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Genetic analysis of water-extractable arabinoxylans in bread wheat endosperm

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Abstract Two mapping populations were used for the analysis of the water-extractable arabinoxylans. One originated from a cross between the hexaploid cultivars 'Courtot' and 'Chinese Spring' and the other from a cross between an amphiploid (Synthetic) and cv 'Opata'. Arabinose (Ara), and xylose (Xyl) contents were quantified for the 91 and 76 lines obtained from the two crosses, respectively. Relative viscosity (η_{rel}) of the wheat flour aqueous extract was evaluated by capillary viscometry. Both crosses gave similar correlation coefficients between sugar contents and relative viscosity. There were strong positive relationships between arabinose, xylose and arabinoxylan contents. The relative viscosity was strongly and positively related to the arabinoxylan content and strongly and negatively related to the Ara/Xyl ratio (arabinose content to xylose content). For one of the two crosses two measurements of relative viscosity were generated from 2 years of consecutive harvesting. As a strong correlation was observed between these two measurements, an important genotypic effect can be deduced for the relative viscosity of water-extractable arabinoxylans. QTL (quantitative trait locus) research did not reveal any chromosomal segments that were strongly implicated in variations in sugar content. However, a QTL was found for relative viscosity values and the Ara/Xyl ratio on the long arm of the 1B chromosome for the two crosses considered. This QTL explained 32–37% of the variations in relative viscosity and 35–42% of the variations in the Ara/Xyl ratio. Genes located at this QTL controlled relative viscosity through modifying the Ara/Xyl ratio. Variations in the Ara/Xyl ratio were supposedly related to differences in the molecular structure of water-extractable arabinoxylans. Minor QTLs were also obtained for relative viscosity and Ara/Xyl ratio, but the chromosomes concerned were different for the two populations evaluated.

Key words Arabinoxylan · Pentosan · Viscosity · QTL · Wheat

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Introduction

The water-extractable arabinoxylans (AX) from wheat endosperm have been studied extensively, and much information is now available concerning their structure and properties. Their structure consists of a long backbone of $(1 \rightarrow 4)$ linked β-D xylopyranosyl residues which may be mono-substituted on position 3 or di-substituted on position 2 and 3 with terminal α-L-arabinofuranosyl residues. The proportions of unsubstituted and mono- and di-substituted xylose residues are approximatively 64%, 18% and 18%, respectively (Renard et al. 1990; Cleemput et al. 1993; Andersson et al. 1994). However, many authors have disagreed over the distribution of mono- and di-substituted xylose residues. Bengtsson and Aman (1990) and Anderson et al. (1994) observed for rye and wheat arabinoxylans, respectively, that the mono- and di-substituted xylose residues were present in different regions of the same polymer or on different polymers. Vinkx

et al. (1993; reviewed in Vinkx and Delcour 1996) and Cleemput et al. (1995) concluded that a whole range of polymer structures exist for rye and wheat arabinoxylans, respectively, in contrast to previous suggestions of two classes.

The main physical property of arabinoxylan lies in its ability to form viscous aqueous solutions (Medcalf et al. 1968; Fincher and Stone 1974; D'Appolonia and MacArthur 1975). The viscous properties of arabinoxylan have a significant influence on the behaviour of processed cereal grain. When arabinoxylan was added to dough it increased dough development time and the viscosity of the dough (Jelaca and Hlynka, 1971). Arabinoxylan viscosity also has an important digestive and metabolic influence on monogastric animals (Fengler and Marquardt 1988).

The wheat flour aqueous extract contains arabinoxylans and arabinogalactans, but arabinoxylans are the main determinant of viscosity since the intrinsic viscosity of arabinogalactans is very weak (Izydorczyk et al. 1991). Saulnier et al. (1995) found that the viscosity of flour aqueous extract was not completely explained by arabinoxylan content, and they noted that the weight-averaged molecular weight of arabinoxylans also influenced the viscosity measurements. Using a sequential precipitation technique, Izydorczyk and Biliaderis (1993) showed that the viscosity of arabinoxylan was mainly influenced by the higher molecular-weight arabinoxylan fraction. This last fraction was the richest in mono-substituted xylose residues and the poorest in di-substituted xylose residues. This same fraction also presents the highest xylose to arabinose ratio.

