REVIEW

Improvement of Durum Wheat Pastamaking and Breadmaking Qualities

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Durum or macaroni wheat (*Triticum turgidum* L. var. *durum*) is an important crop used for the production of pasta, couscous, and in some areas of the world, various types of bread (Quaglia 1988). Durum wheat occupies approximately 20–30 million hectares worldwide, spread over many countries, accounting for 8% of total world wheat production (Bozzini 1988). More than half of the total cultivation lies in the Mediterranean area including southern Europe, North Africa and Southwest Asia, where tetraploid wheats were domesticated around 10,000 to 15,000 BC (Bozzini 1988, Srivastava et al 1988).

The annual world durum wheat production in a three-year period (1991–93) was estimated to be 25.6–34.4 million metric tons (International Wheat Council, London). Historically, the yield level of durum wheat is ≈80% of bread wheat, which has been attributed partly to less favorable crop- growing environments and management practices (Srivastava et al 1988). However, new high yielding semidwarf durums have been produced that have yield potential equal, or even superior to the highest yielding bread wheat in some areas (Breth 1975). As the price of durum is often higher than that of bread wheat, it is a promising and viable alternative crop.

Currently, there are large markets for durum wheat grown in traditional areas, both for domestic consumption and for export to developing countries where there is a greater demand for food due to increasing populations and improving standards of living.

During the last two decades, many advances have been made in our understanding of the chemical and molecular basis of functional quality of durum and bread wheats (reviews by Pomeranz 1971, Payne 1987, Shepherd 1988, MacRitchie et al 1990, Shewry et al 1992, Henry and Ronalds 1993). There has been considerable research on the seed endosperm components affecting pasta quality of durum wheat, particularly in illustrating the requirements in terms of dough rheology, physiology, biochemistry, and processing technology (reviews by Dick 1985, Finney et al 1987, Dick and Matsuo 1988, Cubadda 1989, D'Egidio et al 1993b).

On the other hand, very little work has been done on determining quality requirements of durum wheat used for bread, couscous, and other food products (review by Boyacioglu and D'Appolonia 1994b). In the present review, we shall consider the research undertaken on producing durum wheats with improved baking quality and will discuss the various genetic approaches that could be used to breed durum with modified dough quality.

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In particular, we will describe recent attempts to improve the strength of durum doughs by transferring chromosome 1D of bread wheat, or parts of it, into durum wheats.

DURUM WHEAT AND BREAD WHEAT GLUTENS: A COMPARISON OF PASTAMAKING AND BREADMAKING QUALITY

Durum is a cultivated tetraploid wheat with genomes AABB [$2n = 4x = 28$], and its endosperm has the hardest texture of all wheats. The kernels are also larger and more vitreous than those of bread wheat. The durum endosperm contains about twice the concentration of xanthophylls or luteins (not carotene) pigments when compared to that of bread wheat (Sims and Lepage 1968, Boyacioglu and D'Appolonia 1994a). Unlike bread wheat, durums are grown solely for human food, and many different kinds of food products are available. These include pasta (spaghetti, lasagna, elbow macaroni) used worldwide, and some other regional foods, such as couscous, bulgur (or *burghul*), *frekeh*, puffed cereals, hot cereals, desserts, single- and two-layered flat bread, leavened bread, and noodles (review of Dick and Matsuo 1988). In the regions of West Asia and North Africa, ≈15% of the durum wheat is consumed in the form of pasta products; 50% is processed into single- and two-layered flat breads and the remainder is used for leavened breads. For example, in Syria, Lebanon, Jordan, and Egypt, durum flour is widely used alone or blended with other flours to produce these flat breads (Williams et al 1984, 1988; Williams 1985). In other areas of the world, the durum grain produced is used solely for pasta production domestically, with the surplus being exported (Bozzini 1988). In contrast, in the Mediterranean countries, durums are widely used in breadmaking with a long history tracing back to 500 BC (Quaglia 1988).

Wheat quality is a very broad term, and its definition depends on whether it is being assessed for nutritional or processing purposes. In the present context, the term "quality" refers to the functional properties of a given product. Flour technological or processing quality and dough rheological or dough handling properties will be treated as synonymous, whereas semolina/flour milling and nutritional quality of the end-product are not discussed further.

Pastamaking Quality

Durum wheat has been used traditionally for pastamaking and cooking quality is one of the most important criteria in assessing the quality of durum semolina for this purpose. Cooking quality is determined by two independent parameters: viscoelastic behavior (particularly firmness after cooking) and the surface condition of the cooked pasta (D'Egidio et al 1982, 1993b; Dexter et al 1983; Feillet 1984; Autran et al 1986). This review will focus on the first property, gluten viscoelasticity.

Assessment of quality can be predicted by rheological tests (such as the farinograph or alveograph), but the experimental pastamaking test followed by a proper assessment of the finished products (such as taste panels) is the most reliable assessment of quality (Cubadda 1988). Recently, it was claimed that this can also be empirically predicted by objective experiments (D'Egidio et al 1993a,b).

Traditionally, durum wheats have been thought to have superior pastamaking quality compared to that of bread wheats: cooked pasta from durum maintains good texture, resists surface disintegration, and retains firm structure or *al dente* consistency, characteristics not evident in pasta from bread wheat flours (Cubadda 1989). Generally bread wheat gluten is considered to be too strong for pastamaking, giving dough that is "too tough" for spaghetti (Walsh and Gilles 1971). However, bread wheat flour possessing high protein and strong and elastic gluten with superior rheological characteristics could be acceptable for producing pasta (Cubadda 1993). Nevertheless, strong gluten alone is not sufficient to determine good cooking quality (Dexter et al 1980) because many other factors are known to affect the physical properties required for pasta quality. These include surface stickiness, cooking tolerance, water absorption, degree of swell and solid loss to the cooking water, protein quantity, and quality (Dexter et al 1981, 1983).

Breadmaking Quality

A good breadmaking flour requires strong gluten that is capable of producing an extensive viscoelastic matrix during dough formation, and that has good physical handling properties, such as high resistance to extension (R_{max}) and moderate extensibility (L) as measured by the extensigraph (review by MacRitchie 1984). A large R_{max} value provides a nonsticky and elastic dough whereas greater L values will result in a larger loaf during the baking process. Although various rheological tests are used to indicate the potential of wheat flour for breadmaking, a baking test is still considered to be the final and most reliable test.

