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Genetic control of the amount of some gliadin and glutenin components in durum wheat

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ABSTRACT

Some quantitative aspects of the genetic control for various groups of proteins (HMWG, LMWG, ω-gliadin) were investigated through a diallel cross analysis. The association between the potential effect on durum wheat quality of various allelic types and the quantitative expression of the relevant proteins was confirmed, significant average heterosis effects were demonstrated for some of these proteins (LMWG, ω-gliadin 566). Some genotypes showed significantly greater general combining ability and general reciprocal effect than others. Cultivars Primadur and Brumaire were the best general combiners for determining an optimal protein composition as far as gluten quality was concerned (high proportion of LMWG, low proportion of ω-566). These results should be of great interest for programmes aimed at improving further the wheat breeding stategy.

Key words: Gene dosage, proteins, *Triticum durum* Desf.

INTRODUCTION

Durum wheat (*Triticum durum* Desf.) proteins have been considered as a model because of the very clear-cut relationship previously evidenced between the electrophoretic type 'γ-42' or 'γ-45' of the gliadin components that are encoded by genes on the short arm of chromosome 1B and the intrinsic quality (gluten viscoelasticity or strength) of cultivars (DAMIDAUX *et al.*, 1978; KOSMOLAK *et al.*, 1980; DU CROS *et al.*, 1983).

More recently it was shown that the association involved not one, but a group of γ- and ω-gliadin proteins and that the genes coding for them (*Gli-B1* locus) were tightly linked to genes coding for low molecular weight subunits of glutenin (LMWG) (*Glu-B3* locus) (SINGH and SHEPHERD, 1988). The latter, because of their strong aggregative properties, could be the direct causal agents of gluten viscoelasticity (POGNA *et al.*, 1988). On the other hand, some HMW glutenin subunits, which are encoded by the *Glu-B1* locus, on the long arm of chromosome 1B (SHEWRY and MIFLIN, 1984) have been shown to have a less important but additive effect on gluten properties (AUTRAN and FEILLET, 1967; POGNA *et al.*, 1990).

A breeding strategy based on γ-gliadin type determination by A-PAGE and, more specifically, on glutenin subunit type determination by SDS-PAGE was developed: early generation durum wheat lines with LMW '2' allele, and HMW '7 + 8' allele can be now selected as potentially strong gluten types.

The question was raised as to whether the various contributions made to durum wheat quality by the different alleles might be accounted for by differences in functional properties, or simply due to differences in the amount of certain protein components.

AUTRAN *et al.*, (1987) demonstraed that the strong viscoelasticity of 'γ-45' types occured simultaneously with a great proportion of LMW subunits in total proteins (27.7%), while the low viscoelasticity of 'γ-42' types was associated with lower proportions (15.1%). They suggested that quantitative differences alone in LMW fractions might explain the differences in gluten viscoelasticity between cultivars belonging to types 'γ-42' and 'γ-45'. An opposite situation was found with components that are likely to play a negative role such as ω-gliadins. For instance, 'ω-566' occurred with a lower proportion in 'γ-45' types (1.1%) compared with 'γ-42' types (3.0%). On the other hand, AUTRAN and GALTERIO (1989) showed that HMW alleles

associated with lower gluten strength (i.e. '13 + 16') produced lower amounts of HMW proteins than the others (i.e. '6 + 8' or '20').

Although genetic studies have showed that the major storage protein fractions are coded for by codominant, or equally dominant, alleles (MECHAM *et al.*, 1978, DAMIDAUX *et al.*, 1980, DU CROS and HARE, 1985), we have little knowledge of how these genes are expressed and controlled. Their expression involves a complex polygenic system (SHEWRY and MIFLIN, 1984), which is also influenced by environmental conditions. For instance, gene dosage effects in hexaploid wheats were demonstrated using F1 and F2 seeds (UHLEN and RINGLUND, 1987), or aneuploid and substitution lines (GALILI *et al.*, 1986). On the other hand, the relative amount of the various protein groups (ω-gliadins, α/β-gliadins, LMW-glutenins, HMW-glutenins) was affected by nitrogen fertilization (LEVY *et al.*,, 1985) or sulphur deficiency (CASTLE and RANDALL, 1987).

