Quality (End-Use) Improvement in Wheat: Compositional, Genetic, and Environmental Factors

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SUMMARY. Wheat provides nutrients and the raw materials for industrialized food production. Recent global economic trends and increases in urban population growth have led to an increased demand for wheat-based convenience foods (fast, ready-to-eat, frozen foods, etc.) and for new wheat-based products. These factors have resulted in a greater emphasis than ever on the end-use quality of wheat. This paper reviews grain compositional aspects influencing the processing and quality attributes of the main foods produced with wheat, as well as the breeding strategies and methodologies used to achieve germplasm with desirable end-use quality. Common wheat (*Triticum aestivum*) is used in bread (leavened, flat, and steamed), noodles, biscuits, and cakes. Durum wheat (*T. turgidum* L. var. *durum*) is used globally in alimentary pasta and regional foods (flat breads, couscous, and burghoul) in North Africa and West Asia. Grain characteristics (grain hardness, protein content/qual-

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ity, enzymatic activity, etc.) play a moderate to important role in the processing and end-use quality of wheat-based products. Among these, gluten strength and extensibility, which are determined by glutenin (HMW and LMW) and gliadin composition, are two of the main factors that determine quality. The complex and generally additive nature of inheritance of most quality traits has led to the development of several indirect tests used in early and advanced generations to increase the frequency of high yielding lines with desirable quality attributes. Additionally, characterization of HMW and LMW glutenins and gliadins allows breeders to combine protein content and quality more effectively. The use of molecular-marker-assisted selection and genetic transformation is expected to accelerate the tailoring of new wheat varieties to meet specific end-use quality requirements. Accumulating desirable quality genes will help reduce genotype × environment effects on quality–presently among the major challenges confronting breeders.

KEYWORDS. Biotechnology in wheat quality, breeding methodology, common wheat, durum wheat, end-use quality, genotype × environment interaction, gluten proteins, grain quality, wheat-based foods

INTRODUCTION

Wheat was an important catalyst in the establishment of permanent settlements that gave rise to civilization. Wheat adapts to almost all climatic conditions, with the exception of the very warm tropics. Its wide adaptation and unique property of forming gluten, a viscoelastic storage protein complex that allows the production of diverse foods, makes wheat the most important food crop in the world. Although there are several wheat species within the genus *Triticum,* the most widely cultivated ones are the hexaploid *Triticum aestivum* L., and the tetraploid *Triticum turgidum* L. var. *durum,* known commercially as common wheat and durum wheat, respectively. The two species differ in genomic structure, grain composition, and end-use quality attributes. These differences affect the type of use given the grain from each species: durum wheat is used globally to make pasta and regionally in the production of flat breads and other important foods; common wheat flour is used for making bread and biscuits (cookies). There are also large differences in grain composition among cultivars of the same wheat species, and both quantitative and qualitative compositional differences can make a cultivar suitable or unsuitable for a given baking process or food type.

Wheat breeders must identify specific quality traits to satisfy market and processing demands. These demands are driven more than ever by the consumer. This article reviews the main uses of wheat and the improvement of grain compositional characteristics that affect quality.

CURRENT IMPORTANCE AND TRENDS IN END-USES OF WHEAT

Approximately 90% of the wheat produced in the world–about 585 million metric tons (World Grain, 1999)–is common wheat. Durum wheat production amounts to approximately 27 million tons (Morancho, 2000). Common wheat is generally milled into flour (refined and whole meal) and used for the production of diverse leavened and flat breads, biscuits (cookies), noodles, and other baked products. In contrast, durum wheat is generally milled into semolina (coarse grits) to manufacture alimentary pasta and couscous (cooked grits) in Arab countries. Some durum wheat flour is used in the production of medium-dense breads in Mediterranean and Middle Eastern countries (Quaglia, 1988; Qarooni, 1994).

For many years, several important wheat-based foods were specific to certain regions (e.g., Arabic flat breads, couscous, and oriental noodles) and unknown outside their region of origin. However, migrations from rural to urban areas have permitted the exchange of cultural and dietary habits (Montague, 1998). Today's consumers, particularly those living in urban areas, look for more healthy, nutritious foods and/or convenience foods (frozen foods, instant noodles, etc.). Newly marketed wheat-based foods, such as noodles and flat breads in Europe, the Americas and Australia, or leavened breads and wheat-based fast foods in Asia, are easily accepted by urban populations. For example, the "flour tortilla," a wheat flat bread from Mexico, has become one of the fastest growing products of the baking industry in the U.S.A. (Kohn, 2000).

CLASSIFICATION AND GRAIN COMPOSITIONAL CHARACTERISTICS

Wheat Types and Classes

For trading purposes, wheat is classified into distinct categories of endosperm hardness (soft, semi-hard, and hard) and grain color (red, white, and amber). Wheat can be further divided into subclasses based on growing habit (spring or winter). Each wheat subclass may be grouped into grades that are used to adjust the basic price of a wheat stock, by applying premiums or penalties based on physical characteristics of the wheat lot. Wheat grades are determined by the purity of a wheat class or subclass, by the effects of external factors on grain soundness (rain, heat, frost, insect, and mold damage), and by the cleanliness (dockage, foreign material) of the wheat lot. All these grading factors affect both flour and semolina milling quality. Grain protein content and alpha-amylase activity–enzymatic activity associated with grain germination–are frequently considered grading factors in wheat trading. These two factors are important in determining the end-use properties of wheat and can be tested rapidly.

Grain Hardness

Grain hardness is determined by the packing of grain components in the endosperm cells. It is often referred to as the resistance of the grain to an applied fracturing force or to the energy required to reduce the grain sample into fine particles (whole meal, semolina, refined flour). In general; durum wheat has a harder endosperm than hard-grained common wheat. Grain hardness is a quality trait associated with the milling properties of wheat (Miller et al., 1982; Finney et al., 1987), with the water absorption capacity of flour/semolina, and with the baking quality of the resulting dough.

Milling duration, milling energy requirements, and the level of starch damage produced in the milled flour are all influenced by grain hardness. Hard wheat requires longer milling time, more milling energy and produces a larger amount of damaged starch compared to soft wheat.

A 15 KD protein attached to the surface of the starch granule is associated with grain hardness in common wheat; starch from soft wheat tends to have more of this protein than starch from hard wheat (Greenwell and Schofield, 1986). The actual role of the 15 KD protein (controlled by a gene on chromosome 5DS) in determining grain hardness is not well understood (Rahman et al., 1991).

Starch

Native starch, the main component of the wheat grain (70-75%, dry weight), has little influence on the differences in functional properties existing among flours used in bread, cookie, and cake making; however, it plays an important role in the textural properties of flour noodles (Lee et al., 1987). The amylose and amylopectin components of starch damaged mechanically during flour milling interact with other constituents of the baking formula, thereby influencing the water absorption and fermentation time requirements of bread-making dough and the staling and crumb textural properties of bread. A small amount of damaged starch is desirable in bread-making flours but highly undesirable in cookie and cake-making flours, as it may considerably reduce the expansion capacity of cookie dough (Miller and Hoseney, 1997) and cake batter during baking. For this reason, the cookie and cake industries use flour from soft-grained wheat, which has very low levels of mechanically damaged starch and, consequently, low flour water absorption.