The utilization of durum wheats for breadmaking was recently reviewed by Boyacioglu and D'Appolonia (1994b). They suggested that while the search for suitable breadmaking durums started at the beginning of this century, little progress was made until the 1950s because of the generally weak dough produced by these wheats. Since 1950, several attempts have been made to use blends of durum and bread wheat flours to produce bread with acceptable loaf volume (Harris and Sibbitt 1950, Harris et al 1952, Prabhavathi et al 1976). However, the results from using durum wheat alone for breadbaking have been inconsistent (Prabhavathi et al 1976, Bakhshi and Bains 1987).

The development of durums with strong gluten in Canada, Italy, and the United States during the 1980s raised the prospect of using durums directly for breadmaking. Dexter et al (1981) reported that some Canadian durum cultivars approached acceptable quality for breadmaking, being equivalent to weak hexaploid wheats in their baking performance. In Italy, Boggini and his colleagues (Boggini and Pogna 1989, Boggini et al 1994a) found that durum varieties with poor breadmaking quality are also poor for pastamaking. They concluded that to obtain durum semolina for a better breadmaking, it would be necessary to have varieties with gluten that is less elastic and more extensible.

While some Italian cultivars (Capeiti and Appulo) were found to have better breadmaking quality than others (Boggini and Pogna 1989), they did not include local commercial bread wheats in these tests for a comparison. In the United States, many durums of various sources have been tested for baking performance since the late 1970s and, in general, they had inferior breadmaking quality (Josephides et al 1987, Dick 1988, Boyacioglu and D'Appolonia 1994a).

Although durum flours usually produce a smaller loaf volume than those from bread wheats, the durum bread has a yellowish color, a characteristic taste and smell, a fine and uniform crumb structure, and more prolonged shelf-life, all of which appeal to some customers. Durum bread has also been reported to be less toxic for those who suffer from intolerance to wheat gluten (celiac disease) (Troncone and Auricchio 1991). The stronger durums, when blended with weak and soft wheats or triticale, were reported to give flour mixes with improved breadmaking quality (Prabhavathi et al 1976, Bakhshi et al 1989, Boggini and Pogna 1990).

Rheological and Technological Property Differences Between Durum and Bread Wheats

The semolina/flour from durum wheats generally has higher protein content, and higher wet- and dry-gluten content than bread wheat, but a much lower sodium dodecyl sulfate sedimentation (SDSS) value; hence, durum wheats tend to be much poorer in gluten strength (see reviews of Finney et al 1987, Dick and Matsuo 1988, Boyacioglu and D'Appolonia 1994b). In farinograph tests, durum flours generally give higher water absorption values than bread wheat flours, due to higher levels of starch damage during milling, but they show shorter dough development time and a high mixing-tolerance index (Bakhshi and Bains 1987, Boyacioglu and D'Appolonia 1994a). Durum wheats have been classified as having poor breadmaking quality potential on the basis of farinograph and mixograph tests (Boyacioglu and D'Appolonia 1994a), which is consistent with the views of others (review by Finney et al 1987). Also, durum flours have shown inferior rheological properties compared to bread wheat flours when evaluated by alveograph and extensigraph tests (Matsuo and Irvine 1970, Bakhshi and Bains 1987, Boyacioglu and D'Appolonia 1994a). All of these rheological characteristics indicate that durum gluten is, in general, very weak and inelastic when compared to bread wheat dough (Dick 1981, 1985; Feillet 1988; Boyacioglu and D'Appolonia 1994a).

A dough can be firm but if it lacks elasticity or springiness the product is doughy or pasty. Durum doughs have been described as "mushy" or "firm" but not "tough" (Walsh and Gilles 1971). The durums with low gluten strength usually exhibit more viscous and less elastic dough than bread wheat flour (Bakhshi and Bains 1987, Boyacioglu and D'Appolonia 1994b). Others claimed the opposite (Boggini et al 1994a; Pasqui et al 1991, 1994). Some modern durum cultivars produce doughs with increased elasticity and are, consequently, more suitable for breadmaking, but these are still not as strong as bread wheats (Bakhshi and Bains 1987), resulting in reduced loaf volume (Quick and Crawford 1983, Dexter et al 1994). Quaglia (1988) concluded that to make leavened bread from durum flour, the durum semolina-flour should have <70–75% starch damage, a protein concentration of >13% (dmb), a gluten quality value of >17 as determined by the Berliner method for the proteolytic activity, and an alveograph P/L ratio >1.5 and energy (W) value of ≈200. Milatovic and Mondelli (1991) also pointed out that wheat flours with an alveograph P/L value of 0.8–2.0 generally produced a reasonable pasta or bread product. Recent results of Ciaffi et al (1995) suggested that durums with increased dough strength (from introducing the active *dicoccoides Glu-A1* genes) usually have exceptionally high gluten strength (measured by alveographic indices W and P), which appeared to be very promising for breadmaking. These results were in contrast with those of Pasqui et al (1991, 1994), as they suggested that durum doughs with lower alveograph W and P/L values gave higher loaf volume and a softer crumb.

Although it is universally accepted that breadmaking requires strong and extensible gluten, the strength requirements for pastamaking are less clearly defined. It appears from the literature that good pastamaking quality requires only the dough strength (as measured by the gluten's elastic recovery [R] of the viscoelastograph [Damidaux et al 1978]; alveographic indices W and P; or

extensigraphic parameter R_{max}), but little consideration has been given to dough extensibility of durum semolina/flour. In general, the dough extensibility of durum is not suitable for breadmaking. In spite of this, in some cases, these strong and tenacious gluten durum flours can also bake better bread (Ciaffi et al 1995). Furthermore, too much weakness or strength are not beneficial for pastamaking either, because medium gluten strength is required for the optimal pastamaking quality (Matsuo and Irvine 1970, Dexter et al 1981).

Endosperm Proteins and Technological Quality

The semolina/flour protein content is recognized to be the most important factor influencing the mixing, processing, and functional characteristics of semolina (Matsuo et al 1982, Autran et al 1986, Dick and Matsuo 1988, D'Egidio et al 1990). The semolina/flour protein content is highly environmentally dependent and is usually negatively correlated with grain yield (Johnson et al 1985). Matveef (1966) recommended that durums should possess a protein concentration of ≈13%, because protein levels <11% generally resulted in a very poorly processed product. With high grain yield production, the maintenance of a relatively high protein concentration requires changing management practices, particularly increasing the application of nitrogeneous fertilizers. Genetic improvement of seed protein concentration might also be possible (Joppa and Cantrell 1990). However, durums with high protein content do not necessarily have optimal cooking quality, indicating protein amount is not the only factor influencing the cooking property of pasta.

