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C. Boeuf · S. Prodanovic · G. Gay · M. Bernard

Structural organization of the group-1 chromosomes of two bread wheat sister lines

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Abstract Eureka and Renan are two French bread wheat cultivars derived from a 4-way cross. Using molecular markers (essentially RFLPs), we studied the structure of the group-1 chromosomes of these two genotypes, their parents and a doubled-haploid (DH) population derived from their F_1. Using the DH population (102 lines), a molecular map of the three homoeologous group-1 chromosomes was produced and compared with the map established on another intervarietal cross: Courtot × Chinese Spring (Cadalen et al. 1997). The polymorphic markers were mapped on the DH population and characterized on the four grand-parents, allowing us to compare the structural organization of the group-1 chromosomes of Eureka and Renan and determine their origin. These chromosomes were very different, except for small regions (1AL proximal and 1BL distal) which were identical.

Keywords. Wheat · Intervarietal cross · Molecular mapping · Genetic distances

Introduction

In wheat, genetic maps using molecular markers have been developed initially on interspecific populations, in order to maximize the molecular polymorphism levels and to obtain maps covering the genome reasonably well (ITMI map: Marino et al. 1996; Nelson et al. 1995a, b, c; Leroy et al. 1997; Chinese-Spring × synthetic wheat population: Chao et al. 1989; Devos and Gale 1993; Devos et al. 1992, 1993; Gale et al. 1995; Jia et al. 1996; Xie et al. 1993; or the *Triticum aestivum* × *T. spelta* map: Liu and Tsunewaki 1991); then on intraspecific populations, generally targeted to one chromosome or one chromosome arm (see Gupta et al. 1999 for a review). Intraspecific maps covering the whole genome are still rare in bread wheat, although their interest is evident for a complete exploration of the genome and for a vast number of characters (Sourdille et al. 1996, 1998; Cadalen et al. 1998; Martinant et al. 1998; Tixier et al. 1998). Moreover, such maps can take into account the interactions between loci, which generally are not allowed by maps targeted to one chromosome, where the genetic background remains constant.

Two cultivar 'sister lines', Eureka and Renan, were developed by INRA. Both derive from a 4-way cross involving the varieties Courtot, VPM × Moisson, Maris Hunstman and Mironovskaïa, whose physiological, agronomical and technological characteristics were highly complementary. The two resulting cultivars were fixed at the F9 generation to fulfil the requirements of the French catalogue (distinction from other cultivars, uniformity, stability). They were registered in 1989 and 1991 respectively, and both present many interesting characters: good resistance to abiotic stress (particularly cold, pre-harvest sprouting), to many diseases (eyespot, mildew) and to lodging. On the other hand, they are different regarding earliness, technological properties and productivity, Renan being better for bread-making quality (upper class 'BPS' of French wheats), but less productive than Eureka, classified as 'BAU' (other uses than bread-making).

Surprisingly, preliminary results of diversity evaluation, mainly by RFLP, showed that these two lines do not appear genetically closer to each other than two lines randomly taken from a collection (unpublished results). Taking these characteristics into account, it appeared interesting to us to develop a population of homozygous lines from the cross between the two cultivars, with the following objectives:

the first to characterize the chromosomal structure of Eureka and Renan as compared to those of their parents, in order to assess the contribution of each of them, and

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C. Boeuf (✉) · S. Prodanovic · G. Gay · M. Bernard
UMR INRA-UBP Amélioration et Santé des Plantes,
234 avenue du Brezet, 63039 Clermont-Ferrand Cedex 2. France,
e-mail: Christiane.Boeuf@clermont.inra.fr
Tel.: 33-4-73-62-43-40, Fax: 33-4-73-62-44-53