On the other hand, the swelling and pasting properties of native starch influence the eating quality of wheat flour noodles, particularly white noodles that are smooth, soft, and slightly elastic (Lee et al., 1987; Bhattacharya and Corke, 1996). High starch swelling and desirable noodle softness have been associated with the absence of the granule bound starch synthase (GBSS) protein controlled by genes on chromosome 4A, commonly referred to as Null4A (Ross et al., 1996). Other starch and protein related factors also influence starch swelling and noodle softness and may mask the quality effects of Null4A (Ross et al., 1996). Thus screening for Null4A may not be effective in improving starch properties for noodle making.

Proteins

Protein content in wheat varies between 8 and 17%. The factors that affect protein content are the genetic make-up of the variety, permanent and variable environmental factors, and crop management practices. Most (78-85%) endosperm protein is gluten, a very large complex primarily comprised of polymeric (multiple polypeptide chains linked by disulfide bonds) and monomeric (single-chain polypeptides) proteins known as glutenins and gliadins, respectively (MacRitchie, 1994). Glutenins, through inter-peptide disulfide bonding, confer elasticity, whereas gliadins, with their globular structure, confer viscous flow to the gluten complex (see Shewry and Tatham, 1997, for a review). Gluten is, therefore, responsible for most viscoelastic properties of wheat flour and semolina dough, and is the main factor determining the use of a wheat variety by the baking and pasta-making industries. Although variations in grain protein (gluten) content may significantly influence the dough strength of a wheat variety (Simmonds, 1989), protein quantity alone cannot explain differences in quality characteristics among wheat cultivars. Therefore, protein quality related to the polymeric/monomeric protein ratio and the size of the aggregated protein polymer are important (see Weegels et al., 1996, for a review).

Wheat flour contains similar amounts of glutenins and gliadins, and any change in the glutenin/gliadin ratio may change its viscoelastic properties. The glutenin fraction is, however, the major protein factor responsible for variations in dough strength among wheat varieties (Fu and Sapirstein, 1996).

Genes in the complex *Glu-1* and *Glu-3* loci located in the group 1 chromosomes control glutenins (Table 1). In the *Glu-A1*, *Glu-B1*, and *Glu-D1* loci there are genes coding for 0 or 1, 1 or 2, and 2 high molecular weight (HMW) subunits of glutenin, respectively. The relationships between frequently found HMW subunits and dough strength and bread-making properties are well established (Payne, 1987; Shewry et al., 1992). Quality scores for several HMW subunits of common wheat are shown in Table 2. Low molecular weight (LMW) subunits of glutenin, controlled by genes of the *Glu-3* complex loci, are also important in determining gluten viscoelasticity (see Weegels et al., 1996, for a review). However, much remains unknown regarding the relationship between LMW glutenin subunit composition and gluten strength in common wheat. This is in part due to the larger number of LMW subunits in bread wheat compared to durum wheat (D genome proteins are not present in durum wheat). The large number of components (up to 7) that make up a single LMW subunit makes it practically impossible to resolve them by using the conditions for determining HMW composition, particularly if the gliadins that co-migrate with the LMW are not removed as a first step (Gupta et al., 1990). A new sequential protein ex-

TABLE 1. Wheat gluten proteins and their genetic control.

Proteins	Chromosome Arm			Locus		
Glutenins						
High molecular weight glutenins	1AL	1BL	1DL	*Glu-A1*	*Glu-B1*	*Glu-D1*
Low molecular weight glutenins	1AS	1BS	1DS	*Glu-A3*	*Glu-B3*	*Glu-D3*
Gliadins						
γ- and ω-gliadins	1AS	1BS	1DS	*Gli-A1*	*Gli-B1*	*Gli-D1*
α- and β-gliadins	6AS	6BS	6DS	*Gli-A2*	*Gli-B2*	*Gli-D2*

TABLE 2. Quality scores assigned to HMW glutenin subunits based on gluten quality-related parameters.[a]

	Score[b]	
Subunit	SDS-Sedimentation[c]	Alveograph W
Glu-A1		
2*	3	5
1	3	3
Null	1	2
Glu-B1		
17 + 18	3	6
7 + 9	2	5
7 + 8	3	-
6 + 8	1	1
7	1	2
20	-	1
Glu-D1		
5 + 10	4	6
5 + 12	-	2
2 + 12	2	2
3 + 12	2	-
4 + 12	1	1

[a]: Source: Pogna et al. 1992.
[b]: Higher value indicates better quality effect.
[c]: Source: Payne 1987.

traction procedure combined with ID SDS-PAGE has been developed to obtain well-resolved patterns of HMW and LMW subunits in a single gel (Singh et al., 1991). The procedure has facilitated the study of the relationship between genetic control and impact on grain quality of LMW subunits. This notwithstanding, it remains more difficult to determine LMW subunit composition than HMW composition.

In durum wheat, gluten quality is more closely associated with specific LMW subunits and gliadins than with specific HMW glutenins (Ruiz and Carrillo, 1995; Liu et al., 1996; Peña, 2000). However, some HMW subunits associated with strong gluten type and good bread making quality in durum wheat have been identified (Pogna et al., 1988; Peña, 2000). The role of specific LMW subunits on gluten strength in durum wheat has been determined; LMW-2 and its variants confer stronger gluten characteristics than LMW-1 (Pogna et al., 1988; Peña et al., 1994).

Genes in the *Gli-1* and *Gli-2* loci located in the group 1 and group 6 chromosomes, respectively, control gliadins (Table 1). Some allelic variants at the complex gliadin loci *Gli-1* have been found to influence gluten properties in common wheat (Sozinov and Poperelya, 1980; Branlard and Dardevet, 1985). However, there is still controversy regarding the effects of individual *Gli-1* alleles (Nieto-Taladriz et al., 1994). In durum wheat, gliadin γ-45 is associated with high gluten strength, while gliadin γ-42 tends to be associated with weaker gluten and poorer viscoelastic properties (Kosmolak et al., 1980). These associations are thought to be related to the tight linkage between *Glu-B3* and *Gli-B1*; the causal effects are attributed to allelic variations (LMW-1 and LMW-2) at *Glu-B3* (Payne et al., 1984).

Flour/Semolina Pigments

In many countries, flours used for bread and noodle making must be white with no discoloration or yellow pigment. In contrast, the yellow pigment (xantophylls or luteins) of semolina is extremely important in assessing durum wheat for pasta quality.

Enzymatic Activity

High alpha-amylase activity has a large negative effect on baking dough properties, as it hydrolyzes flour starch excessively. Grain with very high levels of amylase activity may be rejected as a food product and downgraded to feed grain in the market. Polyphenol oxidase (PPO), also referred to as tyrosinase, is an enzyme complex located in the bran layers of wheat. PPO may cause product discoloration in both oriental noodles and durum pasta through the oxidization of phenols into polyphenols, which are dark brown. Low levels of PPO activity ensure that fresh flour noodles and fresh pasta will maintain their luster. Common wheat generally has higher PPO levels than durum wheat (Bernier and Howes, 1994).

