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A direct comparison between the genetic maps of sorghum and rice

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Abstract A direct comparison of the genetic linkage maps of sorghum and rice is proposed. It is based on the mapping of a common set of 123 RFLP probes scattered on the genomes of both species. For each species a composite map was established by merging two individual maps comprising many common loci. This enabled us to confirm the global correspondence scheme that had previously been established between the chromosomes of sorghum and rice. It also provided a more detailed insight into the conservation of synteny and colinearity: 69% of the loci mapped on a given rice chromosome mapped to the corresponding homoeologous chromosome in sorghum; among them, 84% formed a colinear arrangement between the two species. Local inversions and translocations were detected.

Keywords Sorghum · Rice · RFLP · Comparative mapping · Synteny

Introduction

Map comparisons in the grasses have been largely documented in the past 10 years (Chao et al. 1989; Hulbert et al. 1990; Whitkus et al. 1992; Ahn and Tanksley 1993; Ahn et al. 1993; Devos et al. 1994; Kurata et al. 1994; Van Deynze et al. 1995a, b). This allowed Moore et al. (1995) to propose a synthesis of the homoeology relationships between the chromosomal segments of grass species, which indicates a fairly good conservation of large alignments of non-repeated DNA regions which contain genes. This conservation may even extend to dicots in some cases (Paterson et al. 1996). Nevertheless, general schemes do not account for the numerous exceptions to the conservation of synteny observed at different levels. Even if multi-species chromosome correspondences are now well-documented, this only allows refined pair-wise map comparisons from restricted numbers of mapping populations.

For various historical, economical and biological reasons, rice and maize have become the two most-important entry points for knowledge on genome organization in the grasses. These two species are among the most-important cereal crops and have been widely studied by geneticists for decades. Rice has a small genome size (430 Mb) which, among other features, has made it the reference species for monocots in the last few years (Isawa and Shimamoto 1996). An international genome-sequencing initiative has been set up and this task should soon be completed. Unlike rice, maize has a large genome size of around 2500 Mb with a complex internal organization due to its tetraploid origin accompanied by numerous and rapid rearrangements (Helentjaris et al. 1988; San Miguel et al. 1996; Gaut and Doebley 1997; San Miguel et al. 1998; Wilson et al. 1999).

Sorghum is another cereal crop which, like maize, belongs to the tribe Andropogoneae. It has great economic importance in the tropics and also has growing importance in temperate regions. Large stretches of colinearity have been observed between the genetic maps of maize and sorghum (Hulbert et al. 1990; Binelli et al. 1992; Whitkus et al. 1992; Melake-Berhan et al. 1993; Pereira et al. 1994; Paterson et al. 1995; Dufour et al. 1996; Peng et al. 1999). Nevertheless, the sorghum C-value (750 Mb) is smaller compared to that of maize, due to less non-coding DNA regions between the genes (Chen et al. 1997). The sorghum genome is also less duplicated

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and less disturbed by peculiar local rearrangements compared to maize, as assessed by comparisons with other species such as rice (Ahn and Tanksley 1993; Wilson et al. 1999) or sugarcane (Dufour et al. 1997). Sorghum thus appears as an interesting representative genome for the Andropogoneae and related tribes, complementary to that of maize. In this respect, a direct comparison between the genetic maps of rice and sorghum would usefully participate in (1) the fine depicting of synteny and colinearity conservation between the genomes, and (2) the evolution of chromosome rearrangements during grass evolution. Direct comparisons between the sorghum and rice genomes have already been addressed based on recombinational mapping (Paterson et al. 1995; Peng et al. 1999) and sequencing (Chen et al. 1998) but, paradoxically, the most complete studies addressing this issue have so far involved the use of maize as an intermediate (Moore et al. 1995; Wilson et al. 1999). To-date, a clear picture of detailed chromosomal-segment correspondence between the two species is not fully available.

We provide here new data allowing a direct comparison between the genetic maps of rice and sorghum based on 123 common probes revealing 133 and 137 loci on the sorghum and rice maps, respectively.

Materials and methods

The aim of this work was to obtain accurate map positions for loci revealed by the same set of low-copy or single-copy probes well scattered on the genomes of sorghum and rice. To achieve this objective, we employed existing data that were completed by newly produced data.

Existing sorghum mapping data

Two existing data sets were used. They were produced from two populations of recombinant inbred lines, RIL249 and RIL379, derived from two intra-specific crosses within *Sorghum bicolor* ssp. *bicolor* (Dufour et al. 1996; 1997). RIL249 consists of 91 lines from which 131 loci have been identified. RIL379 consists of 110 lines from which 298 loci have been identified. These two data sets had 88 loci in common (Boivin et al. 1999). We selected 339 loci from the two data sets (with 86 in common) and individual maps were merged to construct a composite linkage map with 339 loci. The nomenclature employed for the sorghum linkage groups is the one already used by Pereira et al. (1994), Dufour et al. (1997) and Boivin et al. (1999).