Current research shows genetic effects to be important determinants in arabinoxylan content (Saulnier et al. 1995) and viscosity. Consequently, in order to improve our knowledge of arabinoxylan synthesis, we conducted the study presented here to search for genes or chromosomal segments (QTLs; quantitative trait loci) involved in arabinoxylan content and arabinoxylan-derived viscosity. This was achieved by using two mapping populations of bread wheat.

Materials and methods

Plant material

Two different mapping populations were used in this study.

The first population (CTCS) consisted of doubled-haploid lines developed at the INRA plant breeding station of Clermont Ferrand (France). This population derived from an intraspecific cross between cv 'Courtot' (CT) and cv 'Chinese Spring' (CS) and its reciprocal. Cadalen et al. (1997) mapped 106 lines from this cross using restriction fragment length polymorphism (RFLP) probes. Amongst these, 91 lines were used in this study. Plants were grown at the INRA station in Clermont Ferrand over 2 consecutive years, 1994 and 1995. Grain from the first harvest (1994) was milled to wholemeal using a Cyclotec lab mill (Tecator, Höganas, Sweden), whilst grain from the second harvest (1995) was milled approximately to a 70% extraction rate using a Brabender Junior mill.

The second population (ITMImap – Leroy et al. 1997) consisted of 115 single-seed-descent (SSD) lines at the F_7 generation. They were derived from a cross between a synthetic amphiploid wheat W7984 (= Synthetic or SY) and a hard red spring wheat (= Opata 85 or OP). The synthetic wheat was obtained from a cross between a *T. tauschii* accession and a durum wheat cultivar 'Altar 84'. Recombinant inbred lines (RILs) were mapped by the Plant Breeding Station in Clermont Ferrand (France), the Department of Plant Breeding and Biometry in Cornell University (USA) and the A&M Texas University (Nelson et al. 1995a, b, c; Van Deynze et al. 1995; Marino et al. 1996). A subset of 76 RILs was used in this study. Plants were grown at the INRA station in Clermont Ferrand in 1996. Grain was milled approximately to a 70% extraction rate using a Brabender Junior mill.

Methods

The contents of the water-extractable arabinoxylan and the viscosity of the wheat flour aqueous extracts were determined as described previously (Saulnier et al. 1995). The relative viscosities measured were quite low, and AX in the water extract never exceeded 2 mg/ml. In this condition a solution of water-extractable arabinoxylans exhibits Newtonian behaviour. Soluble arabinoxylans were hydrolysed into sugars, which were then converted to their alditol acetates and analysed by gas-liquid chromatography (GLC). Arabinose (Ara), xylose (Xyl) and arabinoxylan (Ax) content were expressed on a dry flour weight basis. The ratio of arabinose to xylose content (Ara/Xyl) was calculated subsequently. The viscosity of the aqueous extracts was measured using an automated capillary viscometer (AVS 310, Schott Geräte, Germany) at 30°C. The relative viscosity (η_{rel}) was determined from the flow time of the aqueous extract (t) and the flow time of distilled water (t_0) and was expressed as follows: $\eta_{rel} = t/t_0$. Six replicates from the same flour were measured in order to estimate the repeatability of all these variables.

In order to eliminate arabinogalactans from the aqueous extracts, wheat flour water extracts from the ITMImap cross were added to 1.5 volumes of ethanol (95%) and stirred. After 1 h at 4°C, tubes were centrifuged at 1000 *g* for 10 min. The supernatant (containing arabinogalactans) was eliminated and the pellet (containing arabinoxylans) was washed with ethanol and centrifuged (1000 *g* for 10 min). Final pellets were hydrolysed into sugars and quantified by GLC as previously described.