In a programme aimed at improving further the wheat breeding strategy, it is essential, therefore, not only to identify specific alleles that play a positive role in quality, but to consider their quantitative expression in the progeny and their combining abilities in order to identify genotypes, specific crosses and direction of crosses which could determine an optimal expression of the relevant proteins (e.g. maximal proportions of LMWG or HMWG and minimal proportions of ω-gliadins).

Based on an accurate densitometric scanning of electrophoretic patterns, the objectives of this study were to investigate some quantitative aspects of genetic control (general and specific combining abilities as well as maternal effect and specific reciprocal effect) for various groups of proteins involved in durum wheat quality (LMWG, HMWG, ω-gliadin) through a diallel cross analysis.

MATERIALS AND METHODS

Plant Material

The experimental material comprised five *durum* genotypes presenting a large genetic diversity. Primadur is a French commercial cultivar; Brumaire is another cultivar deriving from crosses between a *Triticum turgidum* var. *durum* and a *Triticum aestivum* carried out in "Ecole Nationale Supérieure Agronomique" of Toulouse (SARRAFI *et al.*, 1986); ENSAM 3034 and ENSAM 522-15 are two pure lines from "Ecole Nationale Supérieure Agronomique" of Montpellier; 80 SM 25-6 is a Syrian pure line from ICARDA (International Center for Agricultural Research in Dry Areas). A diallel cross was made between all five genotypes, including the reciprocal combinations. F1 hybrid seeds and their parents were used for electrophoretic purposes, on a per seed basis.