The gluten protein, constituting ≈80% of the total protein in the grain (Osborne 1907), primarily affects the firmness of cooked spaghetti, cooked weight, and cooking loss, whereas starch, the predominant component of the seed endosperm, appears to have less effect on cooking properties (Sheu et al 1967, Walsh and Gilles 1971, Grzybowski and Donnelly 1979, Damidaux et al 1980).

The major components of gluten are the gliadins and glutenins, which have been confirmed by fractionation and reconstitution experiments in both durum and bread wheats to have a functional role in dough formation (reviews by Wall 1979, Miflin et al 1983). These experiments indicated that the albumins and globulins did not have a major effect on these properties. It is widely accepted that with spaghetti, strong gluten with high elastic recovery gives greater cooking stability and higher cooked firmness scores (*al dente*), whereas pasta made from weak gluten with low elastic recovery is prone to deteriorate rapidly and become soft with overcooking (Grzybowski and Donnelly 1979, Feillet 1980). Consequently, gluten strength is recognized to be one of the most important quality criteria in durum breeding.

Protein quality is a highly heritable character and, therefore, only partly influenced by the environment. The protein quality of a particular cultivar is generally believed to be primarily controlled by the type of alleles present at the various loci controlling the gluten proteins, namely the gliadins and glutenins. The genetic control of the wheat storage protein genes has been extensively reviewed recently (see reviews by Garcia-Olmedo et al 1982, Payne 1987, Shepherd 1988, MacRitchie et al 1990).

ASSOCIATIONS BETWEEN STORAGE PROTEIN POLYPEPTIDES AND QUALITY

Durum Wheat Gliadin Bands

A strong relationship has been detected between the banding pattern of gliadin polypeptides and the gluten quality of durum wheat (Damidaux et al 1978, 1980). The presence of the γ-gliadin band 45 and the absence of band 42 was closely associated with strong gluten. This important discovery provided a strong impetus to the search for similar relationships between other protein components and gluten properties. With just a few exceptions, this association between gliadin band patterns and durum cooking quality has proved to be quite reliable (MacRitchie et al 1990). Results consistent with these earlier conclusions (Damidaux et al 1978, Carrillo et al 1990b) were also obtained in a recent survey of a large collection of world durum genotypes with large differences in gluten quality, when grown in South Australia environments. Some other γ-gliadin bands also showed significant correlations with SDSS values ranked in the order: γ-45 > γ-43.5 >> γ-44.5 > γ-42 (Liu and Rathjen 1994), suggesting that use of gliadin markers for selection of durums with better quality might be effective (Carrillo et al 1990a). Besides γ-gliadins, Autran and Galterio (1989) reported that the β-60 or α-73 gliadin types also correlated with higher values of gluten recovery and gluten firmness. Nevertheless, the biochemical basis of the effect of these gliadin polypeptides on functional properties is still not resolved (MacRitchie et al 1990).

High Molecular Weight Glutenin Subunits (HMW-GS)

Earlier studies on the solubility of various seed endosperm-protein fractions demonstrated that the amount of glutenin insoluble in 3*M* urea (Pomeranz 1965), the proportion of "residue protein" extracted by dilute acetic acid (Orth and Bushuk 1972), or the proportion of total glutenin separated by Sepharose 4B/2B chromatography (Huebner and Wall 1976) are good indicators of protein quality (Huebner and Wall 1976, Orth et al 1976, Moonen et al 1982) and mixing strength (Orth and Bushuk 1972). The glutenin fraction also proved to be more important than any other component in imparting gluten strength and cooking quality to durum semolina (Walsh and Gilles 1971; Matsuo et al 1972, 1982), whereas variation in gliadin amount was not associated with physical differences in doughs (Huebner and Wall 1976). Later Payne and coworkers at the Plant Breeding Institute in Cambridge, followed by workers in other laboratories, demonstrated an association between specific high molecular weight glutenin subunits (HMW-GS) of hexaploid wheats and the viscoelastic properties of the dough (Payne et al 1979, Moonen et al 1983, Payne 1987). Extensive studies have since been made worldwide on the variation and genetic control of glutenins in durum and bread wheats and their association with wheat end-use quality (see reviews of Garcia-Olmedo et al 1982, Kreis et al 1985, Shepherd 1988, MacRitchie et al 1990, Shewry et al 1992).

Although the HMW-GS have been shown to be correlated to some extent with the strength of durum doughs, the relationship in durums seems to be much less pronounced than with the bread wheats. Earlier studies showed no clear relationship between HMW-GS and spaghetti quality (du Cros et al 1982, Autran 1981, Vallega 1986), whereas others reported a weak but significant relation between these two sets of attributes (Autran and Feillet 1987, du Cros 1987). Other workers reported that certain HMW-GS were correlated with the rheological quality of durum wheats (Boggini and Pogna 1989, Carrillo et al 1990a, Ciaffi et al 1991), and Autran and Galterio (1989) found that some alleles correlated with poor cooking attributes. The HMW-GS genes on chromosome 1A appear to have a negligible relationship to durum quality parameters when compared to genes on chromosome 1B (Josephides et al 1987, Pogna et al 1990). Certain *Glu-B1* alleles (coding for bands 7+8 or 6+8, and novel bands 6+17 versus bands 20 or 13+16) and one *Glu-A1* allele (band 2* versus the null phenotype) were found to be only weakly correlated with gluten rheological properties (Autran and Feillet 1987, du Cros 1987), but these associations were not so clear as the HMW-GS relationships in bread wheat (Payne et al 1987, 1988a).