CTCS and ITMI maps

The development of the CTCS map was previously described by Cadalen et al. (1997) and the mapping of the ITMImap crosses was as reported by Leroy et al. (1997) using MAPMAKER/Exp version 3.0b (Lincoln et al. 1992). Centimorgan (cM) values were calculated using the Haldane mapping function (Haldane 1919). MAPMAKER/QTL version 1.1b (Lander and Botstein 1989) was used to discover QTLs.

QTL analysis

QTL analyses were carried out for all the above variables using MAPMAKER/QTL. A major QTL was considered significant when its LOD score value was superior or equal to 2.8. When a major QTL was detected for a variable, its effect was fixed in order to search for minor effects. A minor QTL was considered significant when its LOD score value was near or above a "LOD score value of the major QTL" +2. Additive effects of QTLs obtained for a variable were checked using multifactor variance analysis. Multifactor variance analysis and Pearson correlations were computed using the Statgraphics Plus software (Manugistics®, Rockville, USA).

Results and discussion

Preliminary statistical analysis

An analysis of variance was applied to compare variation for intra-genotypic and inter-genotypic effects for all variables cited in Table 1. Results (not presented) showed that, for all parameters, intra-genotypic variance was smaller than inter-genotypic variance ($P < 1\%$ for the different sugar contents and $< 0.01\%$ for the relative viscosity). Consequently, the parameters analysed were exhibiting genetical variation in these populations.

Range and mean of variables

The mean and range of all variables are reported in Table 1. For all parameters, the results indicated that there were small differences between values of the two parental lines. Although the parental lines were not ideal material for studying arabinoxylans, there were strong differences between their derived lines for all of the parameters. This transgressive segragation indicated a polygenic control. Lines derived from the Synthetic × Opata (ITMImap) cross had higher arabinose and xylose contents than lines from the 'Courtot' × 'Chinese Spring' (CTCS) cross. Nevertheless, the means and range of Ara/Xyl ratios were not different. Relative viscosity, measured on samples obtained using the same milling procedure (Brabender Junior) for the two crosses (η_{rel} 95 and η_{rel} 96), showed lower values for the ITMImap cross. Lines derived from the ITMImap cross displayed lower viscosity values with a higher content of water-extractable arabinoxylan, which could be explained on the basis of a difference in molecular structure (length and degree of substitution) which has already been noted with viscosity variations (Saulnier et al. 1995).

Correlations between variables

Results of correlations between variables are presented in Table 2. Pearson correlation coefficients were very similar between the two crosses. Arabinoxylan content was related very strongly and positively to xylose and arabinose content ($P < 0.1\%$). The Ara/Xyl ratio was logically negatively related to xylose content; in contrast, this ratio was negatively related to arabinose content. This contrasting behaviour is undoubtedly a consequence of the strong inter-relationship between xylose and arabinose contents.

Relative viscosity measurements of the flour water extracts showed a strong negative correlation with the Ara/Xyl ratio and a strong positive one to arabinoxylan content. The relationship between viscosity and arabinoxylan content has been already investigated (Saulnier et al. 1995), but the relationship between viscosity and Ara/Xyl ratio is less well known. The Ara/Xyl ratio is often cited in connection with the relationship between the structure of molecules: the degree of substitution and the solubility of the molecule (Mares and Stone 1973; Andrewartha et al. 1979; Izydorczyk and Biliaderis 1993; Cleemput et al. 1995). Therefore, the results from Table 2 indicate that the viscosity of the aqueous extract depends on both the content and structure of arabinoxylan.

The correlation coefficient between the viscosities (η_{rel}94 and η_{rel}95), over years, was strongly significant ($P < 0.01\%$). Such a firm relationship suggests a strong genetic influence on relative viscosity variations. An analysis carried out from multilocal trials have revealed that the heritability coefficient was rather high for the relative viscosity of the aqueous extract (data not shown).

Identification of QTLs

CTCS cross

The CTCS map covered 1772 cM with 266 markers. These markers were mapped on 18 of the 21 chromosomes with a similar distribution of markers in the A and B genomes and only small segments of the D genome (Cadalen et al. 1997).