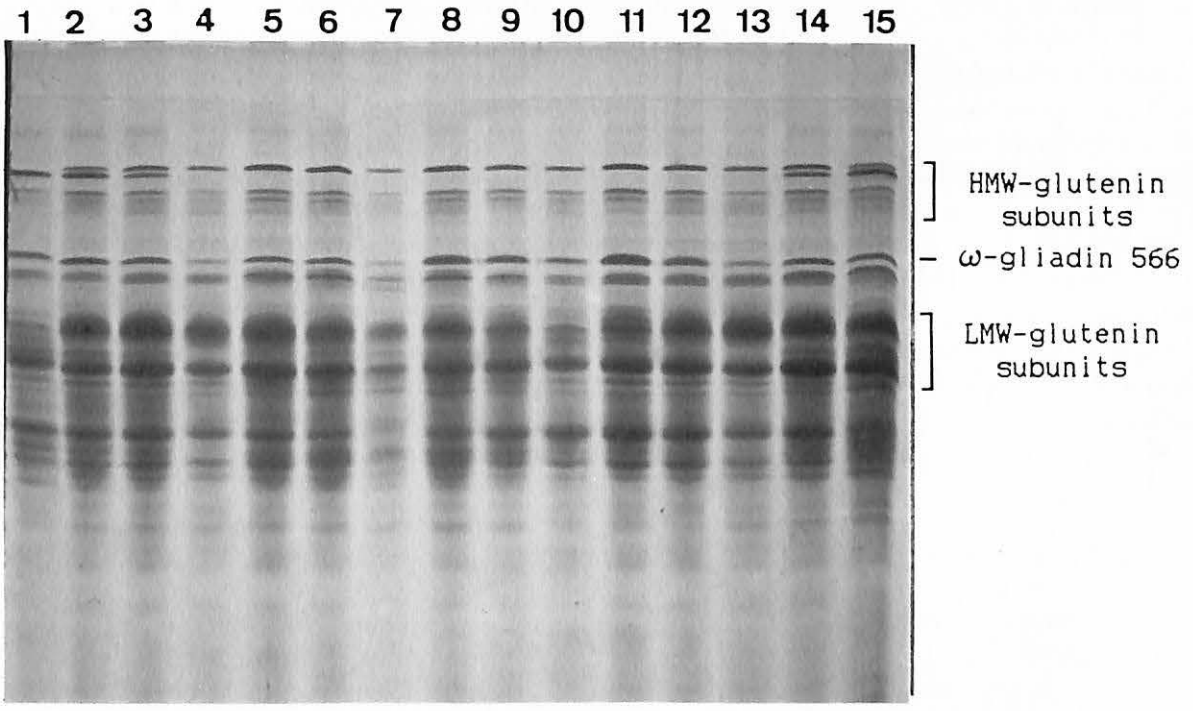

FIGURE 1 - SDS-PAGE patterns of the whole protein fractions extracted from some parental lines and F1 hybrids. 1,80 SM 25-6: 2,80 SM 25-6 × Primadur; 3, Primadur × 80 SM 25-6; 4, Primadur; 5, Primadur × Brumaire; 6, Brumaire × Primadur; 7, Brumaire; 8, Brumaire × ENSAM 3034; 9, ENSAM 3034 × Brumaire; 10; ENSAM 3034; 11, ENSAM 3034 × Primadur; 12, Primadur × ENSAM 3034; 13, Primadur; 14, Primadur × ENSAM 522-15; 15, ENSAM 522-15 × Primadur.

Extraction and Electrophoretic Analysis of Proteins

Reduced proteins were extracted from crushed grains by treatment with Tris-SDS-mercaptoethanol buffer according to PAYNE and CORFIELD (1979). The procedure was expected to extract all the different proteins species in the grain (soluble proteins, gliadins, LMW and HMW subunits of glutenin). Reduced proteins were electrophoresed in vertical SDS-PAGE slabs in a discontinuous, pH 6.8/8.8 Tris-HCl buffer system (PAYNE and CORFIELD, 1979) at a gel concentration of 13% (AUTRAN and BERRIER, 1984) using a 2001 apparatus (Pharmacia-LKB, France). Gels were fixed in 12% trichloroacetic acid and stained overnight with Coomassie Blue. Band nomenclature was based on a three-digit system derived from that of BERGER and LE BRUN (1985), which covered all the groups of components. Attention was focussed on the HMW group of glutenin subunits (mobility: 316-382), one ω-gliadin band (mobility: 566) and LMW group of glutenin subunits (mobility: 750-847), as indicated in Fig. 1. The allelic types for the various protein fractions have been summarized in Table 1.

TABLE 1
Summary of the allelic types of HMWG, LMWG, γ-gliadin and ω-gliadin among the parental lines

Lines or cultivars	HMWG	LMWG	γ-gliadin	ω-gliadin
Primadur	6-8	2	45	35
Brumaire	6-8	2	45	35
ENSAM 3034	6-8	1	42	33-35-38
ENSAM 522-15	7-8	2	45	35
80 SM 25-6	7-8	1	42	33-35-38

Densitometric Scanning

Black and white prints of the gels were scanned with a soft laser Ultroscan densitometer (Pharmacia-LKB, France). The densitometer curves (Figure 2) were prcessed (baseline subtraction, peak identification, integration) with Nelson software (Stang Instruments, France) on an IBM PC-XT microcomputer as previously described (AUTRAN and GALTERIO, 1989). Experiments indicated that the reproducibility of the densitometer analyses was ± 2% when scanning the same electrophoretic pattern and ± 10% when scanning different patterns of the same sample (AUTRAN *et al.*, 1987). Traces amounts of components were not taken into account and were eliminated by baseline subtraction. The absolute amount and relative proportion of each component were determined as well as the total area of the patterns. In all tables, quantitative data correspond to the means of four determinations.

Statistical Analysis

An analysis of variance for each trait was carried out on the five parental seeds and the derived 20 F1 seeds in a random block design with four replicates. All 25 seeds of a given replicate were submitted together to the electrophoresis process.