Existing rice mapping data

We used two existing data sets.

(1) The data set produced from an intra-specific IR64 (*indica*)×Azucena (*japonica*) doubled-haploid (DH) population developed by Cirad and the International Rice Research Institute (IRRI) and comprising a sub-sample of 107 lines derived from the original set (Guiderdoni et al. 1992). Marker data were available for 198 loci (Huang et al. 1994; 1997; Albar et al. 1998).
(2)The data set available from the RiceGenes database (http://ars-genome.cornell.edu/rice/) on an interspecific *Oryza sativa* (BS125)/*Oryza longistaminata* (WL02)//*O. sativa* (BS125) backcross population composed of 113 individuals (Causse et al. 1994). The original file contained segregating data for 617 loci.

From the second set we selected 109 loci also present in the first set, as well as 27 loci revealed by probes previously used to obtain the sorghum composite map. This allowed us to construct a rice composite map of 225 markers. The IR64×Azucena DH population and the inter-specific back-cross BS125×WL02 population will be subsequently referred to as DH and BC, respectively.

Production of new mapping data

The number of common probes mapped on the sorghum and the rice existing composite maps was 40, corresponding to 42 loci in both species. We proceeded in two ways to add new informative loci for comparative mapping. First, on rice population DH, we tried to map probes that were already mapped on the sorghum composite map; and second, we screened probes with a large hybridisation spectrum over grasses and tried to map them on both RIL379 and DH. Polymorphism was tested on the parents of the crosses, with seven restriction enzymes for sorghum population RIL379 (*Bam*HI, *Bgl*II, *Dra*I, *Eco*RI, *Eco*RV, *Hind*III and *Sst*I) and with either six (*Dra*I, *Eco*RI, *Eco*RV, *Hind*III, *Sca*I and *Xba*I) or 12 (*Apa*I, *Bam*HI, *Bgl*II, *Dra*I, *Eco*RI, *Eco*RV, *Hae*III, *Hind*III, *Kpn*I, *Pst*I, *Sca*I and *Xba*I) restriction enzymes for rice population DH.

For some probes, the hybridisation spectrum over species was investigated based on the use of ‘garden filters’ comprising the DNA of various grasses of different tribes, non-grass monocots and a dicot, *Arabidopsis thaliana*.

Sources of probes

Probes were obtained from different sources: rice (RZ prefix), oat (CDO prefix) and barley (BCD prefix) cDNA probes from Cornell University (Van Deynze et al. 1998); rice cDNA probes (R and C prefix) from the Rice Genome Project (RGP) (Kurata et al. 1994; Harushima et al. 1998); maize genomic probes (UMC prefix, from the University of Missouri, Columbia; BNL prefix, from the Brookhaven National Laboratory; PHP prefix, from Pioneer Hi-bred International) and maize cDNA probes (CSU prefix) from California State University; wheat cDNA probes (PSR prefix) from the John Innes Centre (JIC); sugarcane genomic probes (SSCIR prefix) from Cirad (Grivet et al. 1996), and sorghum cDNA probes (SbRPG prefix) developed by Rustica Prograin Génétique (RPG) and Cirad (Boivin et al. 1999). The cloned gene of the maize alcohol dehydrogenase *Adh1* (Gerlach et al. 1982) was also used.

Cornell probes were selected for their large hybridization spectrum over the grasses (Van Deynze et al. 1998). For PSR and a few CSU probes, information about hybridization aptitude over the grasses was kindly provided by P. Stephenson from JIC.

Map construction

Computer program Mapmaker 3.0 (Lander et al 1987) was used to construct a single population map as well as composite rice and sorghum maps. The Haldane mapping function was employed for all maps. The function ‘ripple’ was used to address local uncertain orders, using a window size of 5 markers and a LOD threshold of 2. Centromeres were positioned on the rice composite map according to Singh et al. (1996). The latter authors have determined the centromere location of all rice chromosomes by using secondary trisomics and telotrisomics. They positioned the centromeres relative to a framework map of 170 RFLP markers, essentially those developed by Cornell, that were assigned to chromosomes arms. This permitted us to give a fine location for centromeres relative to the BC linkage map of Causse et al. (1994).