From the CTCS cross one QTL was revealed on the the long arm of chromosome 1B (Fig. 1) for the viscosity parameters obtained from the 2 consecutive harvesting years. The significance level described by the LOD score values were 8.3 and 6.8, and the r^2 coefficients (determined by MAPMAKER/QTL) were 32% and 37% for η_{rel}94 and η_{rel}95, respectively. This same locus was also involved in the Ara/Xyl ratio with a LOD score value of 9.4 and an r^2 of 42%. The LOD score for the sugar content parameters was non-significant at this locus (LOD score value < 2.8).

When the effect of 1BL was fixed by the software, minor QTLs were sought for the viscosity variables and Ara/Xyl ratio. Minor QTLs were identified on chromosomes 6AL and 6DS for the two viscosity measurements and on 6AL and 7BL for Ara/Xyl ratio. Additive effects of each of the QTLs were verified by introducing them together in a multifactor variance model using associated markers.

The mapping population did not reveal any QTLs for sugar content. Nevertheless, variance analysis identified an isolated marker (not mapped) located on chromosome 4DL which had a minor influence on the contents of these different sugars. The r^2 coefficients (determined by variance analysis) were 18%, 19% and 17% for arabinoxylan, arabinose and xylose content, respectively.

Table 1 Abbreviations, average and range of variables (*CT* 'Courtot' · *CS* 'Chinese Spring' · *SY* 'Synthetic' · *OP* 'Opata')

Variables	Abbreviation	Average	Minimum	Maximum	CT	CS	SY	OP
Arabinoxylan content[a]	AX	4.3[CTCS b]	2.2	7.0	5.7	5.2		
		5.0[ITMI b]	3.4	7.9			4.5	5.8
Arabinose content[a]	Ara	1.8	1.0	2.7	2.3	2.2		
		2.3	1.8	3.2			2.2	2.5
Xylose content[a]	Xyl	2.5	1.2	4.4	3.4	3.0		
		2.8	1.6	4.7			2.4	3.3
Ara/Xyl ratio	Ara/Xyl	0.7	0.8	1.1	0.8	0.8		
		0.6	0.8	1.2			0.9	0.8
Relative viscosity cross CT × CS (1994)	$\eta_{rel}94$	1.9	1.3	3.3	1.8	1.9		
Relative viscosity cross CT × CS (1995)	$\eta_{rel}95$	2.1	1.6	3.1	2.1	2.1		
Relative viscosity cross ITMImap	$\eta_{rel}96$	1.7	1.4	2.2			1.5	2.0

[a] Units of sugar content: mg g^{-1} of dry flour
[b] Upper values come from the cross CTCS ('Courtot' × 'Chinese Spring'); lower values come from the cross ITMImap (Synthetic × Opata)

Table 2 Significant ($P < 5\%$) Pearson correlation coefficients

	AX	Ara	Xyl	Ara/Xyl	$\eta_{rel}94$
Ara	0.95***[CTCS a]				
	0.96***[ITMI a]				
Xyl	0.99***	0.89***			
	0.99***	0.91***			
Ara/Xyl	− 0.60***	− 0.34***	− 0.71***		
	− 0.79***	− 0.59***	− 0.85***		
$\eta_{rel}94$	0.64***	0.46***	0.71***	− 0.73***	
$\eta_{rel}96$	0.75***	0.63***	0.78***	− 0.75***	
$\eta_{rel}95$	0.73***	0.53***	0.81***	− 0.84***	0.89***

*, **, *** $P < 5\%$, 1% and 0.1%, respectively
[a] Upper values come from the cross CTCS ('Courtot' × 'Chinese Spring'); lower values come from the cross ITMImap (Synthetic × Opata)