A comparison between F1 hybrids and parents (average heterosis effect) was done from densitometric measurements, based on the relative proportion of each protein component. A comparison based on their absolute values would be biased because of the widely different proportions of protein and starch among the analysed kernels, especially in the case of shrivelled F1 kernels.

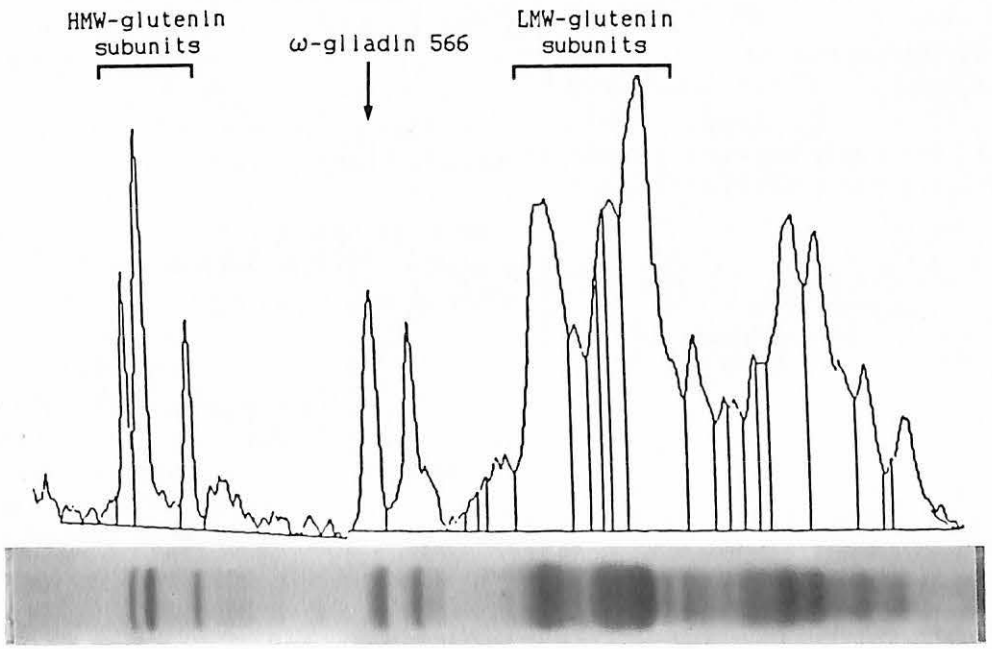

FIGURE 2 - Densitometer scan of the SDS-PAGE electrophoregram of the F1 hybrid ENSAM 522-15 × ENSAM 3034.

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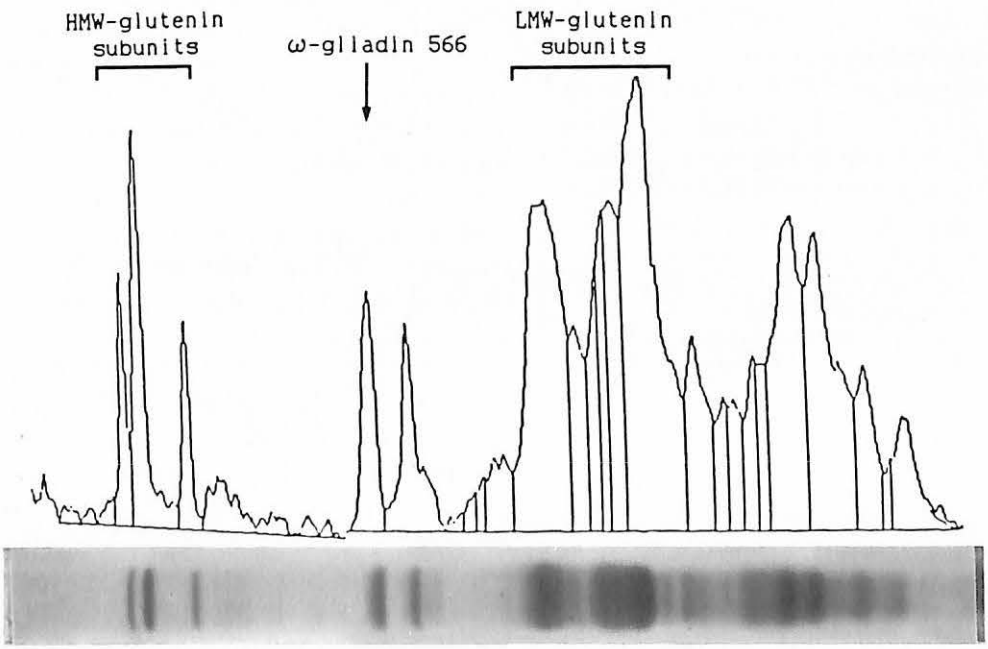

