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ORIGINAL PAPER

Genetic analysis of bread-making quality scores in bread wheat using a recombinant inbred line population

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Abstract Bread-making quality has been evaluated in a progeny of 194 recombinant inbred lines (RILs) from the cross between the two French cultivars Récital and Renan, cultivated in three environments. These cultivars have been previously identified as having contrasting grain protein content and dough rheology properties, although they achieve similar scores for the official bread-making test used for cultivar registration in France. However the progeny displayed a wide range of variations, suggesting that favourable alleles at several loci are present in the two parental lines. Correlation analyses revealed that bread-making scores are poorly correlated among environments, as they are poorly predicted by multiple regression on dough rheology parameters and flour-protein content. However, loaf volume was the most heritable and predictable trait. A total of seven QTLs were found for bread scores, each explaining 5.9–14.6% of trait variation and six for the loaf volume (10.7–17.2%). Most bread-making QTLs, and particularly those detected in all environments, co-located with QTLs for dough rheology, protein content or flour viscosity due to soluble pentosans (Fincher and Stone 1986; Anderson et al. in J Cereal Sci 19:77–82, 1994). Some QTL regions such as those on chromosome 3A and chromosome 7A, which display stable QTLs for bread-making scores and loaf volume, were not previously known to host obvious genes for grain quality.

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Introduction

Bread wheat is one of the most widely cultivated crops around the world, including all temperate zones and altitude regions in the tropics. Out of the nearly 600 Mt collected worldwide, about 80% is used as human food. Among the huge diversity of wheat-derived food products, bread is probably the most important on the basis of the proportion of wheat, which is transformed into bread and for the strong cultural link it has for many people. Bread-making quality is thus very vital for the world wheat trade, and therefore a major target in wheat-breeding programmes. However, its direct estimation through full-scale tests, including milling and baking, is costly, time consuming and requires a large amount of grain, which is usually not available in early-breeding generation. For these reasons, it is generally used only on a limited number of advanced "candidate" lines, and indirect tests have been developed to determine the bread-making ability in earlier generations from simpler measures such as the SDS sedimentation volume or dough rheological characteristics such as those measured by alveograph or dough mixing properties as measured by mixograph. In this way, the effects of some grain characteristics such as hardness (Martinant et al. 1998b; Martin et al. 2001) and grain protein content (Branlard et al. 2001) and the importance of some major genes like Ha-coding for

grain hardness (Symes 1969, Sourdille et al. 1996) and storage-protein encoding genes (Payne 1987; Branlard et al. 1992, 2001) have been well established. Some other studies focused on QTL analyses for indirect tests such as SDS sedimentation test (Blanco et al. 1998), alveograph or mixograph parameters (Perretant et al. 2000; Zanetti et al. 2001, Ma et al. 2005) or relative viscosity of flour extract (Martinant et al. 1998a; Udall et al. 1999). These studies showed that a large number of genetic regions might be involved in bread-making quality related traits.

The relationship between indirect tests and a direct test for the bread-making quality has also been explored (Baker et al. 1971; Briggs and Shebeski 1972; Boggini and Nillson 1976). Concerning the test specifically designed for French-type ("baguette") of bread-making (currently used in French official registration trials), two different studies have been reported. Branlard et al. (1991) analysed 46 distinct parameters (corresponding to 17 technological tests) on 125 varieties grown over 3 years and 18 environments. The study of Oury et al. (1999) summarised the results from 15 years of multi-location experiments. Both studies showed that the relationships between indirect test parameters and the score from a final test are usually weak. Then, it could be interesting to compare the genetic regions involved in the response to direct test and those found for indirect tests. To date, few studies had been reported on the genetic influence on parameters of a full-scale test. In 2001, Rousset et al. analysed the genetic components of bread mixing time and loaf volume, but they focused only on the chromosomes of homoeologous group 1. Recently, Kuchel et al. (2006) used a doubled haploid population and found QTLs for crumb score and loaf volume on chromosomes 2A and 3A.

The aim of this study was thus to analyse a segregating population developed from a cross between two modern French bread wheat for identifying genetic regions influencing bread-making quality evaluated through a full-scale test and the genetic relationships between bread-making scores and related traits, particularly with dough rheology parameters.

Material and methods

Plant material and genetic map

The population studied consisted of 194 F_7 recombinant inbred lines (RILs) obtained by single seed descent from a cross between two cultivars of winter bread wheat (*Triticum aestivum* L.), Renan and Récital. These two cultivars were registered in 1989, and are classified as "high bread making" and "strong improving" grades, respectively. Renan has a higher grain protein concentration (GPC) and dough strength than Récital (Groos et al. 2003, 2004). Renan and Récital have similar alleles of high molecular weight (HMW) glutenins genes (alleles 2*, 8, 5 and 10 for the loci HMWG-1Ax, -1By, 1Dx and -1Dy, respectively) and differ only for the allele of the locus HMWG-1Bx; Renan has allele *Glu-B1b* and Récital allele *Glu-B1d*. They are both known as "medium-hard" wheats and share the same alleles at the puroindoline loci (a candidate gene for softness), namely Pina-D1a (presence of puro A) and Pinb-D1b (a glycine to serine change, Giroux and Morris 1997).