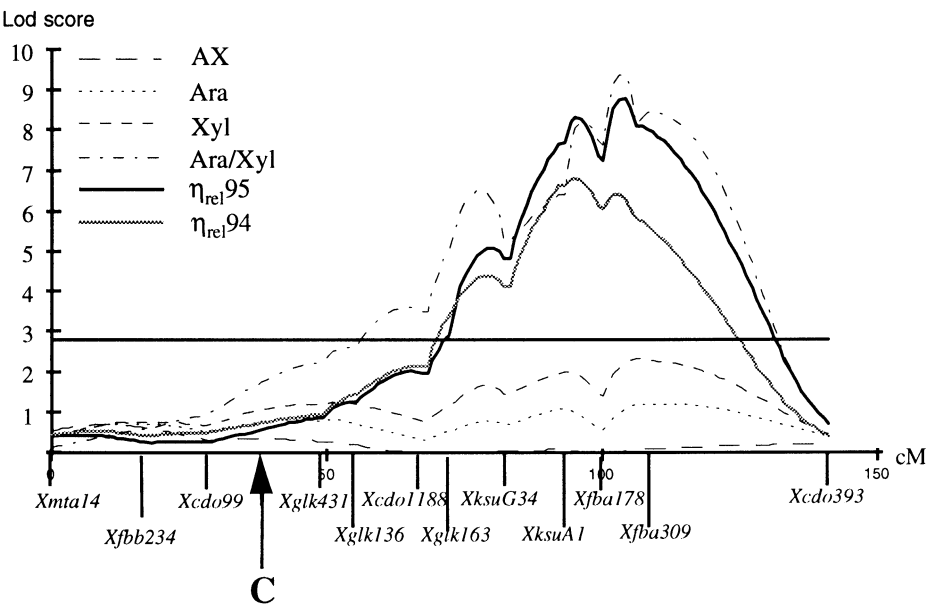

Fig. 1 Representation of the major QTL located on 1BL chromosome for the CTCS cross. *C* Centromere

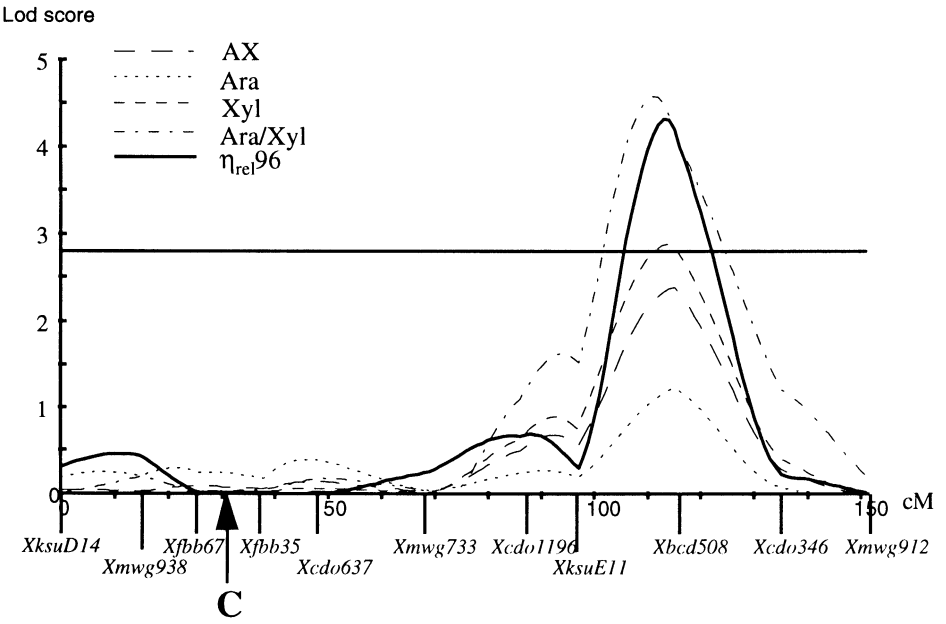

Fig. 2 Representation of the major QTL located on 1BL chromosome for the ITMImap cross. *C* Centromere

ITMImap cross

The ITMImap covered 3488 cM with 1125 markers on 21 chromosomes (Leroy et al. 1997).

As in the CTCS cross a QTL was observed on the long arm of chromosome 1B for relative viscosity and Ara/Xyl ratio (Fig. 2). The r^2 coefficients of 32% and 35% for $\eta_{rel}96$ and Ara/Xyl ratio, respectively, were nearly the same as for the first cross. However, significance levels described by the LOD score values were lower than those observed for the CTCS cross. For a same r^2 coefficient, differences in the LOD score value might be explained by the lower number of lines analysed.