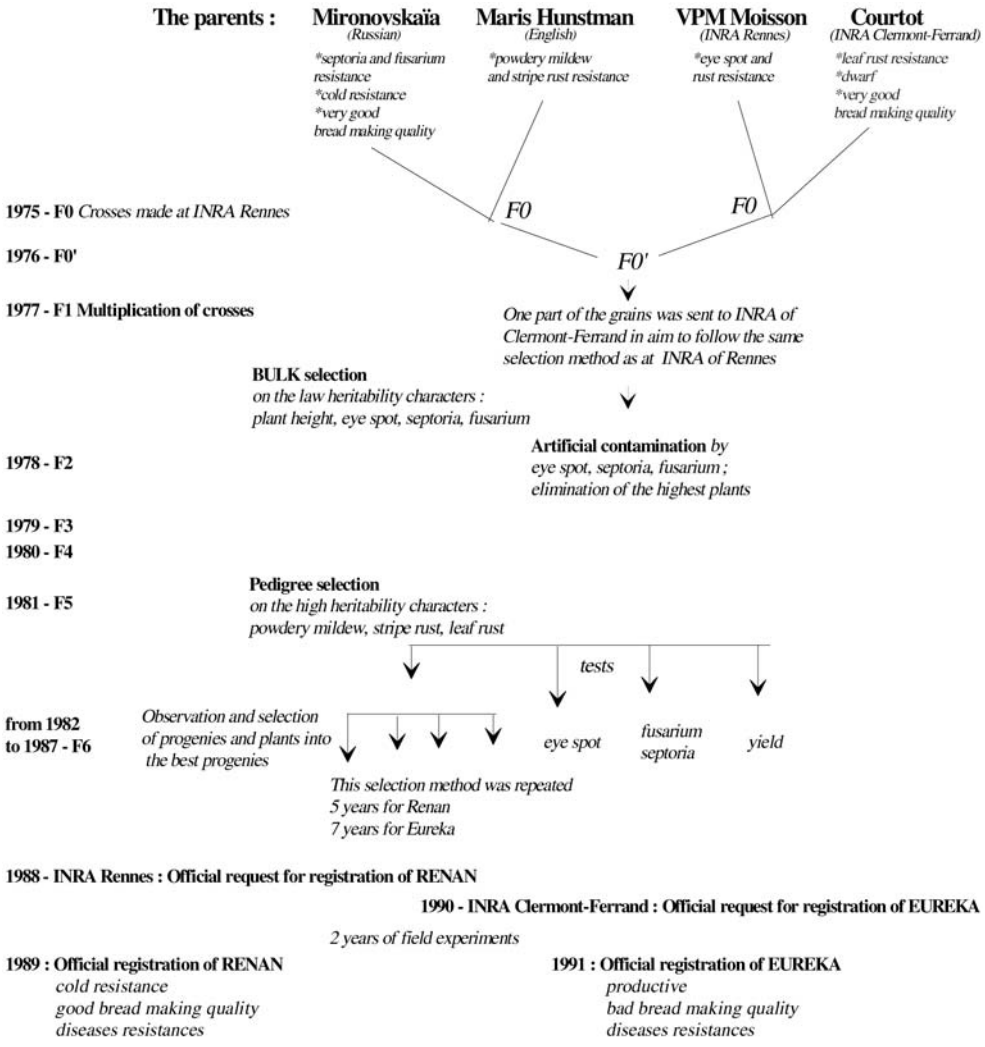

Fig. 1 Origins of Eureka and Renan

to determine whether these chromosomes have been very fragmented by the successive meioses and the selection process;

the second to see whether it was possible to construct maps on chromosomal areas of significant size, amenable to QTL analysis.

Because of contrasts existing between the two genotypes for many characters, we hoped to identify the relevant QTLs without having to map the whole genome, but only the contrasting parts. The two genotypes being agronomically valuable, a population of recombinant lines resulting from their cross represents a good basis to conduct a marker-assisted selection process, aiming at cumulating in one genotype the main positive QTLs for resistances, technological aptitudes and, finally, for yielding ability. To achieve this, the best strategy seemed to associate the phenotypical observations with the tracking of QTLs by molecular markers, following the models described by several authors, including Charmet et al. (1999) for wheat.

Materials and methods

Wheat genotypes

Eureka and Renan are two French sister varieties derived from a cross between four parents: Courtot, Mironovskaïa, Maris Hunstman and VPM × Moisson (Fig. 1). These two lines show differences in several agronomical traits including yielding ability, thousand kernel weight, bread making quality, cold and disease resistances.

One hundred and fifty two DH plants (from which 102 were genotyped) were produced from the F_1 hybrid between Eureka and Renan through anther culture (ten DH) or after crosses with maize and embryo rescue (142 DH).