The population and the parental lines were sown in 1999 at Clermont-Ferrand and Rennes (France; respectively CF99 and RN99) and in 2000 again at Clermont-Ferrand (CF00). The soil in Clermont-Ferrand is a deep, calc-clay soil with high water reserve (~150 mm). The total rainfall during the growing season was 241 and 310 mm in 1999 and 2000, respectively. The year 1999 was characterised by severe drought but moderate temperature during grain filling (only 20 mm but average maximum temperature of 23.1°C in June) while the filling period in 2000 was warmer (average maxima 24.5°C but wet 93 mm). The soil in Rennes is a deep sandy limon with around 100 mm of water reserve. The rainfall during the growing season in 1999 was 570 mm with a very wet autumn, and favourable conditions during grain filling (average max temperature 24.0°C). The experimental field design consisted in a randomised block design with two replications, each block being divided into eight sub-blocks, with the two parental lines and another control variety (cv Soissons) being replicated into every sub-block to allow correction of spatial heterogeneity. Each plot measured 7.5 m^2 and plants were grown using regional farmer's practice (sowing density 250 seed m^{-2} end of October, nitrogen application ~150 kg ha^{-1}, and fungicide application to control main foliar/spike diseases). Unfortunately, since bread-making tests are very costly and time consuming, only one replication per RIL was analysed for each environment. The parental lines and the control line were used to correct sub-block effects. This is a current practice for such heavy traits, and even sometimes QTL analyses are carried out on bulked grain samples from different growing sites (e.g. Kuchel et al. 2006).

The construction of the genetic linkage map has been described by Groos et al. (2003). The map used for the QTL analysis consisted of 254 loci on 38 linkage groups for a total length of 2,722 cm. The linkage groups are distributed throughout the wheat genome but the chromosome 4D is not yet covered. Some unlinked markers, which did not deviate from the expected ratio (1:1) were also integrated for the QTL analysis.

French bread-making quality test

The French bread-making quality test has been evaluated according to the AFNOR method NF V03-016. Three samples

were analysed simultaneously with a control (reference flour) repeated for each analysis and used as reference.

The test consisted in the production of bread following the normal conditions used by a baker. Two kilograms of flour are necessary for each analysis. At each step of the process (kneading, pointing, working...), a score is given by the baker for different characteristics (see Table 1). After the cooking, scores are given for the final product, the bread. Some scores are related to the quality of the bread, others to the quality of the crumb (Table 1). Most scores ranged from 1 to 5 or from 1 to 10, which indicates that they are given different weights in the final scores, as indicated in Table 1. The highest score is always given to the most desired value, which is not always the maximum value of the underlying trait, due to the fact that some characteristics are unfavourable when too high (the elasticity of the dough, as example, is detrimental when too high). This particular construction of bread-making scores should be kept in mind when interpreting QTL results.

At the end, the different scores are partially summed over to yield in three global Scores: one for the dough reaction during the process, one concerning the quality of the bread, and one concerning the quality of the crumb. These three scores are set on 10–100 scale and further summed up to build a Total Score which thus theoretically ranges from 30 to 300. The Bread Score itself is partially influenced by the value of the bread volume (in cm^3). The bread volume was also analysed as a separate variable, as it is the only "true" quantitative trait by nature.

QTL detection and statistical analysis

QTL analysis was performed using a Splus 'home made' program described by Groos et al. (2002). This program is based on the marker regression method (Kearsey and Hyne 1994) after a first analysis by ANOVA and allows the detection of two QTLs on a same chromosome using a two-dimensional scanning of the chromosome (Hyne and Kearsey 1995). The 95% confidence intervals of the QTLs locations and effects were established by bootstrapping (Visscher et al. 1996) using 200 replicates for the one-QTL model and 400 for the two-QTL model. In order to enable comparison with previously published studies, QTL location were projected onto the reference ITMI map (http://www.wheat.pw.usda.gov/GG2) using common markers as bridges.

The other statistic analyses were carried out using SAS 6.1 software (SAS Institute 91). For heritability estimation, we determined the variance components with genotype as random and GxE as error. Then the broad sense heritability is defined as: $h^2 = Vg/(Vg + Ve/3)$, with Vg = genotype variance, Ve = environmental variance.

Table 1 Different steps of the bread-making test considered in the scores

Total score(on 300)		
Dough score (on 100)	Bread score (on 100)	Crumb score (on 100)
Kneading	Cutting (1–10)	Colour (1–10)
Smoothing quality (1–5)	Colour (1–20)	Texture (1–10)
Dough stickiness (1–5)	Thickness (1–5)	Flexibility (1–10)
Extensibility (1–5)	Crusty (1–5)	Elasticity (1–10)
Elasticity (1–5)	Swords stabs	Stickiness (1–10)
Relaxing (1–5)	Development (1–10)	Flavor (1–10)
Pointing	Regularity (1–10)	Alveole
Slackening (1–10)	Tearing (1–10)	Regularity (1–10)
Working	Loaf volume (1–30) (in cm^3)	Thickness (1–40)
Extensibility (1–10)		
Elasticity (1–5)		
Dough stickiness (1–10)		
Finishing		
Quality of fermentation (1–5)		
Dough tearing (1–5)		
Putting in oven		
Dough stickiness (1–10)		
Dough keeping (1–20)		

