Breadbaking Potential of Durum Wheat Lines Expressing Both X- and Y-Type Subunits at the *Glu-A1* Locus

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ABSTRACT

Functionality and protein composition data were obtained for 13 F7 lines derived by a four-way cross, involving two different Italian cultivars (Creso and Lira), a tetraploid breeding line (A327), and an accession of *Triticum dicoccoides*. Three bread wheat cultivars currently grown in Italy and two durum parental cultivars were used as controls. These lines possessed one or two subunits at the *Glu-A1* locus, derived from the uncommon allelic variant at the same locus of both A327 and *Triticum dicoccoides*. Functional quality was assessed by the sodium dodecyl sulfate (SDS) sedimentation test, rheological dough tests (mixograph and alveograph), and an optimized microbaking test. Protein composition was measured by near infrared reflectance (protein content), size-exclusion HPLC, and SDS-PAGE. Rheological and baking properties were strongly associated with the allelic type of proteins encoded by the *Glu-B3* and *Glu-A1* loci. Lines with the best technological performances contained the *Glu-A1* allele from *T. dicoccoides* and the allelic type LMW-2 at the *Glu-B3* locus from the parental durum wheat cultivars. Results indicated that some lines had exceptionally high dough strength and approached acceptable levels for baking, with one possessing dough rheological properties and baking performance as good as those of the bread wheat cultivars used as controls.

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In the Mediterranean area, especially in the southern regions of Italy, in addition to pasta production, durum wheat finds large usage in the preparation of numerous types of bread. Generally bread made from durum wheat is characterized by a yellowish color, fine and uniform porosity, characteristic taste and smell, and prolonged storage life (Quaglia 1988). However, the use of durum wheat in commercial bread production has been restricted, mainly because its breadmaking quality is inferior to that of bread wheat (for review see Boyacioglu and D'Appollonia 1994). The poor breadmaking quality of durum wheats was partly attributed to the lack of the D genome, particularly chromosome 1D, which contains genes that control some of the gluten proteins contributing to breadmaking quality (Payne 1987). However, several studies have shown that there is a wide range of variation in breadmaking quality of durum wheat cultivars (Quick and Crawford 1983, Boggini and Pogna 1989, Peña et al 1994); some genotypes approach the good breadmaking quality of bread wheats. These results indicate that baking quality attributes may also be controlled by A and B genome chromosomes. In durum wheat, chromosome 1B encoded proteins have greater effects on gluten quality than proteins controlled by any other chromosome (Josephides et al 1987). In particular, a very consistent relationship was found between the B group of low M_r glutenin subunits, coded by genes at the complex locus *Glu-B3*, and both pasta cooking properties (Pogna et al 1990) and baking quality attributes (Boggini and Pogna 1989, Peña et al 1994). Two main types of low M_r glutenin subunits, designated LMW-1 and LMW-2, have been detected at this locus in the durum wheat world collection (Payne et al 1984, Carrillo et al 1990, Pogna et al 1990); they are related, respectively, to poor and good gluten viscoelasticity. In contrast to bread wheat, high M_r glutenin subunits appear to be less crucial in affecting both bread- and pasta-making quality in durum wheat, but this remains to be firmly established because of limited genetic variation in the composition of these proteins in durum wheat cultivars. In fact, durum wheats lack the two chromosomes for 1D-encoded high M_r glutenin subunits that are present in all bread wheats, and most cultivars contain only one or two high M_r glutenin subunits that are both encoded by chromosome 1B, more than 80% being null at the *Glu-A1* locus (Branlard et al 1989). The restricted allelic variation detected for *Glu-B1* encoded proteins, even if significant, has less effect on gluten quality than variation at the *Glu-B3* locus. In particular, comparisons within the *Glu-B1* and *Glu-B3* loci indicated that the high M_r subunit pair 7+8 and LMW-2 had greater beneficial effects on gluten strength and breadmaking quality than did subunit 20 or the subunit pair 6+8 and LMW-1, respectively (Boggini and Pogna 1989, Peña et al 1994).