Results and discussion

Map development

In a first step, 140 probes from different sources that were scattered throughout the composite sorghum map were screened for hybridization with rice when necessary, and then for polymorphism between the parents of DH (blots with six restriction enzymes). This allowed us to map 50 new probes on DH, including 6 BNL, 9 CSU, 1 PHP, 11 UMC, 2 BCD, 4 CDO, 5 RZ, 9 SbRPG and 3 SSCIR probes. This revealed 57 loci. For two of these probes (RZ244 and BCD147) a second distinct locus appeared to be mapped on BC. Thus, 59 loci were placed on the rice composite map. These correspond to 55 loci on the sorghum composite map.

In a second step, sorghum SbRPG probes and rice R and C probes were screened on 'garden blots' and selected for their large hybridization spectrum over grasses. Selected probes, as well as other probes from various sources selected for their known large hybridization spectrum (Van Deynze et al. 1998; P. Stephenson, personal communication), were tested sequentially for polymorphism on the parents of DH (blots with 12 restriction enzymes) and RIL379. This allowed us to map 13 new SbRPG probes (revealing 15 loci on DH and 13 loci on RIL379), 12 new R and C probes (giving 12 and 14 loci on DH and RIL379, respectively) and six probes from various sources, 2 RZ, 1 BCD, 1 CSU and 2 PSR (revealing six loci on DH and seven loci on RIL379). For one probe (RZ272), mapped at a different position on BC (Causse et al. 1994), we assumed a duplication. For two probes (C390 and C488), that were mapped on RIL379 but were monomorphic on DH, we used the rice mapping information of the Nipponbare×Kasalath population (Kurata et al. 1994) since map position could be inferred with a fair precision on our map. Altogether, this second procedure allowed us to add 33 probes that revealed 36 loci on both DH and RIL379.

A comparison between sorghum and rice composite maps was made possible through 123 common probes that yielded 133 and 137 loci in sorghum and rice, respectively. Eight loci were duplicated and one was triplicated in the sorghum composite map. Ten loci were duplicated and two triplicated in the rice composite map. Two probes (RZ244 and RZ272) revealed duplicated loci on both maps; one probe (SbRPG825) revealed duplicated loci on the rice map and triplicated loci on the sorghum map. For two probes (RZ244 and SbRPG825), the duplicated loci appeared located on homoeologous chromosomes. This could reflect an ancient duplication which took place before the rice-sorghum divergence.

Global map comparison

The loci simultaneously mapped on the sorghum and rice composite maps are shown in Fig. 1. Chromosomal segments with the highest number of common loci are arranged face to face and orthologous loci are connected by solid lines. This global scheme allows us to bring out the simple correspondence scheme which is summarized in Table 1. This scheme is in agreement with the direct, but partial, sorghum-rice chromosome correspondence established by Paterson et al. (1995) and Peng et al. (1999). Three sorghum chromosomes were not targeted: A, E and J, in Paterson et al. (1995) and one, J, in Peng et al. (1999). This scheme is also very similar to the genome-wide comparison proposed by Moore et al. (1995) and Wilson et al. (1999) who used sorghum-maize and maize-rice map comparisons as intermediates. To sum up, in eight cases, there is fairly good homoeology between one sorghum and one rice chromosome. This concerns sorghum chromosomes G, D, B, E, H, A, J and I which are globally homoeologous to rice chromosomes 1, 2, 4, 5, 6, 8, 11 and 12, respectively. In two other cases, one sorghum chromosome is homoeologous to two rice chromosomes, one being nested inside the other. The first case involves chromosome C in sorghum and chromosomes 3 and 10 in rice; the second case concerns sorghum chromosome F and rice chromosomes 7 and 9. Note that despite the recent addition of 79 new RFLP loci to the sorghum composite map, which now encompasses 416 RFLP loci (unpublished results), the two distal regions of chromosome C are still unlinked in our map. Comparison with other sorghum maps indicates that this gap may be due to a low polymorphism in this region. This possibly hides the real extent of homoeology with rice chromosome 10. This correspondence was, however, also detected by Paterson et al. (1995).

The legitimacy of the global comparative exercise performed here is proved by the repartition of the rice chromosome homoeologous segments on the sorghum map: they appear as disjointed and their sum almost completely covers the sorghum map. The global correspondence between rice and sorghum chromosomes is the simplest one that can be expected from the basic chromosome numbers of these two species, which are x=12 and x=10, respectively. The differences are accounted for by the evolutionary scheme laid down by