Results

Phenotypic variations

Table 2 shows the range of variation of the different scores for the two parental lines and for the segregating population, observed in the three locations. According to the Total Score, the two parental lines are of good quality (by this test, a variety is classified as "high quality bread making wheat" when the total score is greater than 225), with similar final value except in CF99 where Renan is significantly higher than Récital. Similarly, for the three main components of total bread scores, namely dough, bread and crumb scores, the two parental lines also have similar values, Renan being only slightly better than Récital. Bread volume is the only trait, for which Renan has systematically higher values than Récital. However this superiority varies from one location to another: from 212 cm^3 (+15%) in CF99 to only 47 cm^3 (less than 3%) in RN99.

For all traits, the mean of the RIL population is close to the mid-parent value, suggesting that additive allelic effects are the rule for the genetic control of bread-making traits. Moreover, the range of the RIL population was much larger than the range of the parental lines, suggesting that both parents have favourable alleles at different loci.

Figure 1 illustrates the Pearson pairwise correlations for the different scores of the direct test over the three environments. All correlations are below 0.5 and most are not significant, excepted for the Bread Score and the loaf volume, suggesting that non-genetic factors (e.g. GxE) are more influential than true genetic factors. Pearson correlations are particularly weak for the Crumb Score, but are highly significant ($P = 0.001$) for bread volume, and significant at $P = 0.01$ for Bread Score and in two sites out of three for Total Score. The heritability of the traits is also included in this figure. They are all low (crumb score) to moderate for other scores except for bread volume, which is higher than 0.6.

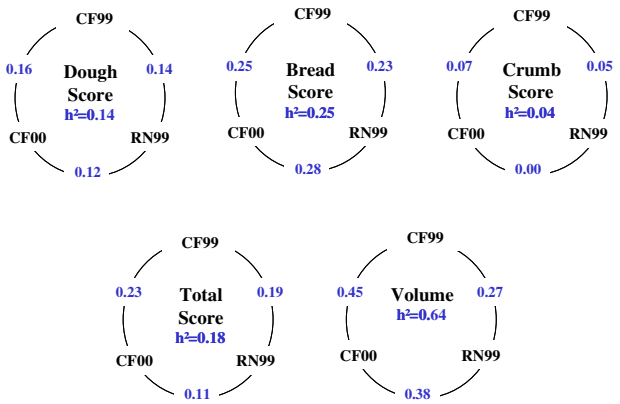


Fig. 1 Pearson correlations between the scores of the French bread-making direct test in the different locations calculated on a subset of 157 RILs. Significant threshold $r = 0.19$ at $P = 0.01$ and $r = 0.25$ at $P = 0.001$. In *bold*, is the mean of the among environments correlation for each trait. In *italic*, is the heritability of each trait

Table 3 summarises the correlations between the scores of the final test and some traits related to bread-making quality and previously studied in the same population (Groos et al. 2003, 2004), calculated on the mean of the three locations. Even if these correlations are still lower than 0.5, some highly significant relationships can be observed. Dough Score is mostly related to the tenacity and the strength of the dough, and the Total Score is more related to dough strength and to grain protein content. Bread volume is highly significantly related to the extensibility and the strength of the dough, and to grain protein content. The Bread Score is not highly related with any of the indirect measures of the bread-making quality, the highest

Table 2 Value of the different French bread-making scores for the parental lines and for the RILs in the three locations

	Loaf volume			Bread score			Dough score			Crumb score			Total score		
	CF99	CF00	RN99	CF99	CF00	RN99	CF99	CF00	RN99	CF99	CF00	RN99	CF99	CF00	RN99
Parental lines															
Renan	1605	1803	1732	69	54	64	85	83	76	98	88	90	249	225	231
Récital	1393	1617	1685	43	48	67	82	85	75	93	88	90	216	221	232
RILs population															
Mean	1509	1773	1703	54	63	65	76	78	77	93	88	84	223	229	226
Min	1132	1318	1306	8	6	4	21	36	16	70	40	43	96	134	112
Max	2011	2210	2135	92	99	90	97	103[a]	102[a]	104[a]	106[a]	100	282	291	277
Error st dev[b]	15.6	22.3	18.8	5.5	6.6	3.8	2.33	4.5	3.6	3.4	5.2	4.4	7.8	12.5	9.5

Trial: *CF99* Clermont-Ferrand 1999, *CF00* Clermont-Ferrand 2000, *RN99* Rennes 1999

[a] Because of the correction by blocks effects, the score can be higher than 100

[b] Error standard deviation was estimated on the two parental lines grown in ten random replicates

Table 3 Pearson correlations between bread-making full-scale scores and indirect tests calculated for the mean of the three locations for 157 RILs