As discussed previously relative viscosity was highly related to Ara/Xyl ratio and sugar content; this result suggests that this QTL on chromosome 1BL controls the viscosity by regulating the Ara/Xyl ratio. Viscosity measurements were made on flour water extracts containing arabinoxylans and arabinogalactans, and thus a part of the Ara/Xyl variation could arise from a variation in arabinogalactan content. Consequently, a further experiment was carried out to separate these two polysaccharides by the selective precipitation of arabinoxylans in an ethanol solution, and a new Ara/Xyl ratio (= Ara/Xyl' ratio) was calculated. The Ara/Xyl' ratio was related very strongly ($P < 0.01\%$) with the Ara/Xyl ratio obtained from the flour water extract, indicating that a variation in the Ara/Xyl ratio is very poorly or not related to fluctuations in arabinogalactan content. Accordingly, the Ara/xyl' ratio showed the same results for the QTL analyses (results not shown). Therefore, the QTL located on the 1BL chromosome implies that the Ara/Xyl ratio based on arabinoxylans is separate from arabinogalactan content.

Sequential precipitation showed that a lower Ara/Xyl ratio is related to a higher molecular weight (Izydorczyk and Biliaderis 1993; Cleemput et al. 1995) and a lower level of paired di-substituted xylose unit for arabinoxylan (Cleemput et al. 1995). Saulnier et al. (1995) found that the viscosity of wheat flour water extracts is dependent on the weight-averaged molecular-weight of arabinoxylans, and Bengtsson et al. (1992) showed that the proportion of arabinoxylan II (containing none and double-substituted xylose residues) obtained for a few rye cultivars has a strong correlation to viscosity. A hypothesis can be formulated concerning the specific gene(s) located at the QTL on chromosome 1BL. Gene(s) could be involved in the substitution of arabinose residues on the xylose backbone or variation in the weight-average molecular weight or a combination of both.

In Fig. 2 the QTLs are approximately located at marker *Xbcd508*. Within the first analyses no markers were present in an interval 18.3 cM on the centromeric side and 20.4 cM on the telomeric side of *Xbcd508*. New markers were then mapped in these two marker regions at 4.2 cM (centromeric side) and 5.9 cM (telomeric side) from *Xbcd508*, and a further analysis was carried out. In this new map the QTL remained located at *Xbcd508*. The QTL was then located in a segment of about 5 cM [= (4.2 + 5.9)/2 cM].

A comparison of both regions on the 1BL chromosome for the two crosses highlighted different molecular markers and, consequently, it is difficult to conclude that the QTLs were located at exactly the same place. Nervertheless, the two QTLs had approximately the

same location, and they both control relative viscosity by influencing the Ara/Xyl ratio. Thus, we can assume than the two QTLs are homologous.

When the major QTL effect was fixed, a few minor QTLs were detected but not on the same chromosomes as for the first cross (CTCS). Minor effects were found on 4BL and 6BS for the Ara/Xyl ratio, whereas nothing were detected for viscosity.

No major QTL were found at the LOD threshold of 2.8 for arabinoxylan and arabinose contents. However, xylose content showed a low but significant effect (LOD score value = 2.9; $r^2 = 21\%$) on chromosome 1BL at the same locus as that for viscosity and Ara/Xyl ratio.

Conclusion

A strong genotypic relationship was observed for relative viscosity from 2 different harvesting years. This result suggests an important genetic effect on water extractable arabinoxylan viscosity. A major QTL responsible for variations in relative viscosity and Ara/Xyl ratio was found on 1BL chromosome for both crosses. Because the two mapped populations were very different from a genetic point of view we conclude that this QTL relates to some important preserved gene(s) for arabinoxylan synthesis. These preliminary results are the first genetic approach to the control of water-extractable arabinoxylan synthesis. Further studies are being carried out to identify the genes involved, and research is underway on other molecular markers, tightly linked to genes, which can be used in plant breeding programmes.

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