FIGURE 2 - Densitometer scan of the SDS-PAGE electrophoregram of the F1 hybrid ENSAM 522-15 × ENSAM 3034.

The error mean square for this analysis was further used to test genetic parameters, based on the F1's only, following the fixed model method n. 3 proposed by GRIFFING and KEULS (1978). This statistical model is the following:

$$Y_{ij} = \mu + GCA_i + GCA_j + SCA_{ij} + RE_{ij}$$

$$RE_{ij} = GRE_i + GRE_j + SRE_{ij}$$

in which:

μ = population mean
GCA_i (GCA_j) = general combining ability of the i^{th} (j^{th}) parent
SCA_{ij} = specific combining ability of the i × j cross
RE_{ij} = reciprocal effect involving the reciprocal cross between the i^{th} and j^{th} parents
GRE_i (GRE_j) = general reciprocal effect due to the i^{th} female or the j^{th} male
SRE_{ij} = specific reciprocal effect due to the cross between the i^{th} female and the j^{th} male

RESULTS AND DISCUSSION

Mean values of the parental lines

The variability of the various traits of electrophoretic patterns (total area, HMWG %, ω-566 %, LMWG %) among the parents is shown in Table 2.

All these traits showed significant differences between genotypes, excepted the total area of the patterns. For instance, the proportion of HMWG fraction showed a rather large variability. Greater values (8.61% and 7.48%) were respectively found with ENSAM 522-15 and 80 SM 25-6, which both belong to type HMWG '7-8'. Smaller values (5.01%, 5.74% and 5.96%) were respectively found with Primadur, Brumaire and ENSAM 3034 which all belong to type HMWG '6-8'. Since genotypes with HMWG '7-8' are now considered as having the greatest potentiel of gluten quality (POGNA *et al.*, 1990), this results develops further with the reports from AUTRAN and GALTERIO (1989) which suggested an association between the natural proportion of HMWG produced in the allelic types previously identified (e.g. '13-16', '6-8' and '20'), and rheological characteristics of gluten.

ω-gliadin 566 has an important genetic variability in our material and the greatest values (5.10% and 4.95%) were respectively found with the two types 'γ-42' 80 SM 25-6 and ENSAM 3034.

Conversely, the greatest values for LMWG % were found in the commercial cultivars Primadur (50.10%) and Brumaire (47.74%), and in line ENSAM 522-15 (43.6%), all belonging to type 'γ-45' (or LMWG '2'), whereas the 'γ-42' lines ENSAM 3034 and 80 SM 25-6 have much lower values (35.4% and 38.6%, respectively), confirming the significant genetic variability for this trait previously reported by AUTRAN *et al.*, (1987).