The yellowness of pasta may also be significantly reduced due to the oxidative degradation of yellow pigment (lutein) by the enzyme lipoxygenase (Irvine and Winkler, 1950). Lipoxygenase (LOX) oxidizes semolina yellow pigments during pasta making. Low LOX activity is more important than high grain yellow pigment content in retaining the yellow color in pasta (Borrelli et al., 1999).

Minor Grain Constituents

Lipids, pentosans, soluble proteins, and other minor grain constituents also play a role in determining wheat flour quality. Their effect on flour and dough functionality can be corrected, generally by adjusting ingredients (e.g., use of additives, improvers) before baking. Thus, they are not considered major factors in grain quality improvement.

WHEAT-BASED FOODS AND GRAIN QUALITY REQUIREMENTS

Flour and Semolina

Milling yield is an extremely important characteristic for millers, particularly in countries where leavened bread is a key product. This is because higher rates of flour extraction result in higher financial returns from the same volume of grain. Breeding lines with potential for release are often rejected in the final round of evaluation because milling yield is a percentage point less than the industry target. Acceptable flour extraction rates may vary from ~70 to 80%, depending on the country/region and the intended use of the flour. Refined flour specifications may also vary widely regarding ash content (.040-0.60%), granulometry, protein content, and levels of starch damage, depending on the intended use and, in some instances, local legislation. In countries where non-leavened breads (e.g., chapatis) are common, such as in the Indian Sub-Continent, whole wheat is milled with very little bran discarded. Grain test weight, thousand-kernel weight, and hardness are the main factors influencing milling yield (Finney et al., 1987). Soft wheat suffers less starch damage during milling than hard wheat and generally yields less flour. Durum wheat is harder than common wheat, resulting in higher semolina yields. Semolina is defined as the purified middling that will pass through a No. 20 U.S. sieve, of which not more than 3% will pass through a finer No. 100 U.S. sieve (Finney et al., 1987). Of 75% milled product, 80-85% should be semolina (semolina yield > 60%, on average about 65%). Ash values of durum semolina are economically important and higher (0.60-0.70%) than those of common wheat refined flours (0.40-0.60%); in countries such as Italy ash content in semolina is specified by law. One particularly important grading factor in semolina milling is the grain discoloration known as black point. This is caused by pathogens such as *Bipolaris* spp. and *Alternaria* spp., and can add undesirable black specks (particles from black point, bran pieces, or other visible foreign materials) to semolina. Up to 15% black point is acceptable. The presence of starchy or yellow berry kernels also reduces semolina (not flour) milling yields and negatively affects end-product quality, because starchy parts of the kernel have lower protein content than the vitreous portion. Minimum requirements for vitreousness vary from 75% to much higher proportions for top grades.

Bread

Wheat bread provides more nutrients to the world population than any other single food source (Pomeranz, 1987). Bread consumption is increasing globally. In developed countries, people consume bread, particularly bread prepared with whole-grain and multi-grain flours, as an inexpensive source of complex carbohydrates, dietary fiber, and proteins (Faridi and Faubion, 1995; Seibel, 1995). In developing countries, bread consumption increases with urban population growth, increased income, and the adoption of processed, convenience foods, particularly in China and Southeast Asia (Owens, 1997) and in North African and Middle Eastern countries (Prior, 1997). Bread consumption in Sub-Saharan Africa is low and varies widely from country to country. It is greater in wheat-producing countries (South Africa, Ethiopia, Sudan, Kenya, Zimbabwe, Tanzania, and Zambia) in Eastern and Southern Africa, and lower in those that rely on wheat imports.

All wheat-based bread types (leavened, flat, and steamed) are made from viscoelastic and cohesive dough prepared from refined or wholemeal flour. There are differences in specific grain quality requirements, processing conditions, and end-product properties within each bread type.

Leavened Breads

Leavened breads are popular in almost all parts of the world. They are made with wheat (and/or wheat-rye blends in Central and Eastern Europe) viscoelastic dough, which expands by the action of gas produced by yeast and/or other fermenting agents. Leavened breads are characterized by a small crust to crumb ratio. The combination of bread formula, dough viscoelastic properties, length of the fermentation stage, and oven-stage conditions determines size, volume, crust thickness, and crumb structure of a given type of bread. Pan breads (pan-type bread, hamburger, hot dog buns, etc.) generally have a thin to medium thin light-brown crust and a light, uniformly distributed crumb structure. Their shape is determined by the panning mold. In contrast, hearth breads, baked on the oven floor (French-type baguette, sweet rolls, croissants, etc.) generally have a semi-hard to hard crust and an unevenly distributed crumb structure. The shape given by hand to the dough determines the shape of hearth breads.

Hard to medium-hard grain is preferred for leavened breads. This is because the levels of damaged starch from these wheat classes result in the high dough water absorption desired by bakers. The type of bread and the bread-making process used, on the other hand, determines flour (or dough) strength requirements. In general, mechanized, high-speed mixing requires stronger dough than manual or semi-mechanized mixing. Hard to medium-hard wheat with strong gluten is more suitable for mechanized production of leavened breads such as pan type bread and hamburger and hot dog buns (Wrigley, 1991). Those with medium-strong gluten are suitable for semi-mechanized or manual production of hearth breads.

To develop wheat cultivars with suitable pan bread quality, breeders must select hard to medium hard-grained wheats with high milling yield, medium to high flour protein, and low yellow pigment. Flour water absorption should be high. Medium-strength and extensible doughs are also favored by most users (Finney et al., 1987). Breeders can use grain hardness estimates, flour protein (> 13%, Wrigley, 1994), medium to high values of SDS-sedimentation, and low yellow pigment scores to favorably skew their breeding populations in the early generations. At an intermediate stage in the breeding process (F4 to F7), when the number of lines is reduced, small-scale milling tests can be applied to further truncate the material. When advanced materials with suitable disease resistance and good yield potential are identified, a more exhaustive examination of physical dough and baking properties is justified.

Steamed Breads

Steamed bread is popular in China and throughout East Asia (Pomeranz, 1978; Lin et al., 1990). Steamed bread is spherical and possesses a spongy crumb and no crust. It is made with yeast-fermented viscoelastic dough that is steamed rather than baked. Steaming prevents the formation of the brown crust characteristic of baked breads. Steamed bread may be plain or filled with sweet bean paste, or with meat and/or vegetables (Nagao, 1995b). There are three main types of steamed bread; northern-style and southern-style Chinese steamed breads, and Cantonese and/or Southeast Asia steamed bread. Northern-style Chinese steamed bread is denser and chewier, while Cantonese style is softer and less cohesive (Crosbie et al., 1998). Southern-style Chinese and Cantonese and/or Southeast Asia steamed breads are consumed in southern China, Southeast Asia, Korea, and Japan.