The object of this study was to evaluate some gluten quality characteristics and breadmaking properties of 13 F7 lines segregating from multiple crosses, including an accession of *Triticum dicoccoides* and a tetraploid breeding line that possess allelic variants at the *Glu-A1*, *Glu-B1*, and *Glu-B3* loci not usually present in durum wheat cultivars. The effects of A and B subunits of glutenin on quality attributes was also studied.

MATERIALS AND METHODS

Plant Material

The 13 F7 lines used in this study were selected for agronomic and qualitative traits from a segregating population obtained by a four-way cross involving two different Italian durum wheat cultivars (Creso and Lira), a tetraploid genotype (A327) derived from an interspecific cross (*T. durum* × *T. aestivum*), and an accession of *T. dicoccoides* with high protein content. During the season 1992–93, these lines, with the parental durum cultivars (Creso and Lira) and three bread wheat varieties (Centauro, Loreto, and Mec) used as controls, were grown in a randomized complete block design containing two replicates.

Electrophoretic and Chromatographic Analyses

A and B subunits of glutenins were analyzed in the parental and derived F7 lines using the one-step 1D sodium dodecyl sulfate polyacrylamide gel electrophoresis (SDS-PAGE) procedure described by Ciaffi et al (1993a). Total unreduced flour proteins were fractionated, by size-exclusion high-performance liquid

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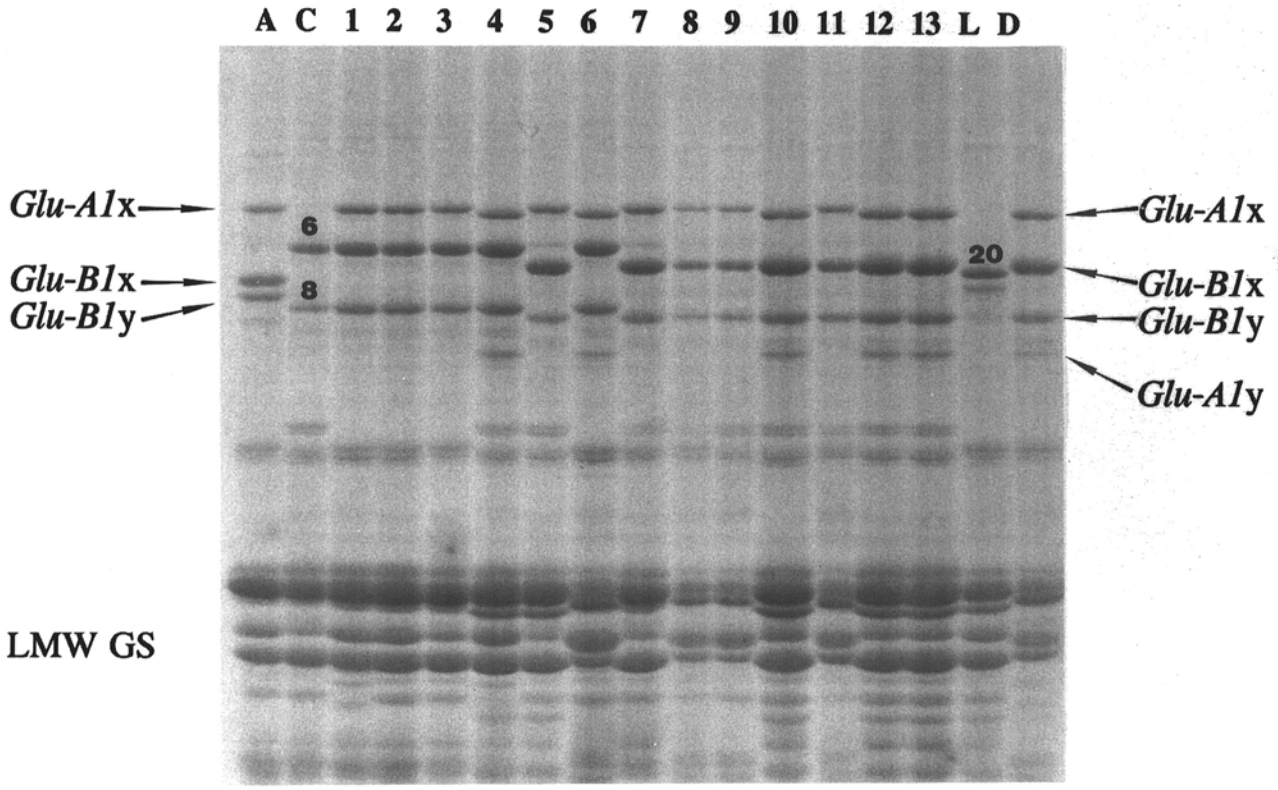

Fig. 1. Sodium dodecyl sulfate polyacrylamide gel electrophoresis (SDS-PAGE) separation of glutenin from F7 lines and their parents. For each subunit, corresponding locus is indicated in A327 (A) and *T. dicoccoides* (D). Numbers indicate alleles in Creso (C) and Lira (L).