	Dough score	Bread score	Crumb score	Total score	Bread volume
FPC	0.19	0.27	0.16	0.33	0.44
Hardness	0.15	0.08	0.20	0.18	0.29
P	0.37	−0.07	0.17	0.15	−0.01
L	−0.17	0.31	0.01	0.16	0.39
W	0.40	0.19	0.24	0.38	0.36
Viscosity	0.18	0.19	−0.04	0.20	0.24
R^2 of multiple regression	0.24	0.17	0.10	0.17	0.33

Within brackets, is the value of the correlation when the sign is opposite to the correlations in the two other locations

FPC flour protein content, *W*, *P* and *L* are strength, tenacity and extensibility of the dough determined using the Chopin alveograph, *Viscosity* relative viscosity of flour extract, proportional to soluble pentosan content

Significant threshold $r = 0.19$ at $P = 0.01$ and $r = 0.25$ at $P = 0.001$

correlation being with extensibility ($r = 0.31$). The Crumb Score is significantly related with hardness and dough strength. On Table 3, R^2 of multiple regression for all bread-making scores with all the related traits studied are shown. These coefficients are still moderate, the highest value being for bread volume, for which around 1/3 of the variation of the trait is explained by predictor variables. Traits related to storage protein composition (e.g. quantity of HMW-GS or gliadin on glutenin ratio...) recently published (Charmet et al. 2005), did not improve these predictions.

QTLs for bread-making quality

Table 4 shows the effects and chromosome positions of the QTLs detected for the different scores of the bread-making test and for bread volume. The confidence intervals for QTL locations and effects are given for the location where the QTL was found with the highest power of detection through bootstrapping. Considering the low heritability of the studied traits and the likely importance of GxE, we decided to make QTLs analyses for each location independently. However, we did also analyse the mean over the three locations, since the "repeatability" of QTLs through different location is of first importance in their possible utilisation.

Seven QTLs were detected for Bread Score, each explaining from 5.9 to 14.6% of trait phenotypic variation, only three for Dough Score and two for Crumb Score. None of these QTLs were detected in all three locations. Six genetic regions were detected for the bread volume. The strongest QTL was found on chromosome 1B, explaining from 10.7 to 17.2% of the trait, but this QTL was only detected in two locations. Two other QTLs on chromosomes 3A and 7A were consistently detected in all locations and for the mean, although they have smaller effects.

Relationships between QTLs for bread-making quality and QTLs for indirect predictors

Figure 2 illustrates the chromosome locations of bread-making QTLs and those of QTLs previously reported for grain hardness, GPC and dough rheology using the same RIL population (Groos et al. 2003, 2004). It also includes a QTL on chromosome 7A for the dough viscosity due to soluble pentosans (data not presented). Despite the large confidence intervals observed for many bread-making QTLs, several co-locations were observed, which are unlikely to have occurred by chance only. Indeed, except on chromosomes 6B and 7B, which carry only bread-making QTLs, all other chromosomic regions have significant effect on both direct and indirect bread-making traits. On chromosomes 1A and 1B, QTLs for bread-making scores, and particularly for bread volume, co-locate with a QTL for grain protein content and a QTL for dough strength, respectively. A similar result was found on the short arm of chromosome 3A, on which QTLs for most studied traits were found to co-locate within a 50 cm region. The QTLs on other chromosomes have larger confidence intervals. However, according to the co-location observed, candidate components can be postulated for bread-making QTLs on chromosomes 2A (GPC) and 7A (soluble pentosans, responsible for flour extract viscosity, Fincher and Stone 1986, Anderson et al. 1994).

Discussion

Measures of bread-making quality through a direct test

Up to now, few studies have been published on the quantitative genetic architecture of bread-making quality. Our study was one of the first QTL analyses on a full-scale bread-making test. Then it is interesting to determine the stability of such a test in a segregating population. The

Table 4 Summary statistics of QTLs affecting bread-making quality

Trait	Chromosome	Environment with significant QTL	R^2	Power	Location	Additive value	+Allele	Closest marker(s)
Loaf volume	1A	CF99, RN99	4.4–6.1	0.93	30-54-106	29-61-99	Rn	gwm164 gwm135
	1B	CF99, CF00, Mn	10.7–17.2	0.94	55-76-81	25-43-61	Rc	gwm456 GluB1
	3A	CF99, RN99, CF00, Mn	4.6–10.5	0.99	12-23-47	25-47-71	Rn	fbb250 gwm666
	5B	CF00	5.3	1.0	33-47-70	28-58-85	Rc	gwm371
	7A	CF99, RN99, CF00, Mn	4.6–13.6	0.91	65-123-154	20-41-67	Rc	cfa2049 bcd1930
	7B	CF99, CF00, Mn	5.1–7.5	0.64	81-112-183	21-44-78	Rn	gpw1045 gwm577
Bread score	1B	CF00, Mn	7.2–13.0	0.98	69-85-102	4.6-8.0-11.2	Rc	gwm456 GluB1
	2B	Mn	6.0	0.92	8-127-154	1.8-3.7-5.9	Rc	gwm148 gwm374
	3A	RN99, CF00, Mn	4.7–7.9	0.92	26-37-47	3.0-5.6-8.9	Rn	fbb250 gwm666
	5B	Mn	5.9	0.98	1-19-73	3.0-4.8-7.1	Rc	psr170
	6B	RN99, Mn	6.0–6.8	0.96	2-11-35	3.2-6.2-9.4	Rn	gwm193
	7A	CF99, CF00, Mn	6.6–14.6	0.90	64-119-132	3.8-6.6-10.5	Rc	cfa2049 bcd1930
	7B	CF99, CF00, Mn	5.0–8.6	0.69	64-104-168	4.8-8.9-15.0	Rn	gpw1045 gwm577
Dough score	1B	Mn	6.9	0.70	9-73-91	1.4-2.7-4.3	Rn	gwm264 GluB1
	2B	RN99	6.9	0.94	112-124-216	3.1-5.8-9.3	Rc	gwm388 gwm501
	3A	CF99, Mn	5.0–5.3	0.88	27-45-63	0.7-2.3-3.9	Rn	fbb250 gwm666
Crumb score	5B	CF99	9.1	0.98	61-70-100	1.2-2.3-3.7	Rc	gwm639 gwm271
	6B	CF99	5.5	0.79	4-22-63	0.7-1.8-3.1	Rn	gwm193