To produce good steamed breads, the grain should be white in color, semi-hard with bright white flour. Milling yield should be high and flour protein intermediate (10-13%, Wrigley, 1994). Hard to semi-hard wheat possessing medium strong and extensible gluten is more suitable for northern Chinese steamed bread. Soft wheat with medium to low gluten strength is better suited to southern Chinese steamed bread, and steamed breads consumed in Southeast Asia (Lin et al., 1990; Nagao, 1995a; Huang et al., 1996; Crosbie et al., 1998). There are visual and texture requirements for steamed bread, but these cannot be selected for with any certainty in the early generations. Breeders should essentially apply the same early generation selection regime as for leavened bread. However, slightly softer grain can be retained and flours must have a very low level of yellow pigment. Final evaluation will require customer "feedback" on texture and appearance.

Flat Breads

Flat breads can be single layered (e.g., the Indian chapati, Mexican tortilla and Arabic tanoori) or double layered (e.g., the Egyptian baladi and Arabic or pita bread). Flat breads are characterized by a high crust to crumb ratio and are generally round or oval-shaped, and less than 1 cm to around 4-6 cm thick. All flat breads are made from viscoelastic doughs prepared with 100% wheat flour or with composite flours that include wheat and other cereals. Some flat breads are made of wheat flour (whole or refined), water, and salt. Others are fermented using sourdough starters or yeast, and still others contain chemical leavening agents. Flat breads may be thin and crisp (e.g., the Israeli matzo and the Iranian lavosh) or soft and flexible such as the Mexican flour tortilla and the Indian naan (Faridi, 1988; Qarooni, 1996; Singh and Kulshresta, 1996).

Flat breads are consumed in northern Europe (bannock, lefse, plank, etc.), North Africa (baladi, Arabic or pita, Moroccan, etc.), the Middle

East (barbari, bazlama, lavosh, tanoori, etc.), the Indian Sub-Continent (chapati, naan, etc.) and North and Central America (tortilla, etc.). Faridi (1988) published an excellent review of the various types of flat breads all over the world. Some flat breads remain ethnic foods, made at home using traditional clay or brick ovens, or baked on a hot clay or metal plate. Others have become very popular, given that they fit the needs of the fast food and/or convenience food industry. This is the case of the Mexican flour tortilla, Indian naan, and Egyptian baladi and Arabic or pita breads (Faridi, 1988; Steinberg, 1996). Mechanized, large-scale production of these breads satisfies the demand of urban consumers (Faridi, 1988; Kohn, 2000).

Breeders aiming to develop good flat bread products target white (red is at times acceptable), hard-grained wheat with high milling extraction and intermediate flour protein (11-13%, Wrigley, 1994). Hard to medium-hard wheats with medium-strong and extensible gluten are suitable for flat-type breads such as the two-layered Arabic baladi, and the single-layered Indian chapati, Mexican flour tortilla, etc. (Qarooni, 1996; Singh and Kulshresta, 1996). Flat bread doughs should be medium in strength and extensible. Breeders can essentially utilize the same early generation selection criteria as those used for leavened bread. The suitability of a variety for flat bread production will be determined once physical dough properties are determined.

Flour Noodles

Wheat flour noodles, a staple food in northern China, are widely consumed all over East Asia (Huang, 1996; Kim, 1996). To make noodles, a stiff, crumbly dough is developed by hand-kneading or slow mixing of the ingredients and then letting the dough rest for 30 min. A dough sheet is then made, cut into noodle strands, and boiled (or dried). Mechanized noodle production predominates in Japan, while most noodles in China are handmade (Nagao, 1995a). There are three main types of noodles: white salted (WSN), yellow alkaline (YAN), and instant (bag and cup noodles). White salted noodles (fresh, dried, boiled and steamed and dried) are made of flour, salt and water. In addition to the ingredients of WSN, YAN includes alkali (roughly 1% of alkaline salts, flour weight basis) to develop their characteristic yellow color. In Japan WSN are known as *udon,* and YAN as *ra-men* (Nagao, 1995b). WSNs are bright, creamy-white, smooth and soft, but slightly elastic to permit a clean bite. In contrast, YAN are light yellow to yellow, smooth but firmer and more elastic than WSN, and offer slightly more resistance to the bite.

The greater firmness and elasticity of YAN is due to the use of flours with higher protein content and stronger gluten (Huang, 1996; Nagao, 1995a). Instant noodles are steamed and fried, or steamed and dried. In instant noodle production, fresh noodles are waved and steamed in a steaming tunnel for 1-3 min prior to cutting. Non-fried instant noodles require longer steaming time than fried ones (Nagao, 1995b). Drying by frying requires the steamed noodles to be passed through a frying tunnel for approximately 1-2 min at 140-150°C for bag instant noodles and 1.5-2.0 min at 160°C for cup instant noodles (Kim, 1996; Nagao, 1995b).

Desirable noodle brightness and whiteness are achieved when low extraction (below 70%) flour having low ash content (less than 0.5%) is used. White salted noodles require intermediate flour protein, whereas YAN will range from high (> 13%) in Japan to low (> 9.5%) in southern China and Indonesia (Nagao, 1995a; Ross et al., 1996). Grain hardness also varies; in WSN soft to semi-hard grain is acceptable, whereas the grain must be hard to produce acceptable YAN. Starch properties are also important, particularly in WSN. Starch paste viscosity must be high (Lee et al., 1987); however, there is more flexibility in the production of yellow alkaline types where medium levels are acceptable. The reaction of flour to the addition of alkali is also important in making YAN, where a clear yellow color is sought. As with steamed breads, noodle texture and taste are very important (Finney et al., 1987), and doughs should generally be medium to strong.

In selecting for flour-noodle quality, breeders can use the same tests as those used for leavened breads; however, their interpretation will depend on the product being sought. This is particularly important when using protein and grain hardness as indicators of eventual noodle quality. The swelling power test may also be applied in preliminary screening, as it correlates well with starch pasting viscosity (McCormick et al., 1991). The role of flour pigment in determining suitable reaction to the addition of alkali is not well defined, so selection for increased yellow pigment may or may not be beneficial in the case of alkaline noodles.

Soft Wheat Products (Cookies and Cakes)

Cookies (biscuits), cakes, and other soft wheat products, such as those made with batter, are produced around the world in a very large variety of shapes, textures, sizes, and flavors. They are generally sweet goods where wheat flour represents 1/3 to 1/2 of the formula. Cookies are usually made with inelastic and stiff dough, but some cookies, cakes, pancakes, and waffles require thick, viscous batters. The development of viscoelasticity in cookie dough is prevented by the inclusion of large amounts of sugar and fat in the baking formula (sugar may equal as much as 2/3 and fat as much as 1/2 the amount of flour used in the formula). Both cookie spread and batter expansion are largely determined by the viscosity of the system and the availability of free water (water acts as a leavening agent as it evaporates) during the baking stage. Soft wheat flour (not hard wheat flour) is suitable for the production of cookies, cakes, and other products from batters, because it has limited ability to form viscoelastic dough coupled with low water absorption capacity (Miller and Hoseney, 1997). Air and chemicals are, in addition to water vapor, the leavening agents in these foods.

To make suitable cookies and cakes, wheats with low flour protein (8-10%, Wrigley, 1994) and weak, extensible dough, possessing low water absorption, are sought. Low water absorption can best be achieved with soft wheat flours characterized by low levels of damaged starch and low protein content. Breeders can use NIR analysis to select for soft grain and low flour protein. Low protein in combination with low SDS-sedimentation values can be used to skew populations favorably in the early generations. Eventually a cookie test is required to determine suitability for specific cookie and cake manufacture (Finney et al., 1987).