TABLE I
Allelic Variation at the *Glu-1* and *Glu-B3* Loci and Relative Size-Exclusion High-Performance Liquid Chromatography Measurements of 13 F7 Lines

Genotypes	*Glu-A1*[a]	*Glu-B1*[b]	*Glu-B3*[c]	%Peak 1	%Peak 2	%Peak 3
N201	1	1	1	46.3	42.4	11.3
N202	1	1	1	46.0	42.1	11.9
N203	1	1	1	45.7	41.4	12.4
N204	2	1	1	51.7	37.3	10.9
N205	1	2	1	50.4	36.4	13.2
N207	2	1	2	46.2	42.2	11.6
N211	1	2	1	48.3	41.5	10.2
N212	1	2	2	42.3	45.0	12.7
N213	1	2	2	42.9	46.5	10.6
N215	2	2	1	50.7	37.9	11.4
N221	1	2	2	44.0	43.1	11.9
N224	2	2	1	49.3	39.1	11.6
N225	2	2	1	49.8	38.1	12.1
Mean				47.2	40.9	11.6
SD[d]				3.1	3.1	1.1
LSD ($P = 0.05$)[e]				2.7	2.4	2.8

[a] 1 = Allelic variant from A-327; 2 = allelic variant from *Triticum dicoccoides*.
[b] 1 = Allelic variant from Creso; 2 = allelic variant from *T. dicoccoides*.
[c] 1= *Glu-B3* LMW-2 type; 2 = *Glu-B3* from *T. dicoccoides*.
[d] Standard deviation.
[e] Least significant difference.

chromatography (SE-HPLC) into three distinct peaks of decreasing size range, representing mainly glutenin, gliadin, and albumin-globulin, according to the method of Batey et al (1991).

Quality Measurements

Flour (straight-run) samples were produced on a Brabender Quadrumat Junior laboratory mill. Protein and moisture was determined by near infrared reflectance (NIR). SDS-sedimentation test (TSDS) was performed according to Dick and Quick (1983). Mixing development time (MDT) was measured using a 10-g mixograph and doughs made with an addition of 70% water (13% mb) and NaCl (2% by flour weight). Alveograph characteristics (*W, P, L,* and their ratio *P/L*) were determined according to the manufacturer instructions, using 250-g flour samples with constant (50%) and variable (55–60%) water absorption for bread and durum wheats, respectively. Variable absorption was used because milling of the typically hard-grained durum wheat into flour was assumed to result in high levels of damaged starch and, consequently, in higher than normal (50%) water absorption requirements in the alveograph determination. Bread was baked using 30.2 g of dry flour according to the optimized method of MacRitchie (1976), except that the improver contained 100 ppm of ascorbic acid and no bromate. For common wheats, bread was baked only for Centauro.

Statistical Analysis

The results were analyzed statistically with the SYSTAT (1990) computer package. Analysis of variance (ANOVA) for the quality parameters was made over the lines and cultivars using a complete randomized block design with two replicates or considering high M_r and low M_r subunits as sources of variation. In the latter case, the *F*-test for variance significance was performed using as residual the variation between lines within high M_r or low M_r subunit groups.