In contrast, Boggini and Pogna (1989) and Pena et al (1994) reported that certain *Glu-B1* coded HMW-GS strongly affected durum breadmaking quality (bands 7+8 > 20 > 6+8 or bands 7+8 > 6+8 > 20), similar to the effect observed in hexaploid wheats (Payne et al 1987, 1988a). However, Boggini and colleagues

(Boggini and Pogna 1989, Boggini et al 1994a) concluded that the flour of some current Italian durums with alveograph ratio *P/L* >1.5 and carrying HMW-GS 7+8 were too tenacious for breadmaking, whereas active *Glu-A1* alleles had a favorable influence on baking properties (Boggini et al 1994a, Ciaffi et al 1995). Kaan et al (1993) noted that the *Glu-A1* null phenotype was associated with low SDSS values, similar to the effect found in hexaploid wheats (Payne et al 1979). A recent survey of a collection of durum wheats also suggested that the presence of certain HMW-GS were closely associated with dough strength, in the order 13+16 > 7+8 > 6+8 > 20 (Liu and Rathjen 1994). However, they did not observe any relationship between the *Glu-A1* alleles and dough strength, unlike previous workers.

There are two points of caution in interpreting the results of these studies. First, the commercial durum varieties grown around the world exhibit a very narrow range of genetic variability. Thus misleading results may be obtained from a small collection of varieties because there will be a far from random association of both HMW-GS and low molecular weight glutenin subunits (LMW-GS), and also because results obtained from just one growing location may be affected by specific genotype-by-environment interactions. Second, the predominant HMW-GS alleles present in durums have low *Glu-1* ratings based on Payne scores (mostly null at the *Glu-A1* locus and the frequent presence of bands 20, 6+8, etc., at *Glu-B1*) (Vallega 1988, Branlard et al 1989, Kaan et al 1993, Liu 1994), with few contrasting genotypes available for investigation. Therefore, it is not surprising to find a general lack of association between individual HMW-GS and durum end-use quality as observed in the earlier studies. Some recent results of Boggini et al (1994b) and Liu and Rathjen (1994) indicated that the effect of HMW-GS on durum dough quality is similar to the functional effect of these alleles in bread wheats (Payne et al 1987, 1988a), suggesting that the results obtained with bread wheats (reviews of Payne 1987, MacRitchie et al 1990) could be used as a guide for improving the dough quality of durum wheats, especially if the LMW-GS are also considered.

LMW-GS and Durum Wheat Quality

The LMW-GS of durums have not been studied extensively until recently, although they account for about 80% of the total glutenin fraction (Autran 1981, Payne et al 1984b). An initial study indicated that the LMW glutenin polypeptides of durum wheat were highly correlated with gluten strength (du Cros 1987). More recent studies suggest that they actually determine the viscoelastic properties of durum wheat doughs whereas the γ-gliadins, the monomeric polypeptides (which are closely associated with the LMW-GS in their coding loci) are merely genetic markers (Pogna et al 1988, 1990; Feillet et al 1989). Very recently, Ciaffi et al (1995) showed a positive effect of *Glu-B3* genes on gluten strength and the breadmaking properties of durums that was consistent with other earlier reports (Boggini and Pogna 1989, Pena et al 1994). These recent studies indicated that the protein genes at the *Glu-1* and *Glu-3* loci influence dough quality in a linear cumulative fashion, suggesting that they might be used to predict the potential end-use quality of a particular breeding line in the future, despite the complex interactions known to occur between genes determining end-use quality and the environment (Boggini and Pogna 1989, Autran and Galterio 1989, Pogna et al 1990, Kaan et al 1993, Pena et al 1994, Liu and Rathjen 1994, Ciaffi et al 1995).

NEW APPROACHES TO QUALITY IMPROVEMENT IN DURUM WHEAT

A major objective in durum breeding is to produce varieties with a strong, elastic gluten that is satisfactory for breadmaking quality, as well as for pastamaking. Such dual-purpose durums would be an ideal crop for future markets, since they could be used in place of bread wheat in high quality flour blends in years of high production (Boggini and Pogna 1989). Although the specific quality requirements for pastamaking and breadmaking quality are still not clear, in general, it is widely accepted that durums possess poorer dough strength than bread wheats. This raises the question: can the dough quality of durum wheats be improved genetically so that they could be used for breadmaking as well as pastamaking?

Modification of the protein composition of the grain by genetic means is a major approach for durum improvement. It seems likely that the selection of the improved gluten strength durums during the 1970–80s in Canada, Italy, and the United States was achieved by the conscious or unconscious selection of the favorable γ-gliadin genotype (γ-45 band), which later was shown to be due to the linked LMW-GS types LMW-1 and LMW-2 (Autran et al 1987, Feillet et al 1989, Pogna et al 1990). Although the new strong-gluten durum cultivars were much superior to the weaker types in breadmaking ability (Quick and Crawford 1983), as well as having improved pastamaking characteristics (Damidaux et al 1978), these new durums still had much less gluten strength than hexaploid wheat. Because there is a narrow genetic base for both HMW-GS and LMW-GS among commercial durum varieties worldwide (Vallega 1988, Branlard et al 1989), and because the effect of LMW-GS on viscoelastic quality is less than that of HMW-GS (Gupta et al 1990, 1991), it would be of interest to incorporate new seed protein alleles from landraces or wild relatives, or alleles with known high *Glu-1* scores from hexaploid wheat (*Glu-A1* bands 1 or 2* and *Glu-B1* bands 17+18, 13+16, and 7+8) in an effort to improve the quality of durum wheats.

Based on our recent studies (Liu et al 1994a,b), we hypothesized that the poorer quality of durum wheat is not only due to the lower baking score of the HMW-GS alleles present, but also due to the absence of the *Glu-D1* alleles, as the introduction of chromosome 1D into durum wheat led to a twofold increase in technological quality attributes when compared to the effects of substituting alleles at the *Glu-B3/Gli-B1* loci (Liu et al 1994a). Thus it was suggested that introducing these 1D alleles might be the most efficient approach for improving the strength of durum gluten.