Durum Wheat Products

Durum wheat is eaten as alimentary pasta in most countries. The most commonly known pasta products are spaghetti and macaroni. Durum wheat is also a major staple food in the West Asia/North Africa (WANA) region where most of the world's durum wheat area is concentrated. In WANA durum wheat is used to make a range of local and processed products, such as pasta and couscous, made with semolina; burghoul, made with boiled and dried grain; flat bread, and several other minor local foods. Other uses of durum wheat include flat bread production in India (chapati) or Mexico (tortilla). In the Andean Region, durum wheat is consumed as a local dish called mote (boiled whole grain).

Alimentary Pasta

Although alimentary pasta originated in Italy, it is now consumed around the world. Pasta is made primarily (and, in several countries, exclusively) from durum wheat semolina. Semolina and water (~30% of semolina weight) are mixed to form a stiff dough that is extruded at high pressure and in a vacuum to produce long and short pasta products of diverse sizes and shapes. Fresh pasta products are dried to 12-12.5% moisture content using short or long drying regimes. Dry pasta is boiled for 6-10 min, depending on pasta type, and then consumed. Good quality cooked pasta should be smooth, firm, and slightly elastic, offering some resistance to the bite ("al dente" texture). Filled pasta ("tortellini," "ravioli," etc.) is made with fresh pasta sheets cut to the desired shape, filled with meat, cheese and/or vegetables, sealed and then dried or canned fresh, with or without sauce. Filled pasta is particularly popular in Italy.

Flat Breads, Couscous, and Burghoul (Bulgur)

Durum wheat flour, alone or blended with other flours, is widely used in Mediterranean countries for making dense leavened breads (Quaglia, 1988). In the WANA region, 50-60% of durum wheat is consumed as single- or double-layered flat bread, and as dense, leavened bread (Williams, 1985). Durum wheat flour flat breads, although similar in processing and general attributes to those prepared with common wheat, are characterized by an appealing yellowish color and slower staling compared to common wheat. The latter is because durum wheat flour dough has higher water absorption capacity than common wheat.

Couscous and burghoul are two of the most important traditional foods in the WANA region. Couscous is a national dish in North Africa, where it is consumed two or three times a day (Qarooni, 1994). Couscous consists of steam-cooked small granules of agglomerated semolina and is consumed with vegetables and/or meat stews. It is prepared by moistening semolina while mixing and rubbing to agglomerate wet semolina particles. Small granules of agglomerated semolina are then steamed and dried. Couscous may be steamed and used, or steamed and dried (to 10-12% moisture) for later use. Couscous is generally dried under the sun during the hot summer season, but large-scale automated production of couscous is now common in large urban areas (Qarooni, 1994). Burghoul (also known as bulgur and boulgur) is a popular food in West Asia (Williams, 1985; Qarooni, 1994). Durum grain is soaked and then boiled in excess water. The cooked wheat is dried (10-11% moisture) under the sun. The dried grain is rubbed to remove outer bran layers and cracked to produce the coarse pieces called burghoul. Burghoul is the basic ingredient of several regional dishes containing vegetables and/or meats. Large-scale automated production of burghoul takes place in large urban areas in the region as well as in the USA (Qarooni, 1994). Durum burghoul possesses a desirable characteristic yellow color and a hard texture that cannot be obtained with common wheat.

Processing requirements of flat breads prepared with durum flours are practically the same as those prepared with common wheat, apart from the stronger yellow color, higher water absorption, and better keeping properties associated with durum wheat. For this reason, flat breads will not be considered further in this section. Pasta and couscous are the main uses of semolina. For reasons as yet not well understood, the grain quality characteristics required to produce high quality couscous are the same, or similar, to those required for high quality pasta production. Therefore, in the following text we will refer only to pasta quality-related factors. Grain factors associated with quality generally include kernel vitreousness, protein content, gluten strength, and yellow pigment concentration. High quality pasta is characterized by a uniform, bright golden yellow color, free of specks, non-stickiness and low cooking loss and maintains the correct firmness or chewiness ("al dente" trait) after some overcooking. The minimum grain protein content required by the pasta processing industry is roughly 12.5% (11.5% semolina protein), but higher concentrations are preferred and often rewarded by higher prices. Protein content is critical in durum wheat, since it can account for 30-40% of the variability in pasta cooking quality.

BREEDING FOR END-USE QUALITY

To satisfy the processing and quality requirements of traditional and new wheat-based products, the wheat industry requires several wheat types, each characterized by specific grain quality attributes that should be consistent from lot to lot. More and more frequently, the value and acceptability of a wheat crop on the market is determined by how much its grain attributes satisfy specific processing and end-use quality requirements. In the current free trade environment, the wheat industry can find on the export-market wheat quality types not encountered locally. Hence, to remain competitive, local farmers look for wheat varieties that satisfy their grain yield expectations and the quality requirements of their target market.

Improving yield potential without negatively affecting grain quality is difficult, mainly because increases in grain yield are generally accompanied by a decrease in grain protein content, which is strongly associated with bread-making quality. Therefore, wheat breeders must give grain quality the same level of importance as yield potential and disease resistance. To develop wheat cultivars for specific food markets, breeders should:

- Understand the genetic control of specific grain components,
- Understand the relationship between grain composition and processing qualities, and
- Achieve rapid identification and manipulation of quality-related traits by using quick, reliable, low-cost methodologies for testing quality.

Table 3 summarizes the major characters sought by breeders in developing common and durum wheat products.

Breeding Methodology

Parameters Considered in Breeding for Quality

The complex and generally additive nature of inheritance of most quality traits (Wrigley, 1994) has led to the development of a range of indirect tests. By applying these tests in the early generations, the population mean is favorably shifted and increased frequency of homozygous lines with the desired quality characteristics can be expected at the end of the breeding process. Tests commonly used for the determination of grain quality are described below. The sample size and approximate time required for each test are provided in Table 4.

Flour and Semolina Milling Quality

A range of small-scale milling equipment to estimate flour yield potential is available, from micro-mills (Finney et al., 1987) to Brabender Quadrumat Jr. and Sr. mills. To obtain a more precise estimation of flour and semolina yield potential, it is necessary to mill larger samples (1-2 kg) using laboratory pilot mills such as the Buhler mill (Simmonds, 1989). These mills contain two to three sets of break and reduction rolls, similar to those used in industrial milling. In addition, they have better flour sifting mechanisms and, in the case of semolina milling, semolina purifiers. Near-infrared reflectance spectroscopy (NIR), if calibrated properly, can provide estimates of potential flour extraction (Burridge

TABLE 3. A rough guide to the key quality characteristics sought by breeders when developing cultivars suitable for some major products.