Molecular marker analysis

DNA was extracted from young leaves (2–4 weeks of growth) using the CTAB protocol (Rogers and Bendich 1985). RFLPs were produced as described in Cadalen et

al. (1997). Only the probes which were previously mapped (on other crosses) to the homoeologous group-1 chromosomes were used. Seventeen microsatellites (previously mapped on the ITMI population by Röder et al. 1998) were also analysed following the protocols described in Tixier et al. (1997) for the amplification and silver staining method.

The map obtained from the DH population was constructed using Mapmaker/exp version 3.0b (Lander et al. 1987). The linkage groups were established by calculating recombination frequencies with the following conditions: threshold for LOD = 3.0 and $\theta = 0.35$.

The four parents were genotyped together with Eureka and Renan in order to attribute the different alleles to one of the parents.

Assignment of linkage groups and unlinked loci

Where possible (i.e. when the examined band was present in Chinese Spring), loci were assigned to chromosomes by using nullisomic-tetrasomic lines of Chinese Spring (Sears 1966). When nullisomic assignment was not possible, we tried to compare the observed RFLP patterns with those used to construct the ITMI map (Leroy et al. 1997) and the CTCS map (Cadalen et al. 1997).

Comparisons between maps

We used several references for comparisons: the ITMI map (Leroy et al. 1997; Röder et al. 1998) and the CTCS map (Cadalen et al. 1997). When a probe was mapped on one of these populations with the same enzyme, and when the mapped bands were identical (same molecular weight), we concluded that the loci were homologous.

In order to locate some non-polymorphic loci on chromosomes 1A, 1B and 1D, the consensus map of Van Deynze et al. (1995) and the map of Devos and Gale (1993) were used.

Results

Polymorphism between parental varieties

One hundred and thirty RFLP clones and 17 microsatellites (previously mapped to one of the group-1 chromosomes) were tested on Eureka, Renan and their four parents. Eighty six probes and 14 microsatellites exhibited polymorphism between the six genotypes, giving at least two different patterns. Among the 86 probes and 14 microsatellites, only 66 probes and 11 microsatellites were polymorphic on one group-1 chromosome, the remaining 20 probes and three microsatellites on other groups. The 86 polymorphic probes yielded from 1 to 24 bands and from two to six different patterns (Table 1). Microsatellites provided from two (gwm135) to five patterns (gwm140).

Genetic distances; comparisons between Eureka, Renan and their parents

The 11 microsatellites and the polymorphic (on the six genotypes) probes assigned to at least one group-1 chromosome (by using nullitetrasomic lines of Chinese Spring or by using the Eureka × Renan map described later) provided 94 loci (55 codominant and 39 dominant) physically represented by 175 bands. The presence of one band was noted as '1', its absence was noted as '0', and the matrix served for calculation of the absolute distance (Nei and Li) (Table 2). Eureka and Renan, although sister varieties, are almost the more distant genotypes among the group of six genotypes, according to the distances.

Table 1 Number of patterns and bands generated by the RFLP probes

Numbers of probes	Number of different patterns	Number of bands
6	6	6 to 24
2	5	9 to 12
12	4	3 to 12
20	3	1 to 12
46	2	1 to 18
Total = 86		

Table 3 Number of markers generated by the RFLP probes

Number of probes	Number of loci given by each probe	Number of loci on group 1
39	1	36 linked + 1 unlinked
12	2	17
6	3	9
2	4	2
1	5	1

Table 2 Absolute distances (Nei and Li)

	Courtot	Maris Hunstman	Mironovskaïa	VPM × Moisson	Eureka
Courtot	0.000				
Maris Hunstman	0.654	0.000			
Mironovskaïa	0.662	0.506	0.000		
VPM × Moisson	0.587	0.438	0.497	0.000	
Eureka	0.443	0.412	0.873	0.597	0.000
Renan	0.602	0.669	0.255	0.618	0.839