Introduction of Genes from Wheat Chromosome 1D

Hexaploid level. There are reports that all three genomes of bread wheat ($2n = 6x$[AABBDD] = 42) contribute to the baking qualities of hexaploid wheat (Schmidt et al 1966; Morris et al 1966, 1968; Boyd and Lee 1967; Boyd et al 1969; Mansur et al 1990). Other evidence points to the primary importance of the D-genome, because removal of the D-genome results in a large decrease in baking quality (Kaltsikes et al 1968, Kerber and Tipples 1969, Orth and Bushuk 1973), and the addition of the *Triticum tauschii* (DD) genome to tetraploids (AABB) generally improves dough quality (Kerber and Tipples 1969, Lagudah et al 1987). Welsh and Hehn (1964) were the first to demonstrate that the loss of chromosome 1D in a cross involving a monosomic line resulted in a drastic reduction in dough-ball fermentation times and a marked weakening of the farinograph curve. Schmidt et al (1966) also noted that 1D monosomics of hard red winter wheats had weak dough strength. Null lines for certain HMW-GS, derived from other bread wheats such as Ottawa, Nap Hal, and Gabo biotypes showed poor dough quality properties (Lawrence et al 1988, Gupta et al 1990, Lafiandra et al 1993). Using the nullisomic-tetrasomic lines of Chinese Spring, Rogers et al (1988, 1990) demonstrated that increases in the number of copies of the 1D chromosome increased the suitability of this poor quality cultivar for breadmaking. In particular, chromosome 1D carrying *Glu-D1* alleles, had a distinct effect on the breadmaking quality of hexaploid wheat (Moonen and Zeven 1985, reviews by Payne

1987, Shewry et al 1992). Furthermore, the null allele at the *Glu-D1* locus alone resulted in contrasting breadmaking quality differences when compared with a sister line carrying this gene (Payne et al 1988b, Lafiandra et al 1993).

Tetraploid level. The extracted tetraploid lines (AABB genome) of the common wheat cultivars Rescue and Thatcher (AABBDD genome) exhibited the extremely poor baking quality that is characteristic of the durum cv. Stewart 63, presumably because of the absence of homoeo-alleles on D-genome chromosomes (Kaltsikes et al 1968). A similar result occurred with another extracted tetraploid (Tetra-Canthatch) in a later study (Kerber and Tipples 1969). These tetraploids contained more gliadin and soluble glutenin, and less insoluble residue proteins than their corresponding hexaploid parents (Dronzek et al 1970). Tetra-Prelude appeared different in that it had baking quality similar to its hexaploid parent, but further biochemical analysis is required to determine the factors involved.

Joppa et al (1983) reported that the substitution of chromosome 1D of hexaploid Chinese Spring wheat for chromosome 1B of durum cv. Langdon resulted in improved gluten quality, suggesting that chromosome 1D may play a larger role in influencing dough quality than 1B, even when it carries the *Glu-D1a* (2+12) allele (a low breadmaking quality gene) (Moonen et al 1983, Payne et al 1984a). Later, Josephides et al (1987) also reported that the products of genes on chromosomes 1D and 1B are the major factors affecting the quality of durum wheat for breadmaking.

1D Substitution Lines

Analysis of a set of D-genome disomic substitution lines in the genetic background of durum cv. Langdon revealed that only the chromosome 1D substitutions had a large beneficial effect on rheological properties (stronger dough) when compared to the other D-genome chromosome substitution lines (Liu et al 1995), as shown in Figure 1. High-performance liquid chromatography (HPLC) analysis of the selected F_2-derived progeny lines involving substituted chromosomes 1D and 1B in durum revealed that the γ-42 type durums possessed the highest proportion of gliadin in both the durum and bread wheat samples studied (Liu et al 1994b) as observed in earlier studies (Walsh and Gilles 1971, Huebner and Wall 1976).

A high proportion of gliadin in durum semolina was also associated with adverse cooking quality (Walsh and Gilles 1971). On the basis that SDSS values reflect dough strength, the γ-42 type (LMW-1) durums were expected to have the weakest doughs of all the wheats studied, whereas the γ-45 type would have stronger dough but only equivalent to the poorest bread wheat, Chinese Spring (Fig. 2). Moreover, substitution of chromosome 1D was associated with even larger increases in the amount of glutenin (P_1% measured by HPLC), SDSS values, mix time, and peak resistance values (Liu et al 1994a) (Fig. 3, Table I), which is most likely due to the effect of the storage protein genes, *Glu-D1* and *Glu-D3/Gli-D1*, located, respectively, on the long and short arms of chromosome 1D (Payne 1987, MacRitchie et al 1990). In fact, substituting chromosome 1D from Chinese Spring, resulted in a twofold increase in technological quality parameters as compared to the introduction of *Glu-B3/Gli-B1* alleles (Table I). The F_2-derived progeny combining a substitution of 1D and LMW-2 gave the highest values for dough strength, indicating that there were cumulative effects of these genetic factors (Fig. 3). Furthermore, the 1D(1A) substitution lines were comparable in gluten strength to that of medium-strength hexaploid wheat, as measured by SDSS values (Fig. 2). The major changes in dough quality observed were not due to changes in the total amount of protein present (Fig. 3a), but mainly to quantitative changes of specific protein types (P_1, P_1/P_2) (Fig. 3b). Thus, an increase in the glutenin proportion (P_1%), and a corresponding decrease in the gliadin proportion (P_2%) were associated with improved dough mixing properties and SDSS values and, hence, dough strength.

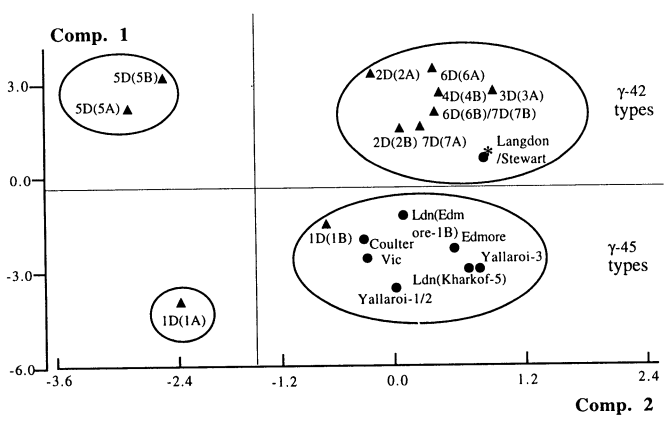

Fig. 1. Distribution of individual lines according to the principal components 1 and 2 from the Principal Component Analysis of Langdon and disomic D-genome substitution lines as well as durum controls. Ten quality parameters (including protein concentration, proportion of glutenin, gliadin, hardness index, most major mixograph parameters, etc.) were used in this analysis. ● = Control cultivars (all γ-45 types except Stewart). * = Langdon and ▲ = Langdon substitution line. Langdon 1D(1A) is γ-42 and Langdon 1D(1B) is absent of chromosome 1B. They are classified as γ-45 type because of improved quality characteristics. Langdon 5D(5A) and 5D(5B) are separated from the rest of the γ-42 types because of their significantly lower grain hardness and white color scores. Figure adapted from Liu et al (1995).