RESULTS

Protein Composition of Parental and F7 Derived Lines

SDS-PAGE migration patterns of reduced proteins from F7 lines and their parents are illustrated in Figure 1. In the region of the high M_r glutenin subunits, the two parental varieties differ; Lira contains one major component and Creso two, coded by genes at the *Glu-B1* locus (lanes L and C in Fig. 1). These allelic variants are indicated as 20 (allele *Glu-B1e*) and 6+8 (allele *Glu-B1d*), respectively. Genes at the *Glu-A1* locus are silent in both

TABLE II
Mean Values of Quality Parameters[a] for F7 Lines and Bread and Durum Wheats Used as Controls

Genotypes	FP, %	TSDS, mm	W, $\times 10^{-4}$J	*P*, mm	*L*, mm	*P/L*	MDT, min	LV, ml
N201	14.6	66.3	240.0	92.0	93.0	0.99	5.3	178.5
N202	15.5	76.7	284.5	105.4	79.7	1.31	4.9	183.0
N203	15.7	76.5	288.5	107.9	83.1	1.29	5.0	184.0
N204	16.4	99.5	467.0	166.0	85.2	1.95	9.9	209.5
N205	14.5	71.2	278.0	98.8	82.0	1.21	5.0	179.0
N207	15.2	59.3	233.5	89.1	79.4	1.12	4.1	163.5
N211	15.5	75.5	275.5	112.1	89.0	1.26	5.2	182.0
N212	15.8	53.9	173.0	82.4	83.7	0.98	3.9	161.0
N213	16.8	51.8	175.0	80.6	87.7	0.91	3.7	162.5
N215	14.7	86.7	289.0	121.7	84.9	1.43	6.3	191.5
N221	14.7	49.5	170.0	85.0	100.2	0.85	4.0	157.0
N224	15.6	91.0	395.5	147.0	92.1	1.60	5.4	188.5
N225	16.5	96.7	397.0	134.0	84.2	1.60	4.9	190.0
Creso	14.2	66.5	247.0	106.0	61.9	1.71	5.0	174.5
Lira	14.2	69.0	246.5	100.0	69.0	1.45	4.7	173.5
Centauro	12.1	90.0	280.0	81.8	81.5	1.03	9.9	202.5
Mec	13.0	86.0	243.0	70.2	105.1	0.66	4.6	...
Loreto	15.8	91.8	438.0	99.7	135.8	0.74	5.8	...
Mean	15.1	75.4	284.5	104.5	87.6	1.23	5.4	180.0
CV[b]	2.78	2.31	3.86	6.49	6.70	9.05	3.37	0.95
LSD ($P = 0.05$)[c]	1.5	5.4	27.6	15.6	12.0	0.33	0.55	5.50

[a] FP = flour protein; TSDS = sodium dodecyl sulfate (SDS) sedimentation test. Alveograph characteristics: *W* = strength, *P* = tenacity, *L* = extensibility, *P/L* = tenacity-extensibility ratio. MDT = mixograph dough development time. LV = loaf volume.
[b] Coefficient of variation.
[c] Least significant difference.

cultivars (allele *Glu-A1a*). The line A327 possesses three novel HMW-glutenin subunits (lane A in Fig. 1). The first, with higher molecular weight, is controlled by the *Glu-A1* locus, the other two are coded by genes at the *Glu-B1* locus. Four high M_r glutenin subunits are present in *T. dicoccoides* (lane D in Fig. 1) each one belonging to a particular subunit group: the first, indicated 1Ax, possesses higher mobility and is coded for by a gene located on the long arm of the 1A chromosome; the subunit with the lowest mobility is also controlled by a *Glu-A1* gene and is indicated as 1Ay; the two intermediate subunits, indicated as 1Bx and 1By, are coded by genes at the *Glu-B1* locus. Assignment of *T. dicoccoides* subunit group to different chromosomes was previously done on the basis of the segregation observed in F2 progenies (Ciaffi et al 1993b). The gene at the *Glu-A1* locus, encoding the y-type subunit, is not expressed in cultivated wheats, whereas the 1Ay subunit was found in cultivated and wild diploid wheats, *T. monococcum* ssp. *monococcum* and ssp. *boeoticum*, in *T. urartu* (Waines and Payne 1987, Ciaffi et al 1992), and in the wild tetraploid *T. dicoccoides* (Levy et al 1988, Ciaffi et al 1993a).

The B subunit pattern, usually referred to as LMW-2, is present in Creso, Lira, and A327 (Lanes C, L, and A in Fig. 1), whereas *T. dicoccoides* possesses a different LMW-glutenin pattern.