In bold, the trial, for which are given bootstrap estimates of parameters

Experiment: *CF99* Clermont-Ferrand 1999, *CF00* Clermont-Ferrand 2000, *RN99* Rennes 1999, *Mn* mean over experiments, R^2 range of QTL heritability in the different environments, *Power* detection power, i.e. percentage of significant models using bootstrap resampling, *Location* confidence interval and estimate of the position of the QTL (from the top of the short arm of the chromosome) determined by bootstrapping, *Additive value* confidence interval and estimate of the additive value determined by bootstrapping and indicate +allele the parent contributing to a higher trait value, where *Rn* Renan, *Rc* Récital

correlations between the different locations were actually quite poor and except for Loaf volume, the heritability of the Scores of such a test appeared rather weak too (Fig. 1).

Different hypotheses can be put forward to explain these low heritability and low repeatability among locations. Bread-making quality measures used in this study are mostly the result of visual scores. Then despite the normalization of the test, it is relative to the subjectivity of the baker doing the test. Unfortunately, due to the cost and the importance of the test, it is not possible to analyse multiple replications and to estimate a true random-source error. This can only be reduced by the replication of a small subset of control lines in every sub-block of the experiment. Alternatively, bread volume is a true quantitative measure. Even if the correlation coefficients between the different locations are higher compared with the scores of the bread-making quality test, they are still weaker compared to the results of the indirect tests (Groos et al. 2004). Otherwise, broad sense heritability measured for bread volume in other studies (determined with the AACC method) is of same magnitude than those obtained in previous studies. Barnard et al. (2002) found a value of 0.61, when Kadar and Moldovan (2003) obtained 0.58, less than the value we calculated (0.64).

Prediction of bread-making quality through indirect tests

No major effect of hardness on the bread-making quality was found in this study, as expected since no correlation was highly significant (Table 3). Moreover no strong co-locations appeared between QTLs for hardness and QTLs for the Scores of direct test, and no QTL were found on chromosome 5D. This is probably due to the fact that both parental lines have the same allele at the major gene for hardness (Groos et al. 2004) since they share the same mutation on pinB gene. In a 15-year multi-site experimentation, Oury et al. (1999) also found no influence of hardness on French bread-making quality itself, but only on parameters of indirect test with constant hydration such as the alveograph.

The influence of GPC on bread-making quality has been largely reported (Branlard et al. 2001). Due to the large difference between the parental lines (Groos et al. 2003), GPC shows a quite a wide variation in the progeny and is indeed highly significantly correlated to bread volume ($r = 0.44$) and Total Score ($r = 0.33$) (Table 3).

Concerning the parameters of indirect tests of bread-making quality, the results have shown the difficulty of predicting bread-making quality with the indirect tests used.