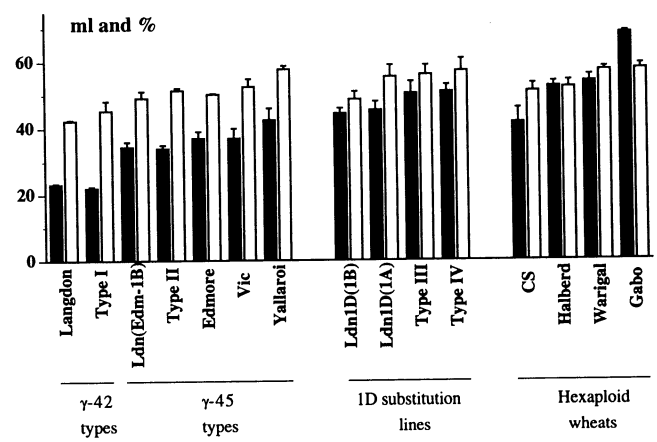

Fig. 2. Mean values for sodium dodecyl sulfate sedimentation (ml) (black column) and proportion of glutenin (%) (white column) determined by SE-HPLC of F_2-derived progeny lines of durum wheat 1D and 1B substitution lines (in Langdon background) and normal tetraploid (Edmore, Vic, and Yallaroi) and hexaploid wheats (Chinese Spring [CS], Halberd, Warigal, Gabo). Types I, II, and III are F_2-derived progeny lines with prolamin phenotypes equivalent to parents Langdon, Langdon (Edmore-1B), and Langdon 1D(1A). Type IV is also a Langdon 1D(1A) type with the 1B prolamin alleles *(Glu-B3/Gli-B1)* from Edmore. Also, Langdon, type I, Langdon 1D(1A) and type III are classified as γ-42/LMW-1 types and the rest are γ-45/LMW-2 types. The error bar of each column represents the standard error of the mean. Figure adapted from Liu et al (1994b).

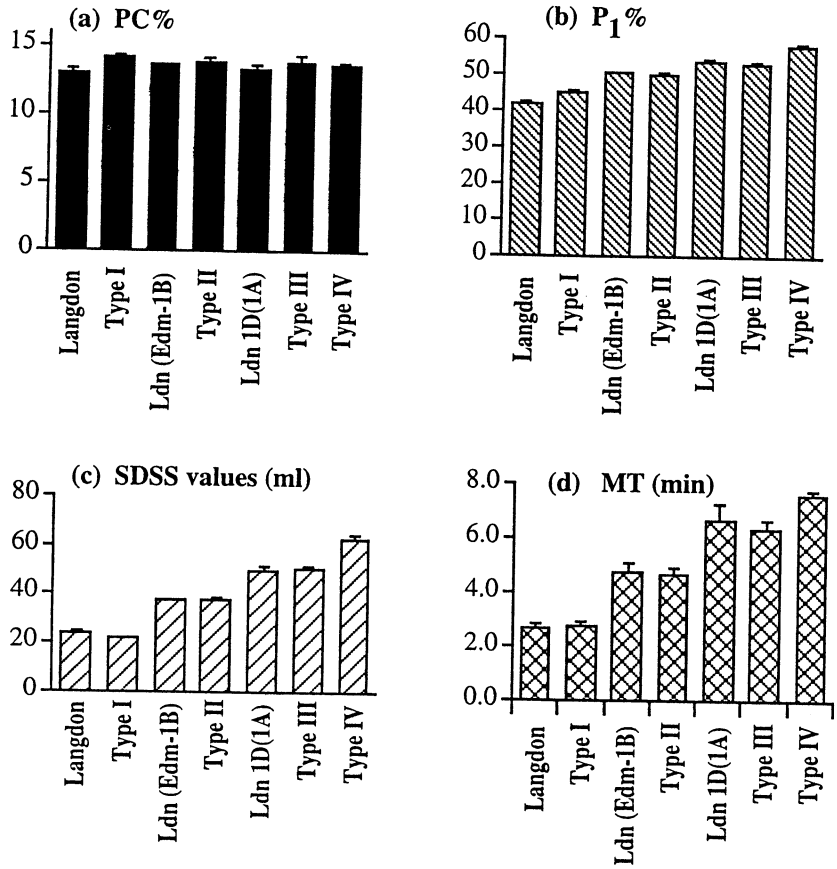

Fig. 3. Mean values of protein concentration (PC%) **(a)**; proportion of glutenin (P_1%) **(b)**; sodium dodecyl sulfate sedimentation (SDSS) values **(c)**; and Mixograph mixing time (MT) **(d)** of four F_2-derived progeny lines and parents from an experiment with six replicates (in Langdon background). The designation of F_2-derived progeny types is the same as in Fig. 2. Error bar of each column represents the standard error of the mean. Figure adapted from Liu et al (1994a).

TABLE I
Mean Effects of Different Chromosome Constitutions on Major Quality Characteristics in the F_2-Derived Progeny of Durum Wheat 1D and 1B Substitution Lines (in Langdon Background)[a,b]

Effect	PC	SDSS	SE-HPLC Parameters				Mixograph Parameters		
			P_{1-1}	P_1	P_2	P_1/P_2	MT	PR	RBD
Chromosome 1B[c]	−0.12	6.81	2.47	2.65	−2.28	0.13	47.9	23.2	−2.8
(*Glu-B3* locus)	ns	***	***	***	***	***	***	***	***
Chromosome 1D[c]	−0.12	13.48	3.53	4.30	−3.93	0.21	97.3	56.5	−3.3
	ns	***	***	***	***	***	***	***	***
Interaction	−0.01	−0.89	0.06	−0.01	−0.02	0.02	−10.8	−7.7	3.2
	ns	ns	ns	ns	ns	ns	ns	*	***

[a] Data adapted from Liu et al (1994a). PC (in %) = protein concentration; SDSS (ml) = sodium dodecyl sulfate sedimentation; SE-HPLC = size-exclusion high-performance liquid chromatography; P_{1-1} = percentage of highly aggregating glutenin; P_1 = percentage of total glutenin; P_2 = percentage of gliadin; MT = mixograph mixing time; PR = peak resistance; RBD = resistance break down (in mixograph Brabender units).
[b] *, **, *** = significant at 5, 1, and 0.1% probability level, respectively. ns = nonsignificant.
[c] Effect of chromosome 1B was derived from major genes at the *Glu-B3/Gli-B1* locus, whereas effect of chromosome 1D was compared with absence/presence of chromosome 1A.