Allelic variation at the *Glu-1* and *Glu-B3* loci of the 13 F7 lines and their relative quantity of different SE-HPLC fractions are reported in Table I. Electrophoretic analyses (Fig. 1) indicated that in these lines, which were selected for agronomic and qualitative characters, some parental alleles were predominant. At *Glu-A1*, only the two allelic variants of *T. dicoccoides* and A327 were found, the first in five lines (lanes 4, 6, 10, 12, and 13 in Fig. 1) and the latter in eight lines. No F7 lines possessed the *Glu-B1* alleles from A237 and Lira, whereas those from Creso and *T. dicoccoides* were detected in six and seven lines, respectively. Finally, at *Glu-B3* the allelic variant derived from Creso, Lira, and A327 (LMW-2) was found in nine lines, whereas that from *T. dicoccoides* was found in the remaining four lines (lanes 6, 8, 9, and 11 in Fig. 1).

Variations for relative quantities of protein fractions among lines were significant (Table I). The highest variability was for the relative quantity of glutenin (% area of Peak 1, 42.3–51.7%) and gliadin (% Peak 2, 36.4–46.5%), whereas the relative quantity of albumin-globulin (% Peak 3) varied least (10.6–13.2%). Table I indicated that F7 lines with LMW-2 had a significantly greater proportion of glutenin than those possessing the *T. dicoccoides* allele at *Glu-B3*, and that the highest relative quantity of glutenin was found in the lines with LMW-2 and the *Glu-A1* allele from *T. dicoccoides*.

Quality Characteristics

Mean values of quality parameters for each of the F7 lines and for the two and three durum and bread wheat cultivars used as controls are reported in Table II. In all lines, mean protein content values (FP) were higher than those detected for the two durum parental varieties used as controls, but only five showed values significantly greater than Creso and Lira. All durum lines were superior to Centauro and Mec in flour protein content but did not differ significantly from Loreto. A large and significant variation for all gluten strength-related parameters was observed between the F7 lines examined. SDS-sedimentation values (TSDS) ranged from 49.5 to 99.5 mm. Seven lines had significantly higher TSDS values than those of the two parental durum varieties, whereas four of these with unusually high values in the SDS-test (86.7–99.5 mm), did not differ significantly from bread wheat cultivars. Alveographic index *W* varied within the F7 lines from 170 to 467 $\times 10^{-4}$ J. Eight lines were superior in *W* index to Creso and Lira, whereas three of these possessed values, ranging from 395.5 to 467 $\times 10^{-4}$ J, significantly higher than those of the two bread wheat cultivars Mec and Centauro. With the exception of four lines (N201, N212, N213, and N221), all the durum wheats had *P/L* values higher than those of the bread wheats used as controls. Although the *P/L* values detected for the F7 lines generally corresponded to tenacious gluten type, some genotypes (N201, N205, and N211) had acceptable values in *W* index and a more equilibrated ratio between tenacity and extensibility *(P/L)* than the two parental durum wheat cultivars.

The F7 line with the highest *P/L* value (N204) showed also the highest value in peak mixograph dough development time (MDT), which differed significantly from all the durum genotypes and from two of the three bread wheat cultivars used as control. The line N215 was also superior in MDT value to Creso, Lira, and Mec. Four lines (N207, N212, N213, and N221) had

TABLE III
Mean Values[a] for Quality Characteristics[b] of 13 F7 Lines Grouped According to *Glu-A1*, *Glu-B1*, and *Glu-B3* Glutenin Subunit Composition

Subunit	Number	FP, %	TSDS, mm	W, $\times 10^{-4}$J	*P*, mm	*L*, mm	*P/L*	MDT, min	LV, ml
Glu- A1[c]									
1	8	15.4a	65.2a	235.6a	95.5a	87.3a	1.08a	4.6a	173.3a
2	5	15.7a	86.6b	356.4b	131.6b	85.2a	1.54b	6.1a	188.6b
Glu-B1[d]									
1	5	15.5a	75.7a	302.7a	112.1a	84.1a	1.32a	5.8a	183.7a
2	8	15.5a	72.0a	269.1a	107.7a	87.9a	1.22a	4.8a	176.4a
Glu-B3[e]									
1	9	15.4a	82.2b	323.9b	120.5b	85.9a	1.40b	5.8a	187.3a
2	4	15.6a	53.6a	187.9a	84.3a	87.8a	0.95a	3.9a	161.0b