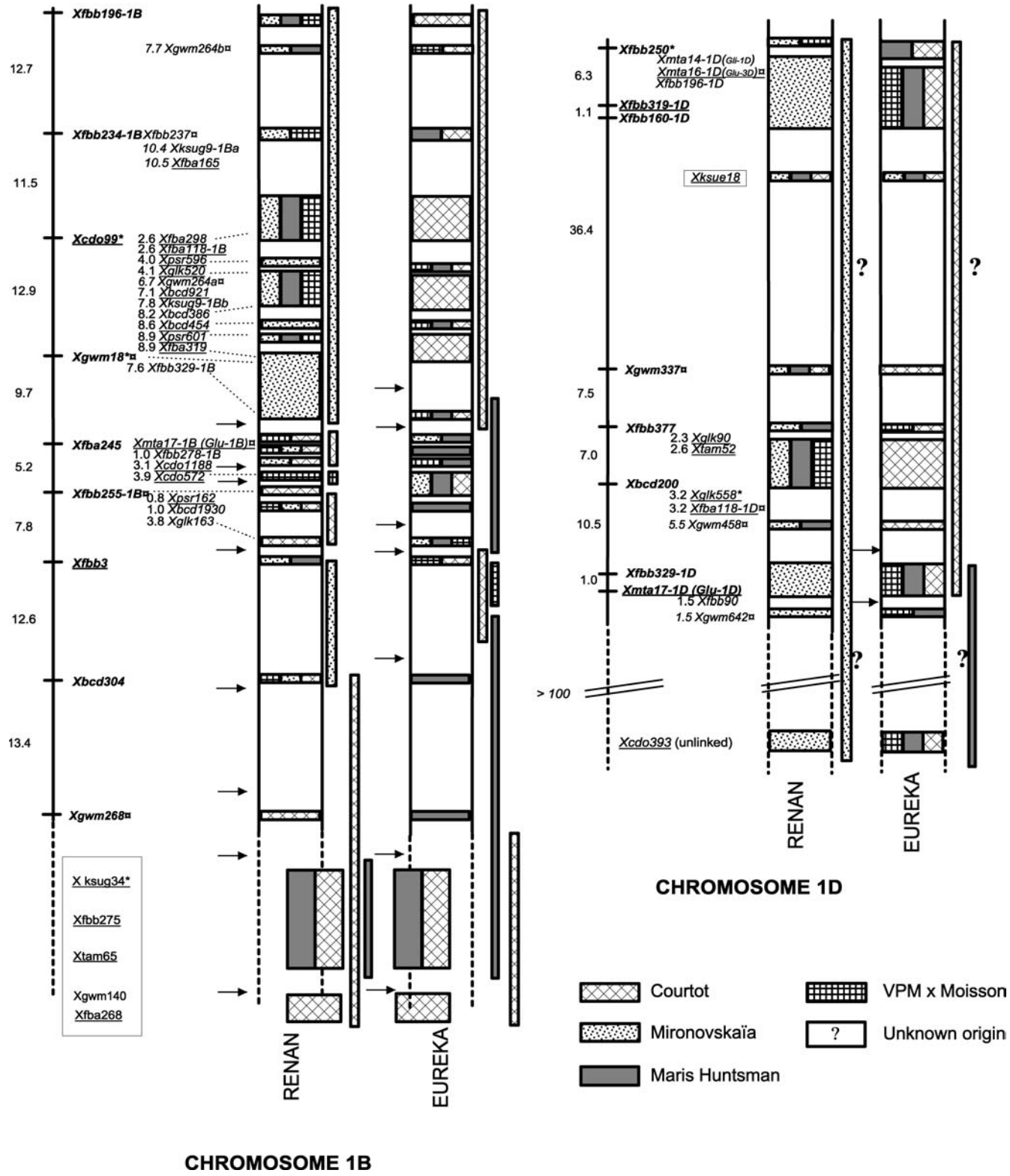

Fig. 2 Molecular map derived from the Eureka × Renan cross (102 DH lines) for chromosomes 1A, 1B and 1D. Recombination fractions are on the left of the chromosomes. Unmapped markers (polymorphic between the four parents but not on Eureka and Renan) are in a frame. *Underlined markers* were assigned to specific chromosomes by nullitetrasomic lines of Chinese Spring. Anchor markers are in *bold characters*. Numbers attached to the other markers indicate the distance (cM) from the anchor markers. The symbols *,¤, denote the loci which are mapped on other crosses (CTCS and ITMI populations respectively). Chromosomes of Eureka and Renan are represented on the right of each map. The *arrows* on the left indicate the possible recombination sites. *Boxes* along the right of the chromosomes indicate from which parental loci the genotype was inherited; *dashed lines* indicate which markers have come from which ancestor. When it was not possible to determine which of the two or three parents was implicated (in absence of polymorphism), the two or three 'parental symbols' were represented