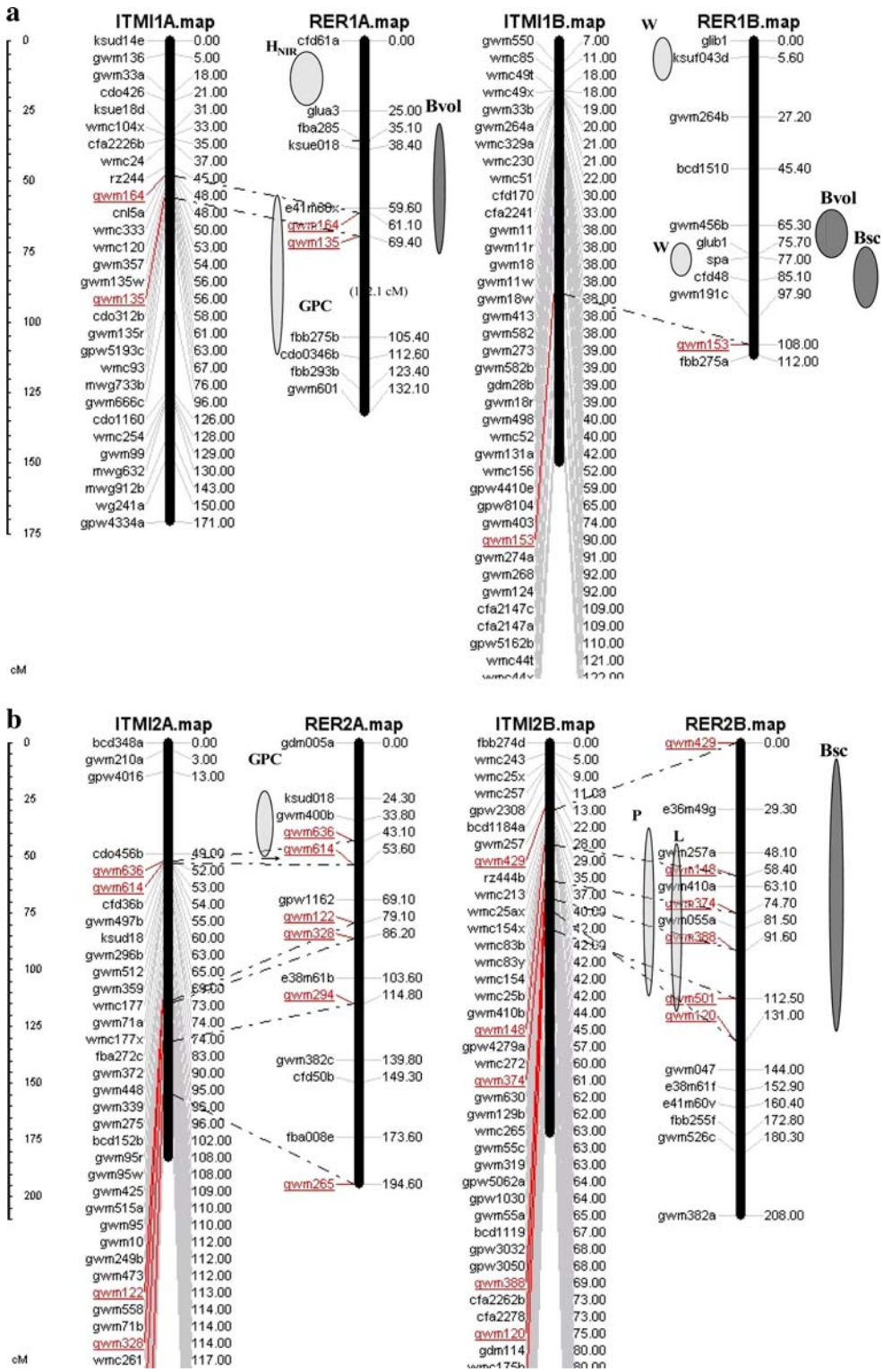
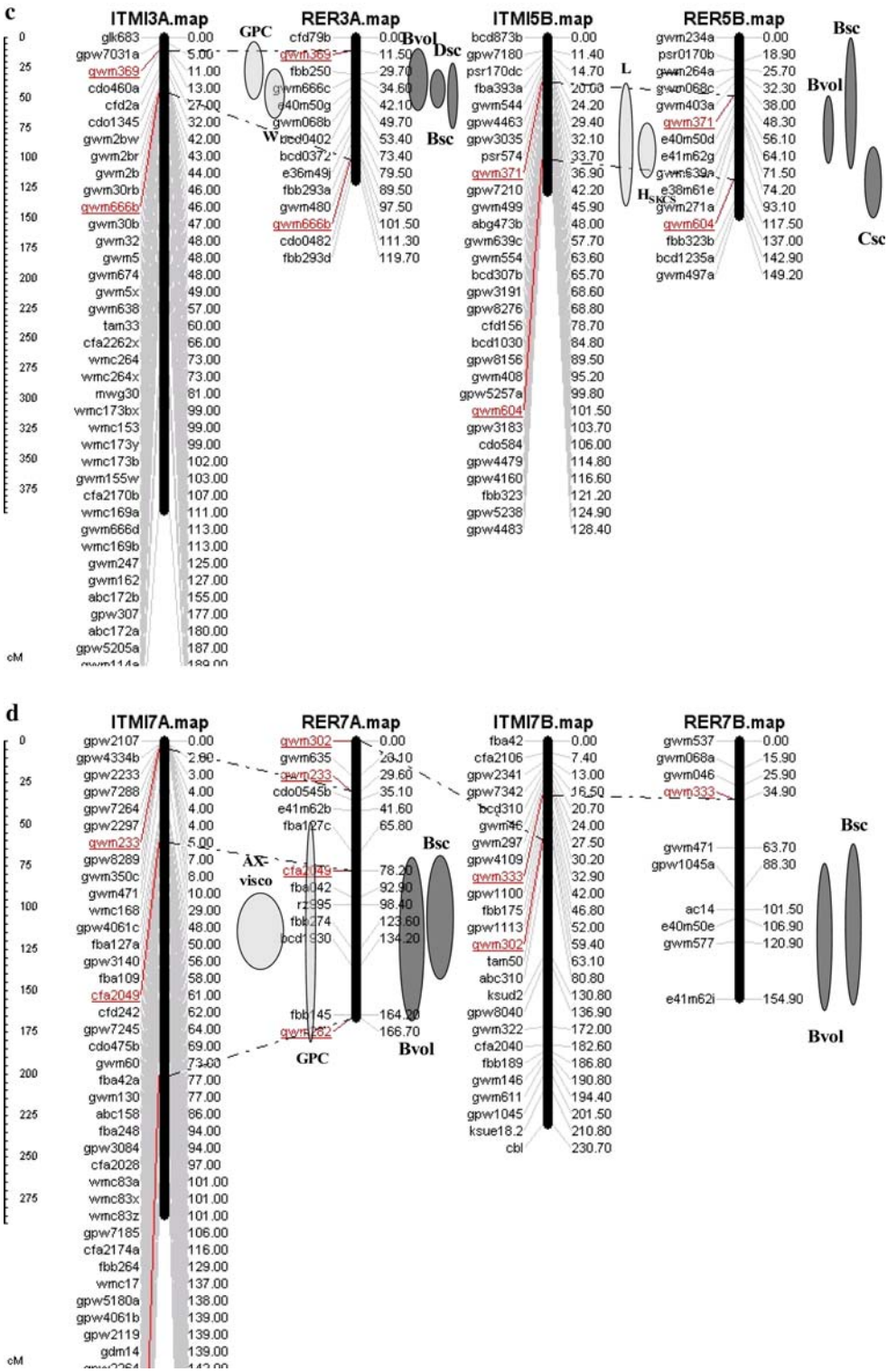