[a] Means with the same letter in columns within the same group are not significantly different.
[b] FP = flour protein; TSDS = sodium dodecyl sulfate (SDS) sedimentation test. Alveograph characteristics: *W* = strength, *P* = tenacity, *L* = extensibility, *P/L* = tenacity-extensibility ratio. MDT = mixograph dough development time. LV = loaf volume.
[c] 1 = Allelic variant from A-327; 2 = allelic variant from *Triticum dicoccoides*.
[d] 1 = Allelic variant from Creso; 2 = allelic variant from *T. dicoccoides*.
[e] 1= *Glu-B3* LMW-2 type; 2 = *Glu-B3* from *T. dicoccoides*.

TABLE IV
Mean Values[a] for Size-Exclusion High-Performance Liquid Chromatography of 13 F7 Lines Grouped According to *Glu-A1*, *Glu-B1*, and *Glu-B3* Glutenin Subunit Composition

Subunit	Number	%Peak 1	%Peak 2	%Peak 3
Glu- A1[b]				
1	8	45.73a	42.30b	11.83a
2	5	49.54b	38.92a	11.54a
Glu-B1[c]				
1	5	47.18a	41.08a	11.74a
2	8	47.21a	40.95a	11.71a
Glu-B3[d]				
1	9	48.68b	39.57a	11.73a
2	4	43.85a	44.20b	11.70a

[a] Means with the same letter in columns within the same group are not significantly different.
[b] 1 = Allelic variant from A-327; 2 = allelic variant from *Triticum dicoccoides*.
[c] 1 = Allelic variant from Creso; 2 = allelic variant from *T. dicoccoides*.
[d] 1= *Glu-B3* LMW-2 type; 2 = *Glu-B3* from *T. dicoccoides*.

values of MDT significantly lower than those of Creso and Lira. Bread loaf volume also varied widely (Table II). The genotype with the strongest gluten (N204) produced bread with large volume (209.5 ml), significantly greater than that obtained for the bread wheat cultivar Centauro. Six genotypes gave loaf volumes (LV) significantly greater than those of the two parental durum cultivars, although none exhibited loaf volume as good as that of Centauro. Two other genotypes had intermediate bread volumes that were not significantly different from Creso and Lira, whereas four other genotypes (N207, N212, N213, and N221) gave lower loaf volumes (157– 163.5 ml).

Effect of Allelic Variation in Protein Components at *Glu-1* and *Glu-B3* Loci on Quality Characteristics and Chromatographic Parameters

To examine the relationship between protein composition at the loci investigated and breadmaking quality parameters, the F7 lines were grouped into *Glu-A1*, *Glu-B1*, and *Glu-B3* genotypic groups. The mean values for quality characteristics of genotypic groups for each locus considered are reported in Table III. Results of analysis of variance (not shown) indicated that flour protein, dough extensibility *(L)* and MDT were not significantly affected by the allelic variation at the *Glu-1* and *Glu-B3* loci. The results showed, however, that genotypes with *T. dicoccoides* allele at *Glu-A1*, and LMW-2 at *Glu-B3*, tended to have longer MDT than those with the A327 and *T. dicoccoides* allelic variants at the same loci, respectively. TSDS, alveographic indices *W* and *P*, tenacity, *P/L* ratio, and loaf volume were strongly affected by the allelic variation at the *Glu-A1* and *Glu-B3* loci, whereas variation at the *Glu-B1* locus had no significant influence on these qualitative parameters. F7 lines that contained the LMW-2 type at the *Glu-B3* locus showed higher values in the dough strength–related parameters and in bread loaf volume than those of lines carrying the *T. dicoccoides* allele (Table III). Similarly, the two high M_r glutenin subunits of *T. dicoccoides* encoded at the *Glu-A1* locus were associated with greater TSDS and *W* and *P* values, and loaf volume than the A327 allele showing only the x-type high M_r glutenin subunit.