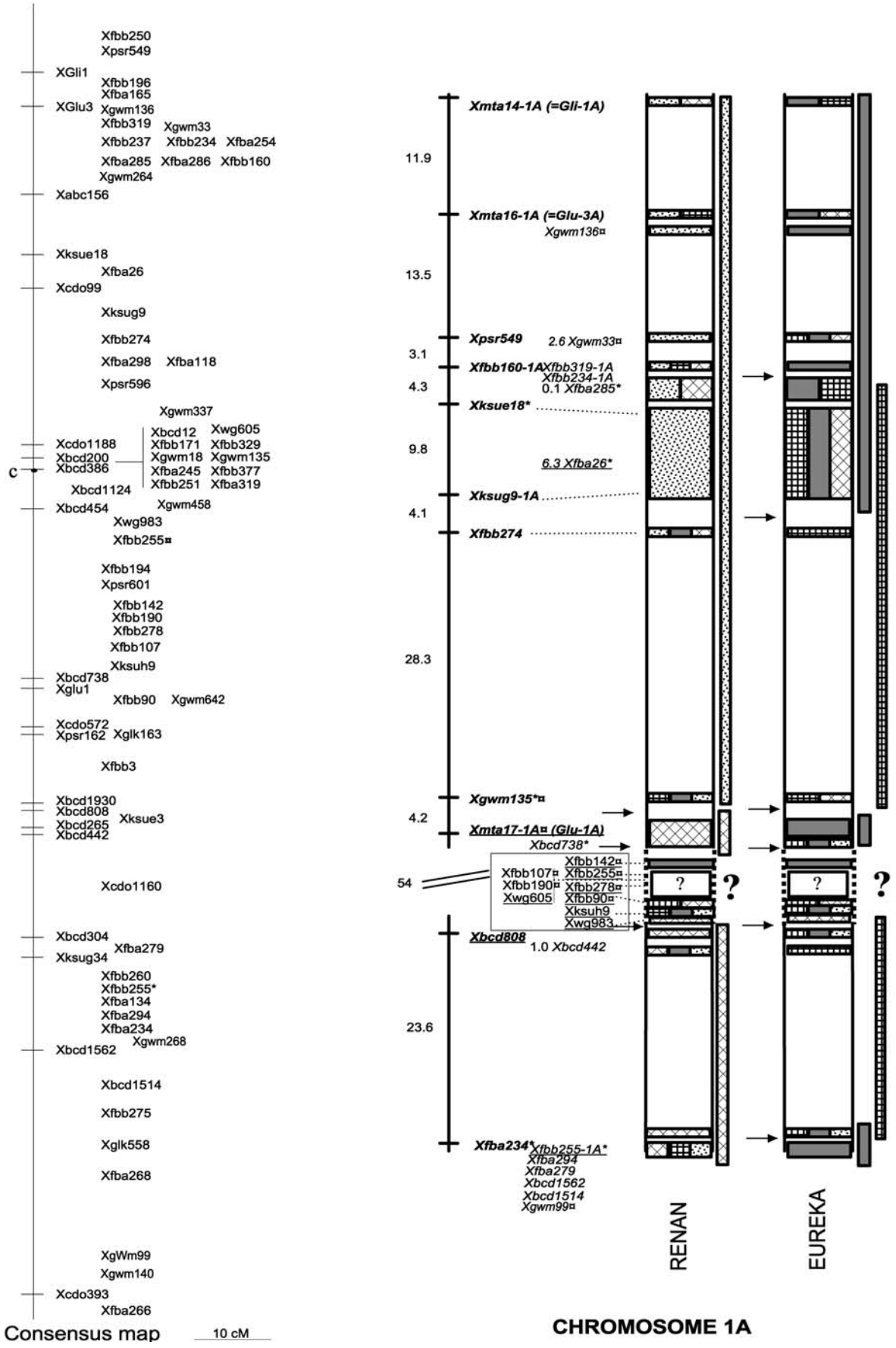

Fig. 2 continued

Mapping the Eureka × Renan population

Only ten microsatellites and 60 probes were polymorphic between Eureka and Renan. They provided 106 polymorphic loci. The probes gave from one (39 of them) to five (only one probe) loci (Table 3). Ten markers deviated from the expected 1:1 ratio at a significant threshold $\alpha = 0.05$. Among the 106 loci, seven were unlinked, but three of them were assigned to chromosomes 1D (*Xcdo393*), 2D and 7B. The 99 remaining loci were structured into 13 linkage groups. Of these groups, seven were made from two or three markers and were not assigned to the group-1 chromosomes. A group of seven markers could not be assigned to any chromosome because markers were neither present in the nullisomic lines nor mapped in another cross (using the same restriction endonuclease). Four groups involving 75 loci were assigned (using nullisomic lines) to a group-1 chromosome (Fig. 2). Two groups including respectively nine and 16 markers and accounting for 23.6 and 79.2 cM represented chromosome 1A; one group consisting of 32 loci and measuring 85.8 cM was assigned to chromosome 1B; and chromosome 1D was represented by one group of 71.3 cM involving 18 loci, plus the marker *Xcdo393*, not linked but assigned to chromosome 1D by a nullisomic approach.

Identification of the donor parents of Eureka and Renan's chromosomes