Fig. 2 Location of the QTL for the full-scale bread-making test in relation with QTL for indirect parameters on the Renan × Récital map, and projection onto the ITMI map (http://wheat.pw.usda.gov/GG2) using common markers. a Group 1 chromosomes, b Group 2 chromosomes, c Group 3 and 5 chromosomes, d Group 7 chromosomes. *Symbol length* corresponds to the confidence interval of the QTL. *Symbol width* corresponds to the QTL additive effects. *Dsc*, *Bsc* and *Csc*: Scores of the direct bread-making quality test, namely dough score, bread score and crumb score, respectively. *Bvol* bread (loaf) volume, *GPC* grain protein content, *Hard* hardness estimated by NIR prediction. Alveograph parameters: dough strength (*W*), tenacity (*P*) and extensibility (*L*), *AXvisco* relative viscosity of flour extract (associated to soluble pentosans)

For example, it could be expected that alveograph parameter, measuring the rheological characteristics of the dough would be highly related to Dough Score. In fact rheology parameters have the same weak influence on all the Scores of the final test. However, some highly significant correlations were found (Dough Score with P and W, Total Score with W, bread volume with L, GPC and W), but the values are still too weak to be of practical use for bread-making prediction. Moreover, by multiple regression, the part of variance explained is still quite low (Table 3). The results found in our study are weaker than those found by Oury et al. (1999). They determined the correlation coefficient to

Fig. 2 continued



0.55 and by multiple regression, were able to explain up to 60% of the variability of the Score, while we explained at best about 1/3rd of the variation for bread volume. This is due to the larger genetic background of the Oury et al. (1999) study including wheat both of high quality and poor quality. The conclusion of both studies is that the indirect tests only allowed definition of threshold values under which one the genotype can be eliminated for high bread-making quality.

This lack of prediction power of indirect tests is probably due to the complexity of the final test. Even if this test is precisely normalised, it is influenced by the baker making

the experiment. Moreover, the three Scores of the test are results of partial scores (Table 1). All those partial scores are not necessarily related to the same parameter and can also be antagonistic. This could explain the weak correlation found. However, the analysis of each component of the Scores did not reveal higher predictive power. (data not shown). Compared to other bread-making practices, French baking and quality evaluation practices leads to more complex scores, which are less related to protein or dough rheology than other tests used worldwide. Particularly, the best crumb scores are not obtained with a high density of many small bubbles, but with a balanced distribution of small and large bubbles, which is difficult to quantify and thus subjective in human interpretation. The very low heritability of this trait may be a consequence of its lack of clear definition. Although French baguette is left free to develop, its final volume is the most heritable trait, and probably also the most reliable and comparable with loaf volume obtained by other tests.

Location of QTLs, relation with QTLs for related traits

Most detected QTLs have relatively small effects on the final test and few of them have been detected in more than one location. These results are probably related to the low heritability of the different Scores of the final test. However, some interesting regions have been established for their influence on bread-making quality and in most of the case, the QTLs found for the Scores of the final test collocated with QTLs for indirect measurement of the bread-making quality (Fig. 2). On chromosome 1B, QTLs for bread volume, Bread Score and Total Score are probably the results of allelic variation for GluB1, coding for HMW-Glutenin Subunits (GS). The importance of the storage protein allele has been largely studied now and score for the importance of the effect of each allele has been estimated (Branlard et al. 1992). Surprisingly, our results are opposite to the expected results: favourable effects come from Récital allele (*Glu-B1d*), while Branlard et al. (1992) gave a coefficient of quality for Renan allele (*Glu-B1b*) of 18 against two for Récital allele (*Glu-B1d*). This result is probably due to the high quality of the population studied. Those QTLs are collocated with a QTL for tenacity, with the favourable allele brought by Renan. Thus the tenacity is relatively high in this population, and perhaps too high to be favourable to the loaf volume. Otherwise, these results showed that the scores given to the different alleles of storage proteins could be modified by the genetic background.