Product	Grain Color	Flour Protein %	Grain Hardness	Flour Pigment	Dough Strength	Dough Extensibility
Leavened Bread	Red/white	High	Hard/semi-hard	Low	Strong/medium	High
Flat Bread	White	Intermediate	Hard/semi-hard	Low	Medium/strong	High
Steamed Bread	White/red	Intermediate	Semi-hard	Low	Medium	High
White, Salted Noodle	White	Intermediate	Soft/semi-soft	Low	Medium	Intermediate
Yellow, Alkaline Noodle	White/red	Low/High	Hard/semi-hard	not defined	Medium/strong	Intermediate
Biscuits (cookies) and Cakes	Red/white	Low	Soft	Low	Weak	Intermediate
Alimentary Pasta (Durum wheat)	Amber	Intermediate/high	Vitreous	High	Strong	Low

TABLE 4. Approximate sample size and time required for small-scale quality tests.

Test Name	Sample (g)	Time/Sample (min)	Test Name	Sample (g)	Time/Sample (min)
Milling (grain)			**Enzymatic Activity** (whole meal /flour)		
Micro-mills (whole mill, UDY, Tecator)	5	1	Falling Number (alpha amylase)	10	1-5
Brabender Quadrumat Junior mill	100-500	10-15	Dyed-Substrate Test (alpha amylase)	2	60*
Brabender Quadrumat Senior mil	500-1000	15-25	Polyphenol Oxidize (PPO)	1g	30*
Buhler or Similar mill	> 500	25-40	**Starch Pasting Properties** (whole meal/flour)		
NIR Analysis (whole meal/flour)			Flour Swelling Volume Test	10	20-30*
Grain hardness, Moisture, Protein, etc.	10-15	< 1	Rapid Visco Analyzer (Newport, Scientific)	10	5
NIR Analysis (grain)	>10	< 1	**Dough Rheology** (flour)		
Gluten Strength (whole meal/flour)			Mixograph (National Mfg.)	2-35	5-10
SDS-Sedimentation (whole meal flour)	1-5	20*	Farinograph (Brabender)	10-60	15-30
Gluten Index (Glutomatic, FN)	10	10	Alveograph (Chopin)	60-250	40-60
Flour Color (whole meal/flour)	10	< 1	Extensograph (Brabender)	60-200	100-130
Pigment Content			**Baking Tests** (flour)	2-250	100-300*
(whole meal/flour/semolina)	1-10	80-120*	**Pasta Making and Pasta Cooking Quality**	1000-5000	2 days

*Indicates many test can be run concurrently et al., 1994). Wishna (1998) examined back illumination imaging, and light and near-infrared transmission as improved predictors of semolina milling parameters.

Small-Scale Tests to Determine Physical, Chemical, and Functional Grain/Flour Quality Factors

Protein content. Several methods can be used to estimate protein content, including the Kjeldahl and Dumas methods, calorimetric/spectrophotometric assessments, and near infrared reflectance (NIR). Of these, the NIR analysis using either milled flour or whole grain is the most versatile and provides the fastest estimate (Williams et al., 1982; Delwiche et al., 1998).

Grain hardness. Rapid small-scale tests (based on grinding time, grinding volume, or particle size distribution) used to determine grain hardness make it relatively easy to screen for hardness as early as the F3 generation. NIR analysis of the particle size distribution of whole grain flour or analysis of intact grain samples are very quick and useful in early generation screening. Rough estimates of hardness can also be made visually or by simply biting the grain.

Flour/semolina yellow pigment. Easy-to-use reflectance and pigment extraction methods are available to breeders. Semolina color is determined by xanthophylls, especially lutein, measured as pigment concentration or by calorimetric instruments. Semolina color heritability is high (Johnston et al., 1983; Clarke et al., 2000) and largely additive. Color can be determined visually by comparison with standard samples or directly with a reflectance colorimeter. The pigment may also be extracted and pigment concentration measured by a spectrophotometer. NIR has been used more recently to assess pigment (McCraig et al., 1992) and is a rapid, inexpensive screening tool. In early generations, pigment is frequently determined from whole meal samples (Clarke et al., 2000) to reduce costs and turnover time, while in later stages of the breeding process, semolina and pasta color are measured. In the latter case, the CIE 1976 L*, a*, b* color system is widely used in breeding programs and standard in the pasta manufacturing industry.

Enzymatic activity. Rainfall at or prior to harvest can cause seeds to germinate on the spike, significantly reducing grain quality. Tolerance to preharvest sprouting is linked to grain dormancy (Mares, 1989). Dormancy inhibits the production of germinative enzymes, particularly alpha-amylase. Breeders can indirectly measure alpha-amylase levels using the Falling Number test (AACC, 1983) to measure the viscosity of a flour suspension, or dye-labeled starch substrates that measure alpha-amylase activity by change in the dye color over time to indicate tolerance to preharvest sprouting (Meredith and Pomeranz, 1985). A calorimetric microtiter plate assay is available for detection of polyphenol-oxidase (PPO) activity (Bernier and Howes, 1994).

Sedimentation test (Zeleny and SDS). The Zeleny (Zeleny, 1947) and SDS-sedimentation (Axford et al., 1979) tests can be used to obtain a semi-quantitative estimation of the amount of glutenin (or indirectly, of general gluten strength). These tests are based on the expansion of glutenins (also known as gel proteins) in isopropanol/lactic or SDS/lactic acid solution and currently the most rapid and reliable single small-scale tests (see Weegels et al., 1996, for a review). The tests are widely used to screen early generation wheat lines for gluten strength (strong to weak). Heritability of SDS-sedimentation is intermediate to high (Clarke et al., 2000). Correlation between protein concentration and predictors of gluten strength differs among methods (Ruiz and Carrillo, 1995; Peña, 2000), while SDS-sedimentation, used widely in early generation selection, and industrial standards, such as Alveograph and Mixograph parameters, are high (Clarke et al., 2000; Peña, 2000). Selection in early generations using SDS sedimentation is frequently practiced from F2 onwards (Clarke et al., 1997).

Glutenins (HMW and LMW) and gliadins. Sodium dodecyl sulfate-polyacrylamide gel electrophoresis (SDS-PAGE) of whole protein extracts can be used in early generations to select lines with desirable HMW subunit composition and in advanced stages to define desirable HMW combinations in the progeny of new crosses. Selecting for HMW-glutenins has proved effective in improving the gluten strength of both bread and durum wheat. Low molecular weight (LMW) glutenins, comprising approximately 80% of total glutenin, have for some time been neglected by breeders because assay methods were unreliable. The sequential protein extraction procedure (to separate gliadins from glutenins) combined with 1D SDS-PAGE provides well-resolved patterns of HMW and LMW subunits in a single gel (Singh et al., 1991). Although this procedure has facilitated the study of the relationship between genetic control and quality of LMW subunits, it is not simple enough to rapidly screen for desirable LMW glutenins.

Screening for gliadin bands γ-42 and γ-45 (by APAGE) and LMW gluten subunit LMW-2 has been implemented in many durum breeding programs (Federmann et al., 1994; Clarke et al., 1997). Early generation selection for pasta making quality using monoclonal antibodies (Howes et al., 1995) to identify desirable gamma gliadins (γ-45) or LMW glutenin subunits (LMW-2) has been proposed. The linkage of γ-42 with bronze (brown) glume color and γ-45 with white glume color (Leisle et al., 1985) can be exploited for selection in early generations, although recombinants do exist. Furthermore, indirect selection for gluten strength via direct selection for SDS-sedimentation has resulted in high frequencies of LMW-2; also, LMW-1 was nearly eliminated and favorable HMW-glutenin allelic variants were accumulated (Peña, 1995; Pfeiffer, 2000).