TABLE 2
Mean values for densitometric measurements of various protein components in the parental lines

Lines or cultivars	Total area	HMWG %	γ-566 %	LMWG %
Primadur	46.0 a	4.01 a	1.61 a	50.1 c
Brumaire	48.6 a	5.74 a	2.21 a	47.7 c
ENSAM 3034	48.9 a	5.96 a	4.95 b	35.4 a
ENSAM 522-15	61.6 a	8.61 b	1.45 a	43.6 b
80 SM 25-6	45.4 a	7.48 b	5.10 b	38.6 a
LSD 5%	32.34	1.55	1.44	5.74

Means followed by the same letter are not significantly different.

Average heterosis effects

Because endosperm tissue originates by the fusion of two polar nuclei contributed by the female parent with a sperm nucleus from the male parent, endosperm is triploid and its nuclei contain three sets of chromosomes. For instance, the F1 seeds of the cross Primadur × Brumaire received two doses of genes from Primadur and one dose from Brumaire, the opposite situation being found in the F1 seed of the reciprocal cross. A dosage effect, therefore, is expected that should be observable in F1 seeds.

However, average heterosis effects (all F1 means/all parents means, referred to as the $\bar{F}\bar{1}/\bar{P}$ ratio), based on the relative proportion of each protein component, were found significant and strongly different depending on the protein components. For instance, the ratios $\bar{F}\bar{1}/\bar{P}$ were 1.02, 1.42 and 0.80 for HMWG %, ω-566 % and LMWG %, respectively. These results are apparent from Fig. 1. Whereas most of the previous reports concluded, generally from visual observations of the patterns, that the protein components were approximately in proportion to the gene dosage in the endosperm, an accurate densitometric scanning suggests that the ratio of some fractions (ω-gliadin) is significantly enhanced in the F1 seed, whilst it is reduced for LMWG and unchanged for HMWG. Although a synchronous accumulation of all major groups of storage proteins has been gen-

erally reported, different rates of expression are likely to exist amongst the various groups. A such effect could be explained on the basis of a different control mechanism of biosynthesis for the various storage protein fractions, this situation being perhaps emphasized in the F1 seed contest.

Combining ability and reciprocal effects

As far as general combining ability (GCA) is concerned, it was found (Table 3) that only the proportions of ω-566 and of LMWG exhibit significant effects, whereas the effects on the proportions of HMWG were not significant (not shown). Also, for both ω-566 % and LMWG %, the GCA effect was highly significant whereas the SCA effect was not significant. This result suggests an exclusively additive determinism for the relative area of the relevant components.

TABLE 3
Analysis of variance of four densitometric traits in the diallel experiment (F1's and reciprocals, no parents)

Source of variation	D.F.	Mean squares			
		Total area	HMWG %	ω-566 %	LMWG %
GCA	4	359.29	0.9856	8.8535**	63.666**
SCA	5	153.59	0.8492	0.2334	10.277
RE	10	161.30	0.7920	1.1245*	12.731*
GRE	4	241.08	0.8454	2.6415**	29.546**
SRE	6	108.12	0.7564	0.1132	1.521
Error	57	212.64	0.7103	0.4250	5.317

Sources: GCA = general combining ability
SCA = specific combining ability
RE = reciprocal effect
GRE = general reciprocal effect
SRE = specific reciprocal effect

*,** Significant at 0.05 and at 0.01 level respectively.

Furthermore, as shown in Table 4, the highest positive GCA values for LMWG (along with the highest negative GCA values for ω-566) were found with the two cultivars Primadur and Brumaire. This result indicates that these two cultivars are the best general combiners for determining an optimal protein composition as far as gluten quality is concerned (high proportion of LMWG, low proportion of ω-566). Conversely, lines such as ENSAM 3034 and 80 SM 25-6 appear as the less suitable for determining an optimal expression of proteins associated with quality. It must be concluded,

TABLE 4
General combining ability (GCA) and general reciprocal effect (GRE) of the parental lines for ω-566 and for LMWG