The comparison of the Eureka and Renan patterns with those of their parents allowed the respective contribution of each parent to the constitution of the group-1 chromosomes in each cultivar to be established (Fig. 2). Eureka's chromosome 1A was composed of five different regions derived from only two parents: Maris Huntsman and VPM × Moisson. Five different parts essentially provided by Courtot and Maris Huntsman constituted chromosome 1B. It was difficult to conclude about chromosome 1D because of the low number of markers. This chromosome seemed to come mainly from Courtot, with a small part from Maris Huntsman or VPM × Moisson. Renan's chromosomes were also made of multiple parts. Chromosome 1A comprised two regions inherited from Mironovskaïa (from the short arm to the middle of the long arm) and from Courtot (the distal part of the long arm). Chromosome 1B included six regions essentially provided by Mironovskaïa and Courtot. One marker, *Xcdo572*, indicated that a very small part of this chromosome came from VPM × Moisson. Chromosome 1D was probably inherited in totality from Mironovskaïa.

We observed in the two genotypes a monomorphic region defined by nine markers assigned to chromosome 1A. These markers (namely *Xfbb107, Xfbb190, Xfbb90, Xfbb255, Xfbb142, Xwg605, Xfbb278, Xwg983* and *Xksuh9*) were located near G*lu-1* on our consensus map. Subsequently, they were placed between the two linkage