Starch pasting properties. Starch pasting viscosity is very important in determining the quality of flour-noodles (Lee et al., 1987) and of Arabic flat breads (Quail et al., 1990). The Amylograph/Viscograph and, more recently, the Rapid Visco Analyzer (RVA) are used to obtain a complete profile of starch pasting properties. While the first requires a large sample size and a considerably longer testing time, the RVA requires a 3-4 g sample and only a few minutes to reveal the pasting profile of the tested material. Therefore, the RVA is now considered a rapid test suitable for the early selection of wheat lines with desirable starch pasting viscosity for noodle-making (Panozzo and McCormick, 1993). As an alternative to the RVA test, starch-pasting properties can be measured inexpensively using the flour swelling power test (McCormick et al., 1991).

Measures of dough strength and extensibility. Direct measures of dough rheology (mixing properties, strength, and extensibility) are much more time-consuming and require more flour compared to the indirect tests described above. However, the Mixograph (Finney and Shogren, 1972) potentially offers breeders the most versatility because it allows evaluation of more samples per day, using smaller quantities of flour, than alternatives like the Brabender Farinograph and Extensograph, and the Chopin Alveograph. The correlation between the Mixographic parameters, mixing time and tolerance to over mixing, and more specific measures of strength and extensibility obtained with the Chopin Alveograph or the Brabender Extensograph is high (Finney et al., 1987). For the same reasons indicated above for the Mixograph, the Alveograph is considered a better alternative than the Extensograph in determining dough strength and extensibility.

Small-scale baking. To properly evaluate loaf volume and crumb structure, baking tests must be performed. Finney et al. (1987) describe the process in some detail. Baking tests are performed only on breeding materials deemed to have, from other measures of grain quality, suitable bread-making quality. The tests range from micro-bakes using 2-5 g of flour (Grass et al., 1997) to larger traditional bakes using 100 g of flour.

Traditional Breeding Approaches

Breeding Methods

Selection and testing for quality begins in early generations. Crop management × quality interactions are of critical importance, and agronomic practices suitable for both visual field selection and identification of quality attributes must be employed. If a breeding program employs a pedigree or modified pedigree breeding method, early generation quality tests are potentially very valuable. However, in a bulk system where selected progenies are carried to homozygosity in a bulk before head rows are taken, early generation testing will be of little value, as the lines with the desired quality will be obscured in the mean of the bulk population. This does not preclude the use of such tests to remove bulks with low mean quality parameters. Obviously, a much higher frequency of derived lines must be screened in a bulk system once the bulk is finally broken up into its constituent homozygous lines.

Selection of Parents

Plant breeders select at least one parent with the desired quality when designing their crossing strategies, particularly as end-use requirements frequently determine the fate of potential new cultivars.

All potential progenitors should be characterized for the requisite quality parameters before crossing. Exploration of genetic variation for quality traits present in wild relatives and alien species may require pre-breeding or progenitor building before such species are crossed widely in the breeding program. The value of new glutenin subunits obtained from crossing durum wheat with *T. tauschii,* the donor of the D-genome in hexaploid wheat, which results in man-made synthetic hexaploid wheat, has yet to be determined. However, evidence suggests that some of these new alleles may enhance quality when optimally recombined with the appropriate glutenin and gliadin combinations found in hexaploid wheat (Peña et al., 1995).

The use of wild emmer wheat (*T. turgidum* L. var. *dicoccoides*) has been investigated and proposed to enhance grain protein concentration and protein quality in durum wheat (Levy and Feldman, 1989; Joppa et al., 1991). Research on quality improvements in durum wheat via common wheat *Glu-D1* HMW glutenin subunits (D-genome), *Glu-D1* alleles 5 + 10 and 2 + 12 suggests there is scope for further quality enhancement (Liu et al., 1996).

Application of Quality Tests in the Breeding Process

Genetics, environmental conditions, and crop management practices influence protein concentration in the grain. In contrast to the low heritability of protein content, grain hardness, yellow pigment, and bread and pasta processing quality are highly heritable and can be readily improved through conventional breeding. Protein heritability estimates vary from low to moderate (Clarke et al., 2000) and selection for protein is complicated by a negative association with grain yield. For instance, if a population is too severely truncated on the basis of grain protein, then the probability of selecting high yielding lines with the desired quality is limited. Hence, selection for protein is not efficient in early generations (Legg et al., 1991) and should be restricted to intermediate segregating generations from F4 onwards. Heritability of protein content can be improved by using statistical procedures to remove environmental trends. Adjustment of protein for environmental trends using the moving mean procedure tended to improve realized heritability for protein concentrations (Clarke et al., 1998). However, this technique may be difficult to apply in early generations, since selection intensities are high and not all entries are harvested. Higher heritability estimates can be realized via replications, locations, and years of testing; however, these options are impractical in early generations. Consequently, molecular markers may have great potential (Humphreys et al., 1998).

Plant breeders must also cull populations with some care on the basis of parameters such as the SDS-sedimentation index (sedimentation/protein content) and HMW-glutenin subunits, if grain yield potential is to be maintained (O'Brien et al., 1989; Trethowan et al., 2000). The stage in the breeding process at which quality determination takes place will influence which tests are applied. If a series of F2-derived F3 or F4 populations is to be screened, then the large number of lines generally found in most breeding programs at this stage and the limited seed amounts will restrict the choice of test. In these instances, the breeder should consider NIR analysis of grain hardness and protein, SDS-sedimentation (rough measurement of gluten strength), HMW-glutenins, grain yellow color/pigment (durum wheat), Falling Number (amylase activity), PPO (noodle wheat), and RVA analysis of starch (noodle wheat). These tests are repeated in the F5 and F6 generations. Advanced lines entering multi-location yield trials are screened for specific quality attributes using more time-consuming procedures. This can also be achieved by screening a considerably smaller set of advanced materials for flour/semolina yield, yellow color, and dough viscoelasticity. Gluten Index and the Mixographic parameters, mixing time, and mixing tolerance/stability are particularly useful for identifying gluten strength. Time-consuming, yet accurate, measures of dough rheology (Farinograph, Extensograph or Alveograph) and quality (bread, cookie, pasta, etc., using laboratory-scale methods) must be applied on relatively small numbers of elite advanced lines before considering them for varietal release. In durum wheat, elite advanced lines and progenitors are tested for milling parameters (e.g., semolina yield, ash) and for actual pasta processing and cooking quality attributes, including spaghetti water absorption, cooked weight, cooking loss, over-cooking features, firmness or "al dente" trait, stickiness, speck count, pasta color, and brightness. Applying pressure for quality traits at both the segregating and advanced stages allows breeders to develop wheat varieties that are not only adapted to cropping conditions, but also have the quality attributes required by the baking and pasta industries.