On chromosome 1A, the QTL for bread volume is not due to a known protein storage gene. There is no difference for HMW-GS on chromosome 1A in the population studied and GliA1 locus is not in the confidence interval of the QTL. This QTL is probably due to an effect of the QTL for GPC detected on this chromosome and of which the confidence interval largely overlapped (Fig. 2). These QTLs could be homologous with the QTLs detected by Rousset et al. (2001), closed to the centromer on chromosome 1D. As us, Rousset et al. (2001) found in the region QTLs influencing both GPC and bread volume (measured with AACC method) not related with the storage protein genes. These results show that the influence of group 1 chromosome is not only due to storage protein allele. Similar co-locations between HMW or LMW glutenin loci and a number of QTL for dough rheology have been reported recently (Kuchel et al. 2006).

In our study, another important region influencing bread-making quality has been found on chromosome 3A. On this chromosome, we detected QTLs for all scores of the full-scale test except for Crumb Score. Moreover, for bread volume the QTL was detected in all locations and the mean. Those QTLs strongly overlapped with QTLs for GPC and dough strength previously reported (Groos et al. 2003, 2004), as well as with QTL for LMW-GS and total gliadin content (Charmet et al. 2005) We can then put forward the hypothesis that all these QTLs are due to a single gene or a gene cluster influencing protein content and/or gluten strength. No obvious candidate genes for bread-making related traits are known of this chromosome. There are known quality-related genes on chromosome 3A associated with pre harvest sprouting (Bailey et al. 1999) but they were mapped on the long arm while the QTLs in this study have been located on the short arm. More study should be done to identify which genes could explain this QTL region. It is noteworthy that QTLs for baking traits (bread volume and crumb score) were also recently reported in the same region of chromosome 3A (close to marker Xgwm666) in an independent wheat population between two Australian cultivars (Kuchel et al. 2006). These authors also found QTLs for baking traits on chromosome 2A, but in a region different from that found in the present study.

On chromosome 7A, we detected a strong QTL for loaf volume, found in all locations and for the mean. The influence of bread volume on the calculation of the bread score probably explained the detection of QTLs for those scores in the same chromosomal region. These QTLs are overlapping with QTLs for GPC, LMW-GS (Charmet et al. 2005) and for dough viscosity due to soluble pentosans (Fig. 2). It is difficult to determine which component has actually an effect on loaf volume, but the dough viscosity is linked to the quantity of pentosans (Rouau 1996) and its soluble part would have a positive effect on bread volume (Feillet 2000). On this chromosome, the Waxy gene, coding for starch synthase protein, was mapped (Nakamura et al. 1993), but it is probably not in the interval confidence of the QTL. Moreover, a gene coding for an alpha-amylase is located in this QTL region, which may affect baking quality.

On chromosome 7B, we found also QTLs for bread volume and Bread Score. The effect of these QTLs appeared weaker than those on chromosome 7A and they do not co-locate with QTLs for indirect tests. Because of the lack of homoeologous loci mapped in our population between chromosome 7A and 7B, it is not possible to determine whether these QTLs are in homoeologous regions. As on chromosome 7A, only a gene coding for alpha-amylase is mapped on this chromosome (Mc Intosh et al. 1998), which could have an effect on bread-making quality.

On chromosome 5B, we detected QTLs for all Scores, excepted for Dough Score. Their effects are weak (less than 8% of the score variance explained) and they were detected only in one location and for the mean. However, their detection powers are high and hence we can estimate that they are not experimental artefacts. These QTLs co-located with QTLs for extensibility and hardness (Fig. 2). Because of the length of their confidence intervals, it was not possible to determine whether these QTLs are due to the influence of one unique gene or several distinct genes. Different genes have been mapped on this chromosome (as Vrn-B1 for response to vernalisation, Mc Intosh et al. 1998; Kr for crossability with rye, Tixier et al. 1998) but none is obviously known to have an influence on bread-making quality.

In this study, no QTL for bread making was found on chromosome 7D, where a stable QTL for grain protein content (Groos et al. 2003) and for most storage protein fractions (Charmet et al. 2005) was reported. This probably illustrates the lower sensitivity of French baking scores to flour protein content (this latter being highly correlated to grain protein content) compared to other baking tests used worldwide. Using this particular population, which segregates only at the Glu-B1 locus, we did not found QTL for bread-making scores collocating with other HMW-GS encoding loci. However, in another doubled haploid population derived from a cross between cv. Apache and Ornicar (data not shown), a QTL explaining 17% of loaf volume and 14% of bread score was found behind the Glu-D1 locus, which was polymorphic in this cross. Thus results presented in this study cannot be considered as covering the diversity of genetic populaions and bread-making methods. Other studies must be carried out using a wider range of parental lines, before a synthetic view can be obtained, using meta-analysis methods such as those described in Goffinet and Gerber (2000).

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