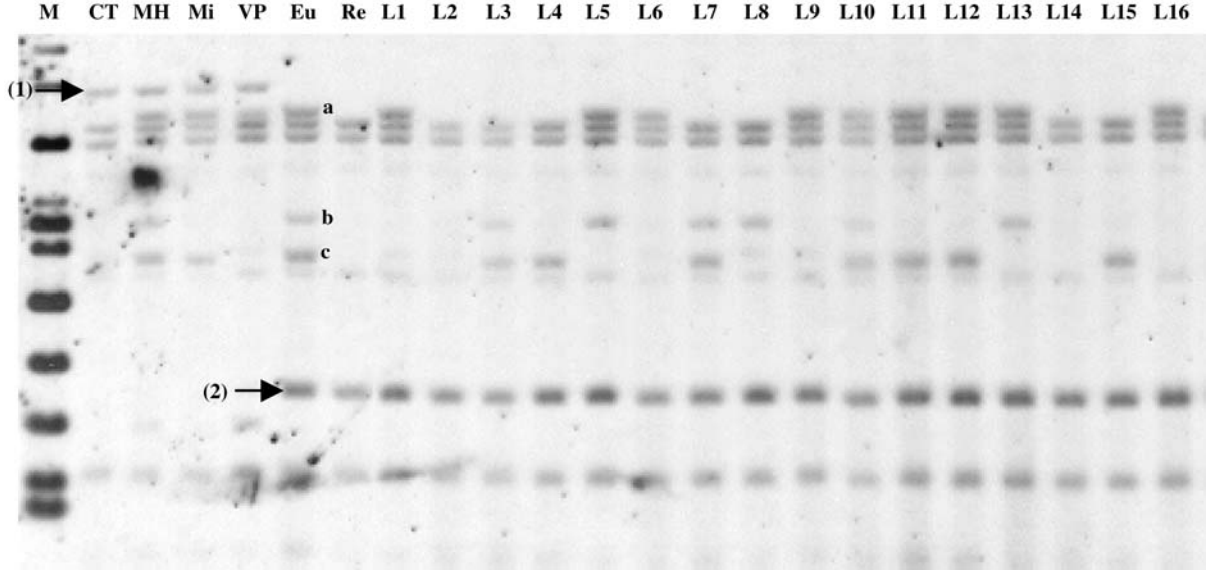

Fig. 3 Hybridization of probe fbb255 to *Dra*I-restricted genomic DNA from Eureka (*Eu*), Renan (*Re*), their four parents: Courtot (*Ct*), Maris Huntsman (*MH*), Mironovskaïa (*Mi*) and VPM × Moisson (*VP*) and one part of their progeny (*L1 to L16*). *M* = molecular weight marker (Raoul, Appligene). *a*, *b*, *c* = mapped markers on the Eureka × Renan population. The *a* locus of Eureka comes from one of three parents (MH, Mi or VP), and the *a* locus of Renan (no *a* band), comes from Courtot. The *b* locus of Renan was provided by MH and its *c* locus was provided by MH or Mi. The band *a* belongs to chromosome 1B on the ITMI map (P. Leroy, personal communication) and thus was named *Xfbb255-1B* on our map (see Fig. 2). The *b* band was assigned to chromosome 1A on nullisomic lines of Chinese Spring and mapped to chromosome 1A in the ITMI map; this locus was named *Xfbb255-1A* in our map. Band *c* was mapped on a linkage group but unassigned (this band is not present in Chinese Spring nor in the ITMI population) (*1*) indicates a band (assigned to chromosome 1A by nullitetrasomic lines) present in the four parents and absent in Eu and Re, (*2*) indicates a non-polymorphic band present in Eureka and Renan but not existing in any of their four parents. Bands (1) and (2) co-segregate in the ITMI population, they correspond to a locus mapped on chromosome 1A

groups belonging to chromosome 1A. Five of these markers (*Xfbb190, Xfbb107, Xfbb278, Xfbb255* and *Xwg605*) indicated that both Eureka and Renan lacked a common 1A band (assigned on nullisomic lines or on the ITMI map) of their four parents but exhibited a 'new' non-parental band assigned on the ITMI population to chromosome 1A with the same restriction enzyme (P. Leroy, personal communication) (Fig. 3). The other four markers in this region gave contradictory information: *Xfbb90* showed for Eureka and Renan one band also present in Courtot and in VPM × Moisson. Moreover, *Xwg983* indicated that they had the same band as Courtot, while *Xksuh9* revealed that the band coming from Courtot was not present in Eureka nor in Renan. *Xfbb142* showed that the non-polymorphic locus present in Courtot, VPM × Moisson and Mironovskaïa was not present in Eureka nor in Renan which had an unassigned band coming from Maris Huntsman.

Discussion

The level of polymorphism between Eureka and Renan was relatively high (47%) regarding their common origin, and was sufficient to establish a map of the three chromosomes. The order and distance between the markers mapped on other populations were generally preserved.

Chromosome 1A, which had the longest genetic map, harboured 25 markers and a total length of 102.8 cM by adding the two linkage groups (vs 154 cM in the CTCS map and 150 in the ITMI map). The nine markers clearly assigned to chromosome 1A by hybridization on the nullisomic lines or comparison with the ITMI map, non-polymorphic between Eureka and Renan, and that were located between the two linkage groups, gave contradictory results concerning the origin of this fragment. Four markers suggested a specific parent cultivar for the region, but the four presumed origins were not consistent with each other. Moreover, five markers showed that the origin of this region had no correspondence with the parents in the studied genotypes. These elements lead to the hypothesis that there is a common part of unknown origin due to an outbreeding event, which might have occurred at an early stage of the selection process, since these two genotypes were selected in two different locations.

Although having more markers (32), the chromosome 1B map was much shorter, since it only measured 85.8 cM. This was explained by the fact that Eureka and Renan were identical for the major distal part of chromosome arm 1BL, tagged by the probes KSUG34, TAM65, FBB275 and FBA268, and the microsatellite gwm140 mapped to the same arm in other populations. However, the overall level of polymorphism seemed higher for chromosome 1B than for the other homoeologous chromosomes, since there were more markers over a shorter length. Our results confirmed that the level of polymorphism of the B genome of wheat is always higher than that of the two other genomes, this being generally related to its origin. Chromosome 1B of our two genotypes was generally more recombined than others of the same group.