This result implied that these F_2-derived 1D(1A) substitution types might have the potential for improving both breadmaking and pastamaking quality.

The specific HMW glutenin bands 5+10 (coded by *Glu-D1d*) have contributed more to the dough rheology (Bekes and Gras 1993) and baking characteristics of bread wheat than have bands 2+12 (coded by *Glu-D1a*) (Burnouf and Bouriquet 1980, Moonen et al 1983, Payne et al 1984a). The beneficial effect of bands 5+10 was shown recently to be due to their ability to form significantly higher proportions of insoluble polymeric proteins than their allelic counterparts 2+12 (MacRitchie et al 1992). Hence, introduction into durum wheats of the *Glu-D1d* allele (bands 5+10) instead of *Glu-D1a* (bands 2+12) from hexaploid wheat should provide a further improvement of the durum gluten strength. Initial results, obtained from a glasshouse experiment, showed that progeny with bands 5+10 had a significantly higher average micro-SDSS height and specific SDSS values (=100*SDSS/PC) than those carrying bands 2+12 in two backcross populations (Fig. 4) (Liu 1995), supporting the above hypothesis. Similar projects aimed at transferring 1D genes into durum wheat were reported elsewhere (Ceoloni et al 1993, Tsunewaki and Matsuda 1993). The chromosome 1D segment carrying

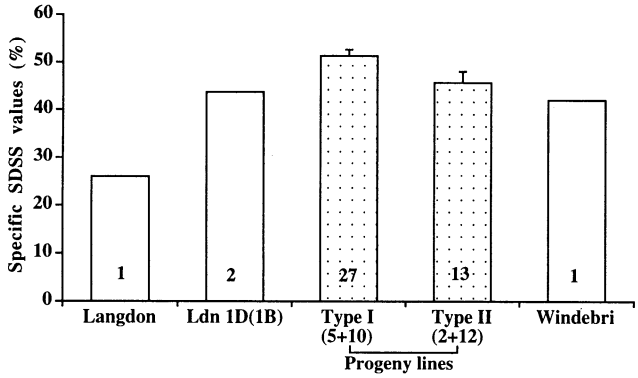

Fig. 4. Average specific sodium dodecyl sulfate sedimentation (SDSS) values (100 × SDSS/PC) of the two BC_1F_4 progeny populations (pooled values) and the parents. The data are the combined values of the an/euploid progeny lines from the two backcross progeny populations (adapted from Liu 1995). Both progeny phenotypes I and II are Langdon 1D(1B) substitution types, carrying the *Glu-D1* encoded HMW glutenin subunits 5+10 and 2+12, respectively. The number in each column represents the number of lines analyzed. Error bars represent the standard error of the mean.

the *Glu-D1* gene coding for HMW-GS bands 5+10 has also been transferred to triticale (Lukaszewski and Curtis 1992, 1994).

It is likely that the accumulation of favorable alleles in durums at the other three glutenin loci (*Glu-A1, Glu-A3,* and *Glu-D3,* or *Glu-B1, Glu-B3,* and *Glu-D3*) coupled with the introduction of *Glu-D1d* or *Glu-D1a* genes from bread wheats, could result in even higher gluten strength. For example, improved dough strength is likely to be associated with durums carrying the *Glu-B1i* allele (bands 17+18), which is known to have a strong influence on breadmaking quality in bread wheat, but which does not currently occur in durum wheats (Lawrence et al 1988, Gupta et al 1994). Introduction of active alleles such as *Glu-A1a* or *Glu-A1b* to replace the null allele *Glu-A1c* on chromosome 1A is also expected to result in improved technological quality (du Cros 1987, Branlard et al 1989, Kaan et al 1993). Introgression of these HMW and LMW glutenin genes into durum wheats is expected to be relatively easy, as these protein markers can be easily screened by electrophoretic or HPLC analyses during early generations of a breeding program (Bietz 1986, Payne 1987).

Other Approaches to Improving Durum Wheat Quality

Novel HMW-GS. It was recently demonstrated in bread wheats that alleles at different loci influence dough strength (here R_{max}) to different degrees in the order: *Glu-D1* > *Glu-B1* > *Glu-B3* > *Glu-A3* > *Glu-D3* > *Glu-A1,* and that the total effect of the *Glu-1* loci is relatively larger than that of *Glu-3* loci (Gupta et al 1991, 1994). Therefore, introduction of superior HMW-GS is likely to be more efficient than changing LMW-GS. As shown in bread wheat, a greater number of HMW-GS or darker bands give enhanced dough quality (Payne et al 1984a, Ng et al 1989, Singh et al 1990), whereas fewer bands or the 'null' alleles have detrimental effects on quality (Lawrence et al 1988). Many alternative approaches have been suggested to improve the gluten quality of hexaploid wheat by the manipulation of HMW-GS (reviews of Payne 1987, Pogna et al 1992), and these may also be applicable to the durums. One strategy is to increase the number of HMW-GS genes controlling the synthesis of quality related polypeptides, for example, the introduction of the HMW-GS at the *Glu-A1* locus from *T. monococcum, T. urartu,* or *T. dicoccoides,* which have active genes coding for both x and y HMW-GS and which are not expressed in bread or durum wheat (Waines and Payne 1987, Levy et al 1988, Ciaffi et al 1991). The first example of such introgression of active *Glu-A1* genes into durum background was reported recently (Ciaffi et al 1995). Introduction of unique genetic blocks coding for more copies of the HMW glutenins (Israeli wheat cv. TAA 36) or introduction of genes that have increased transcription or translation efficiency (Canadian cv. Glenlea) are other suggested approaches (Lukow et al 1992).