Hybrid wheat may also offer breeders the opportunity to tailor end-use quality through the selection of parents with high or complementary quality characteristics while exploiting potential heterosis for both quality and yield. Most authors report an intermediate expression of grain quality traits in hybrid wheat somewhere between the two parents (Borghi and Perenzin, 1994; Cukadar et al., 2000). However, since this intermediate quality is obtained at higher yield levels, hybrid wheat may still offer farmers a considerable advantage in some environments.

BIOTECHNOLOGY IN QUALITY IMPROVEMENT

Application of Genetic Transformation

Biotechnology offers the possibility of investigating the genetic and biochemical basis of individual protein subunits and other molecules contributing to the end-use quality of wheat. Using genetic transformation, new cultivars with improved quality can be developed through the insertion of genes coding for key grain quality attributes. Some researchers have reported improved functional properties from the transformation of wheat with HMW glutenin subunits (Anderson et al., 1996; Blechl and Anderson, 1996; Barro et al., 1997). These authors found improvements in dough strength among plants expressing the transgenes; however, the level of expression of the inserted genes and their contribution to quality in wheat advanced lines suitable for varietal release are yet to be determined (Anderson et al., 1996; Blechl and Anderson, 1996; Blechl, 1998).

The functional properties of starch can also be modified using transformation. Li et al. (1999) have cloned a gene encoding wheat starch synthase 1, responsible for extending starch polymers (hence the balance between amylose and amylopectin). This gene, if expressed in transgenic plants, may affect starch quality. The proportion of amylose to amylopectin and starch granule size affect water adsorption and pasting viscosity (Dengate, 1984). Anti-sense gene constructs may also be used to suppress expression of some deleterious characters such as the rye secalins associated with the 1B/1R translocation in wheat (Blechl, 1998). Transformed plants have been produced using this construct; however, the effects on grain quality have not yet been determined (P. Langridge, personal comm). Other potential applications include neutralization of undesired yellow flour pigment associated with a yield enhancing gene-complex (*Lr-19*) located on chromosome 7D (Knott, 1984).

Application of Molecular Markers

Molecular marker technology is expected to increase the efficiency and speed of breeding for quality. Instead of selecting progeny by determining gene action (determination of their effect on quality), breeders will use marker assisted selection (MAS) to select germplasm carrying desirable genes. Although MAS has been useful in selecting plants carrying genes associated with resistance to pests and diseases, it has not yet proved to be an efficient alternative to traditional chemical and biochemical small-scale testing. The identification of molecular markers in wheat is hampered by a general lack of polymorphism (Helenjaris et al., 1995). It will be difficult to identify markers for milling and dough handling properties of complex heritability (Parker et al., 1996). However, there may be some application for specific traits controlled by one or two genes. For example, in bread wheat a single gene located on chromosome 5D controls grain hardness. A restriction fragment length polymorphism (RFLP) has been developed that allows discrimination among some hard and soft wheats (Jolly et al., 1993). A marker for high grain protein identified from *T. dicoccoides* has been used to select durum and common wheats with higher grain protein (Howes et al., 1994). Other studies have suggested that markers can be applied to simply inherited traits like flour color (Parker et al., 1996).

EFFECTS OF GENOTYPE × ENVIRONMENT INTERACTIONS ON QUALITY IMPROVEMENT

The interaction of genotype with environment has been and still is one of the major challenges confronting plant breeders. Peterson et al. (1998) reported that the interaction variance (G × E) for flour protein in their study of 30 genotypes across 17 locations was lower than that for genotypes. Similarly, Lukow and McVetty (1991) reported significant, but considerably smaller, G × E for flour protein compared to the variance attributed to genotypes. Although a cultivar may have the potential to produce a specified end-use quality, realizing this quality is dependent upon flour protein content and quality. Yellow berry, closely related with vitreosity in durum wheat (Dexter et al., 1989), is strongly affected by crop management practices such as rate and timing of N application, irrigation, and planting date (Sombrero and Monneveux, 1989; Shashi-Madan and Rajendra-Kumar, 1998). Several characters contributing to good quality have high heritabilities and relatively small G × E effects, including SDS-sedimentation (Lukow and McVetty, 1991; Peterson et al., 1998), HMW subunits (MacRitchie et al., 1990), flour pigment (Parker et al., 1996), flour yield (Lukow and McVetty, 1991; Fenn et al., 1994), and grain hardness (Fenn et al., 1994). However, previous studies have shown G × E effects to be significant for many quality tests, although generally smaller than genetic and location effects (Lukow and McVetty, 1991; Robert and Denis, 1996). Robert and Denis (1996) found the Alveograph gave relatively small G × E effects for W (strength) and P (tenacity) but significantly larger effects for P/L (extensibility). Peterson et al. (1998) found the variation attributed to environment was greater than that for genotype for the Mixograph and many baking parameters, even though the G × E interaction variance was generally lower than that of genotype. In contrast, Lukow and McVetty (1991) reported genotypic variance to be much greater than that of environment for the same characters. Reports of G × E associated with loaf volume have been inconsistent, with authors finding large (Peterson et al., 1998) to relatively small (Lukow and McVetty, 1991; Fenn et al., 1994) interactions. In the Lukow and McVetty (1991) and Fenn et al. (1994) studies, the G × E effect on flour protein was relatively small; since protein and loaf volume are highly correlated, this result is not surprising.

The implications of G × E on selection for quality, while significant for plant breeders, are less than those associated with yield. Many of the key quality traits measured by breeders as indirect indications of potential end-use quality are not greatly affected by G × E. While location effects can be large, genotypes tend to rank the same way across locations. Selection for SDS, grain hardness, grain or flour protein, flour pigment, and seed appearance in early generations can greatly assist breeders in identifying wheats with good quality. The SDS-sedimentation/flour protein ratio allows correction for variable protein levels associated with particular locations and correlates well with physical dough properties and baking quality while maintaining variability for yield potential (Trethowan et al., 2000). The relatively low G × E associated with Mixograph and Alveograph measures of physical dough properties also indicates that these more time-consuming measurements can be conducted on samples collected from a small range of representative test sites. Therefore, while most breeding programs conduct yield evaluations over many locations, a subset of locations will provide an adequate representation of end-use requirements.

CONCLUSIONS

The globalization of wheat markets, improved communications, and demographic changes are having an impact on the various uses of wheat. Plant breeders need to better predict these changes in regional demands if they are to position their breeding programs to meet those demands. In countries currently exporting wheat and particularly in countries that traditionally import wheat, breeders must also be conversant with global trends in wheat consumption. Understanding the basic compositional characteristics of the desired end product will enable researchers to apply the most appropriate indirect quality tests in early breeding generations. Application of these tests will depend heavily on their expense, correlation with key end-use characteristics, and speed and ease of use. The potential interaction with environment of key quality characteristics, measured using both indirect and direct techniques will also influence the breeders' choice of test locations.

Researchers working in isolation cannot develop wheats with the quality characteristics necessary to satisfy changing market requirements. More than ever, multidisciplinary approaches involving cereal chemists, plant breeders, agronomists, and market economists will be fundamental to meeting changing consumer demands.

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