ANOVA results for SE-HPLC measurements, performed considering allelic variants at *Glu-A1*, *Glu-B1*, and *Glu-B3* as sources of variation, indicated that the relative quantity of glutenin (% Peak 1), and gliadin (% Peak 2), were significantly affected by the allelic variation at the *Glu-A1* and *Glu-B3* loci, whereas variation at the *Glu-B1* locus had no significant influence on the relative quantity of these two fractions. Results also showed that the relative quantity of albumin-globulin (% Peak 3) was not influenced by the allelic variation at the considered loci. The presence of the *T. dicoccoides* allele with both x and y high M_r glutenin subunits at the *Glu-A1* locus, increased the proportion of glutenin by about 4%, when compared with the A327 allele with only the x subunit (Table IV). Also, the LMW-2 type at *Glu-B3* was associated with a larger proportion of glutenin than the *T. dicoccoides* allele. The situation was completely reversed when the relative amount of gliadin was considered (Table IV).

DISCUSSION

The availability of durum wheat cultivars with satisfactory breadmaking characteristics as well as excellent pasta quality is a desirable goal. A dual-purpose durum would have alternative markets in years of high production (Boggini and Pogna 1989) and might also be used instead of common hard wheat as a filler in high-quality flour blends (Boggini and Pogna 1990, Boyacioglu and D'Appollonia 1994).

Present results indicate that some durum wheat lines used in this study appeared to be very promising in breadmaking ability, being superior to the two durum wheat cultivars used as controls, and nearly equaling the three bread wheat controls in overall evaluation. This shows that, although durum wheat has typically tenacious gluten, in some cases, it is possible to produce bread with good quality. In this respect, although the *P/L* values detected for the F7 lines generally corresponded to tenacious gluten type, some genotypes showed acceptable values in *W* index and loaf volume but a more equilibrated ratio between tenacity and extensibility *P/L* than the two parental durum wheat cultivars.

Though the number of lines used in this study was small, considering all the possible HMW and LMW allelic combinations, these preliminary results indicate that the differences in breadmaking quality-related characteristics among the durum wheats

examined may be partly explained by variations in both high M_r and low M_r glutenin subunit composition. Durum lines that contained LMW-2 type at the *Glu-B3* locus showed higher values in the dough-related parameters and in bread loaf volume than those of lines carrying the *T. dicoccoides* allele, confirming the positive influence of these *Glu-B3* encoded subunits on breadmaking properties (see also Boggini and Pogna 1989, Peña et al 1994). Also, the two high M_r glutenin subunits of *T. dicoccoides* encoded at the *Glu-A1* locus had significantly greater beneficial effects on quality parameters than the A327 allele showing only the x-type high M_r glutenin subunit. More genotypes, with all the possible allelic combination at the *Glu-1* and *Glu-3* loci, or appropriate genetic lines (isogenic lines) are needed, however, to evaluate the contribution of the *Glu-A1* allele from *T. dicoccoides* on dough strength and baking quality.

Gene dosage for high M_r glutenin subunits might represent an interesting novel approach to improving breadmaking quality, not only in bread wheat, as discussed previously by Law and Payne (1983), but also in durum wheat, where in most varieties the genes at the *Glu-A1* locus are both silent. Evidence that an increase in the number of high M_r glutenin subunits might produce an increase in gluten strength was largely indirect, due to the reductions in quality observed when certain subunits were removed (Lawrence et al 1988). However, it has been reported that the introduction, in hexaploid and tetraploid wheats, of a *Glu-A1* locus encoding two subunits from *T. thaoudar* and *T. dicoccoides*, respectively, increases gluten strength (Rogers et al 1990, Ciaffi et al 1991).

Recent studies indicated that quantitative and qualitative effects may contribute to quality differences associated with specific high M_r and low M_r glutenin subunit alleles. In our study, quantitative analyses performed on total protein extracts from the 13 F7 lines show that the presence of the *T. dicoccoides* allele with both x and y high M_r glutenin subunits at the *Glu-A1* locus, increased the proportion of glutenin by ≈4%, when compared with the A327 allele with only the x subunit. Thus, the increase in gluten strength and breadmaking properties associated with the presence of both 1Ax and 1Ay subunits may result from an increase of polymeric proteins due to the greater amount of the high M_r glutenin subunits.

More detailed biochemical and molecular studies are needed to elucidate the precise role of the two *Glu-A1* encoded subunits in gluten structure.

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