Lines or cultivars	GCA		GRE	
	ω-566 %	LMWG %	ω-566 %	LMWG %
Primadur	−0.52*	2.22*	−0.54*	2.28*
Brumaire	−0.88*	3.27*	−0.19	−0.01
ENSAM 3034	1.68*	−2.44*	0.62*	−1.95*
ENSAM 522-15	−1.14*	1.32*	−0.36	1.02
80 SM 25-6	0.86*	−4.38*	−0.48*	−1.34*
Standar error 5%	0.48	0.69	0.37	1.31

The general reciprocal effect is indicated for the parental lines used as female (opposite sign when used as male).
* Significant at P = 0.05 level.

therefore, that in spite of a negative average heterosis effect for the proportion (on a percent of total proteins basis) of LMWG fractions, some cultivars have a better ability to transfer these fractions in the progeny. Clearly, these cultivars are those with high values for LMWG such as γ-45 types. The highest positive GCA values for LMWG were found in genotypes that contain themselves the highest proportion of this fraction. Therefore, in the case of LMWG, the higher the proportion of this protein fraction in a cultivar, the greater its ability to transmit this fraction. Conversely, in the case of HMWG, no cultivar exhibits a significantly greater GCA value, even those with great values of this protein fraction.

In the same way, the general reciprocal effect (GRE) was found significant only for the % in ω-566

TABLE 5
Reciprocal effect (RE) in the F1 hybrids between the five parental lines for ω-566 % and for LMWG %

F1 hybrids	ω-566 %	LMWG %
Primadur × Brumaire	−0.30	3.02
Primadur × ENSAM 3034	−1.44*	3.31*
Primadur × ENSAM 522-15	−0.15	1.02
Primadur × 80 SM 25-6	−0.82	4.06*
Brumaire × ENSAM 3034	−0.54	1.26
Brumaire × ENSAM 522-15	0.06	−0.06
Brumaire × 80 SM 25-6	−0.79	1.75
ENSAM 3034 × ENSAM 522-15	0.99*	−3.52*
ENSAM 2024 × 80 SM 25-6	0.11	−1.64
ENSAM 522-15 × 80 SM 25-6	−0.92	2.53
Standard error 5%	−0.92	3.27

* Significant at P = 0.05 level.

and LMWG, as indicated in Table 5 by its value for each cross combination. It clearly appears that RE values are antagonistic for ω-566 and LMWG (opposite sign and roughly similar magnitude).

Interestingly, since the GRE effects are highly significant and the SRE effect are generally not significant (Table 3), it can be suggested that this reciprocal effect is exclusively due to the influence of some parents (Table 4), depending on their use as female or male, on the hybrid kernel. If such an effect was entirely the consequence of the triploid nature of the endosperm, the direction of the cross would be of no interest to the wheat breeder, unlike an eventual extranuclear influence. Because the next progeny was not analysed in the experiment, it is not possible to decide this point.

CONCLUSION

The present investigation supported previous reports about the association between the potential effect on durum wheat quality of various allelic types and the quantitative expression of the relevant proteins (LMWG, HMWG, ω-gliadin) and demonstrated the occurrence of significant heterosis effects for some of these proteins (LMWG, ω-gliadin 566). Although genotypes belonging to type 'γ-45' (which always contain much greater proportions of LMWG) appeared as better combiners for LMWG %, some of them (e.g. cvs Primadur and Brumaire) have significantly better general combining abilities than others (e.g. line ENSAM 522-15).

All these considerations should be taken into account in breeding programmes. The significant differences in general combining ability and reciprocal effect, and the consequent additive genetic control of the ω-566 and LMWG fractions are encouraging for the breeder since they are the most involved in the determination of gluten quality in durum wheats. Conversely, non significant combining abilities were found for the HMWG components, but the effect of these fractions is less critical in the determination of quality in the case of durum wheats.

It remains to understand on a more fundamental basis the opposite behaviour of ω-566 and LMWG fractions observed by densitometric scanning of their electrophoretic pattern, which indicated different rates of expression during their biosynthesis in the F1 generation.

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