Chromosome 1D had the shortest map with a length of 71.3 cM for a total of 18 markers, but including a large gap (36.4 cM). These results are to be compared with those of the CTCS map (36.6 cM for 12 RFLP markers). The lack of polymorphic RFLP markers on genome D is to be underlined. This constitutes a general problem in wheat which was pointed out by many authors, e.g. Chao et al. (1989) and Cadalen et al. (1997). The development of new markers like microsatellites and AFLPs is contributing to solve this question (Pestsova et al. 2000; Guyomarc'h et al. 2002).

The common origin of the two genotypes Eureka and Renan probably explains the gaps in our group-1 map. Markers on 1A and 1B showed that many parts were identical between the two genotypes. Despite this, distance evaluation between the six studied genotypes (Eureka, Renan and their four parents) calculated on the group-1 chromosomes showed that the absolute distance (AD) between the two sister varieties was the second highest (AD = 0.839; the highest being 0.873 for the couple Eureka/Mironovskaïa). This is probably due to the fact that these two genotypes were selected in two different places in which the selection pressures were different. Thus Renan is highly related to Mironovskaïa (the nearest parent: AD = 0.255), and both express good cold resistance and good bread-making quality. This latter character implies different chromosome groups, among which group-1 was shown to be important (Perretant et al. 2000).

The nearest parents of Eureka are Maris Hunstman (AD = 0.412) and Courtot (AD = 0.443). Eureka is a very productive wheat, and Courtot and Maris Huntsman are better than Mironovskaïa and VPM × Moisson for this trait. Further studies are needed to determine if the group-1 fragments coming from Courtot and Maris Hunstman are involved in yielding ability. On the other hand, Eureka is a wheat of poor bread-making quality, whereas Courtot has the opposite characteristics. Therefore, the chromosome parts inherited from Courtot do not seem to have a particular role in this character. Indeed, the markers *Xmta14, Xmta16* and *Xmta17* correspond to cDNAs of genes coding for storage proteins *Gli1, Glu3* and *Glu1* respectively. The observed allelic composition for Eureka and Renan was confirmed by the observation of the proteins on SDS-PAGE (G. Branlard, personal communication). The HMW glutenins of Eureka came from Maris Huntsman: the null allele for *Glu1A*, allele 6–8 for *Glu1B*, allele 2–12 (either from Maris Huntsman, Courtot or VPM × Moisson) for *Glu1D*. Alternatively, Renan had the favourable alleles provided by Courtot (2* for *Glu1A* and 7–8 for *Glu1B*) and by Mironovskaïa (5–10 for *Glu1D*).

The origins of chromosome 1A in Renan, which showed a majority of alleles from Mironovskaïa on the short arm and from Courtot on the long arm, were completely different from those of chromosome 1A in Eureka, composed of alternate segments from the two parents

Maris Hunstman and VPM × Moisson. Chromosomes 1B of both Renan and Eureka were highly recombined. At least three parents (Mironovskaïa, VPM × Moisson and Courtot) were involved in the formation of the five clearly identified regions of chromosome 1B in Renan, and at least two (Courtot and Maris Hunstman) contributed to the organization of chromosome 1B in Eureka, also divided into at least five segments. It seems that the assembly of chromosomes 1A and 1B occurred mainly at the F_0' stage of the 4-way cross (Fig. 1), since the donor parents of each of these chromosomes came from different F_0 hybrids.

Concerning the origins of chromosomes 1D, the regions with available markers were contributed by only one parent, Mironovskaïa for Renan, or two parents, Courtot plus a small part of Maris Huntsman or VPM × Moisson for Eureka. The whole chromosome of Renan may be inherited from Mironovskaïa, but it is also possible that the fragments located between the markers may be of one or more different origins. Only more markers for this chromosome (microsatellites, AFLPs) will allow us to distinguish between these two assumptions.

Although made difficult due to inbreeding, the production of a molecular map on this cross is of actual agronomical interest. Indeed, the gaps in the map are regions of the same chromosomal origin, which thus should not carry genes or QTLs implied in the variation of agronomical characters which differentiate these two cultivars. This is what we now want to check by carrying out the complete genome map and then performing a QTL analysis for several agronomical traits.

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