New LMW-GS/Gliadins. Modification of LMW-GS/gliadin alleles is also promising. However, the functional effect of particular LMW-GS alleles with the quality attributes is still largely unknown in durum wheat, except for the LMW-1 and LMW-2 (γ-42/-45) types. Earlier, Boggini and Pogna (1989) suggested introducing the rare γ-43.5 and γ-47 types into a durum background as these γ types appeared to be correlated with improved dough quality whereas Autran and Galterio (1989) reported that some α- or β-gliadin allelic types improved cooking quality characters.

Translocation of chromosome segments carrying quality-related genes resulting from interspecific hybridization could also be effective. For instance, a 1AS/1DS translocation was reported in the Russian cv. Perzivan (Metakovsky et al 1990, Redaelli et al 1992), though the effect of this translocation on quality remains to be determined. Conversely, Pogna et al (1992) suggested that removal of gliadin genes could shift the balance of nitrogen assimilation towards synthesizing more proteins such as HMW-GS, and various spontaneous mutants with a *Gli-1* locus deleted have already been isolated (Lafiandra et al 1987, 1988; Benedettelli et al 1992).

As LMW-GS are more likely to be the causal factors for technological quality, the gliadins are only useful as genetic markers and efforts should be made toward characterizing their corresponding LMW-GS components (Autran and Galterio 1989, Pogna et al 1990). Several research workers have started to collect useful information of the functional influence of the LMW-GS (Carrillo et al 1990a,b; Liu and Rathjen 1994). *T. dicoccoides* could provide novel HMW-GS alleles for the cultivated species (Nevo and Payne 1987, Ciaffi et al 1991). Also it is rich in allelic variants at the *Glu-3* loci (Ciaffi et al 1993, Liu 1994), some of which might confer superior technological properties once they have introgressed into the durum wheat background.

Molecular biology approaches. There have been several recent reports of the successful introduction of foreign genes into monocotyledonous plants, suggesting that genetic improvement of the protein quality in wheat will soon be achievable using transformation techniques. The introgression of the HMW and LMW glutenin genes or gliadins through a suitable transformation system is likely to have a significant impact on the improvement of dough quality in wheat (Anderson et al 1994). Expression of particular prolamin genes (natural or synthetic) can also be altered specifically, for example, by the introduction of additional gene copies, by the modification of *cis*-acting regulatory sequences, or by the synthesis of antisense mRNAs. The genes of several different storage proteins have been isolated, and preliminary studies are beginning to unravel the molecular controls that subject them to developmental regulation. Methods for transforming wheat plants are now available (Anderson et al 1994). Furthermore, several HMW-GS genes have been successfully expressed in exogenous systems (Galili 1989, Robert et al 1989).

PROPOSED FUTURE WORK

Our recent work demonstrated that a poor dough quality durum such as Langdon can be improved to a quality level equivalent to a medium quality bread wheat by genetic manipulation. All this work was assessed under small-scale tests. Large-scale quality evaluations, including finished product assessments, are essential to characterize the further quality potential of these new durums with 1D protein genes. Rheological tests are not always correlated with the results of experimental pastamaking and breadmaking testing (MacRitchie 1984, Cubadda 1989). Once the favorable influences of such genes has been confirmed at the tetraploid

level for use in pastamaking and breadmaking durums, they could be readily introduced into locally adapted cultivars with good yield potential (Liu et al 1994a). If the new 1D substitution lines are still poor in grain yield, the introduction of a small segment of a chromosome carrying the particular gene (by cytogenetic means), or of a single gene (by gene transformation) could be the next step. Attempts on the development of superior lines of high grain yield carrying D-genome proteins have so far not been successful (Joppa et al 1978, Liu et al 1995).

Our recent preliminary dough testing of wholemeal samples of these 1D substitution lines showed that they are stronger in dough strength but have lower dough extensibility (measured by R_{max} and extensibility) when compared to normal durums and hexaploid wheats (Liu, *unpublished data*). These quality results are in agreement with those of Ciaffi et al (1995), who produced exceptionally strong durums by introducing the active *Glu-A1* allele from a *T. dicoccoides* line.

New high quality durums must be beneficial for both producers and consumers. Therefore, we may need to turn our attention to other endosperm components, including starch and lipids, and not just concentrate on the protein fraction alone.

The elucidation of factors controlling the surface state of cooked pasta requires further research (Lin et al 1974, Dexter et al 1983, Matsuo et al 1986, Alary and Kobrehel 1987, Kobrehel et al 1991), although it seems to be relatively independent of dough rheological quality. Spaghetti stickiness after cooking appears to be affected by many factors including cooking loss, cooking weight, degree of swelling, compressibility, recovery, and firmness (Dexter et al 1983, Autran et al 1986, Autran and Feillet 1987). Recently, it was shown that the surface condition of cooked pasta is positively correlated with the amount of -SH plus S-S groups in the glutenin (Alary and Kobrehel 1987, Feillet et al 1989). Nonpolar lipids also appear to have an effect on the stickiness of cooked spaghetti (Matsuo et al 1986). There seems to be much scope for further work in this area.

Despite recent progress in understanding the biochemical basis of functional properties of gluten proteins, Cubadda (1989) concluded his review with the statement that "we are still unable to completely identify the nature of the protein components and the mechanisms of the phenomena involved in determining cooking quality of pasta". For example, the role of other durum endosperm components, such as starch and minor constituents (soluble and insoluble pentosans, lipids, lipoproteins, various enzymes, and products of enzyme reactions), and the interactions among these constituents and with the proteins needs further study. The importance of starch in pastamaking is not well understood (Lintas and D'Appolonia 1973, reviews by Finney et al 1987, Cubadda 1989). Moreover, when considering the whole array of differences of durum and bread endosperm, durums apparently differ from bread wheat not only in gluten protein composition, but also in grain hardness and milling characteristics, including starch damage, which contributes to their different mixing properties (Lindahl and Eliasson 1992). Interchange of endosperm fractions between durum and bread wheats (such as lipid, gluten, etc.) have shown quite different quality characteristics between them (Dexter and Matsuo 1978, Dexter et al 1981, Boyacioglu and D'Appolonia 1994b).

Environmental effects, such as sulfur deficiency, heat stress, level of CO_2, nitrogen fertilizers and other weather and soil factors (B, Na^+, etc.) have also been shown to exert a pronounced effect on the overall functional quality of wheat flours (Moss et al 1981, Wrigley et al 1984, Lafiandra et al 1991, Blumenthal et al 1993, Wrigley 1994). The detailed effect of these factors also awaits further study.

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