Fig. 1 Comparison of rice and sorghum genetic maps. The maps used for the comparison are a sorghum composite map based on mapping information from two recombinant inbred-line populations (RIL379 and RIL249), and a rice composite map based on mapping information from a back-cross population (BC, Causse et al. 1994) and a doubled-haploid (DH) population (see text). The map regions with an ambiguous order (LOD<2) are *blackened*. Chromosomes with the highest number of common mapped probes have been put *face to face*. Orthologous loci are joined by *horizontal lines*. The chromosome where a given probe is mapped in the other species is indicated when it is not the facing chromosome (*horizontal outside line*). It appears in *brackets* when several loci are identified with the probe and one of those is in a syntenic position. When a probe yields duplicated or triplicated loci, chromosomes bearing paralogous loci are given in *brackets*. Markers positioned to RIL249 only for sorghum, and BC only for rice, are in *italics*. Concerning the rice map, two markers positioned from the Nipponbare×Kasalath map (Kurata et al. 1994) are *boxed*. The position of centromeres is indicated by *striped boxes* (see text)

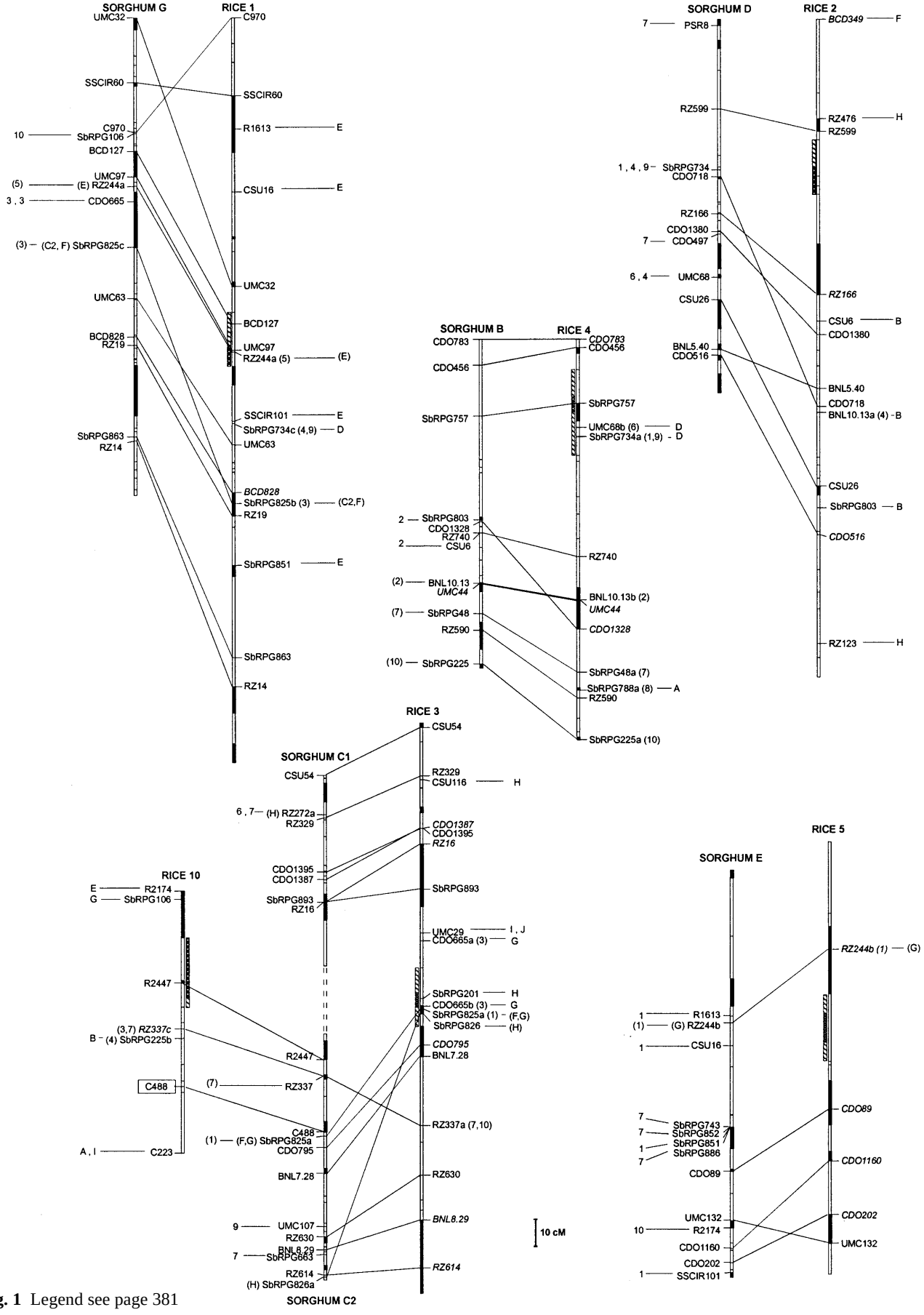

Fig. 1 Legend see page 381

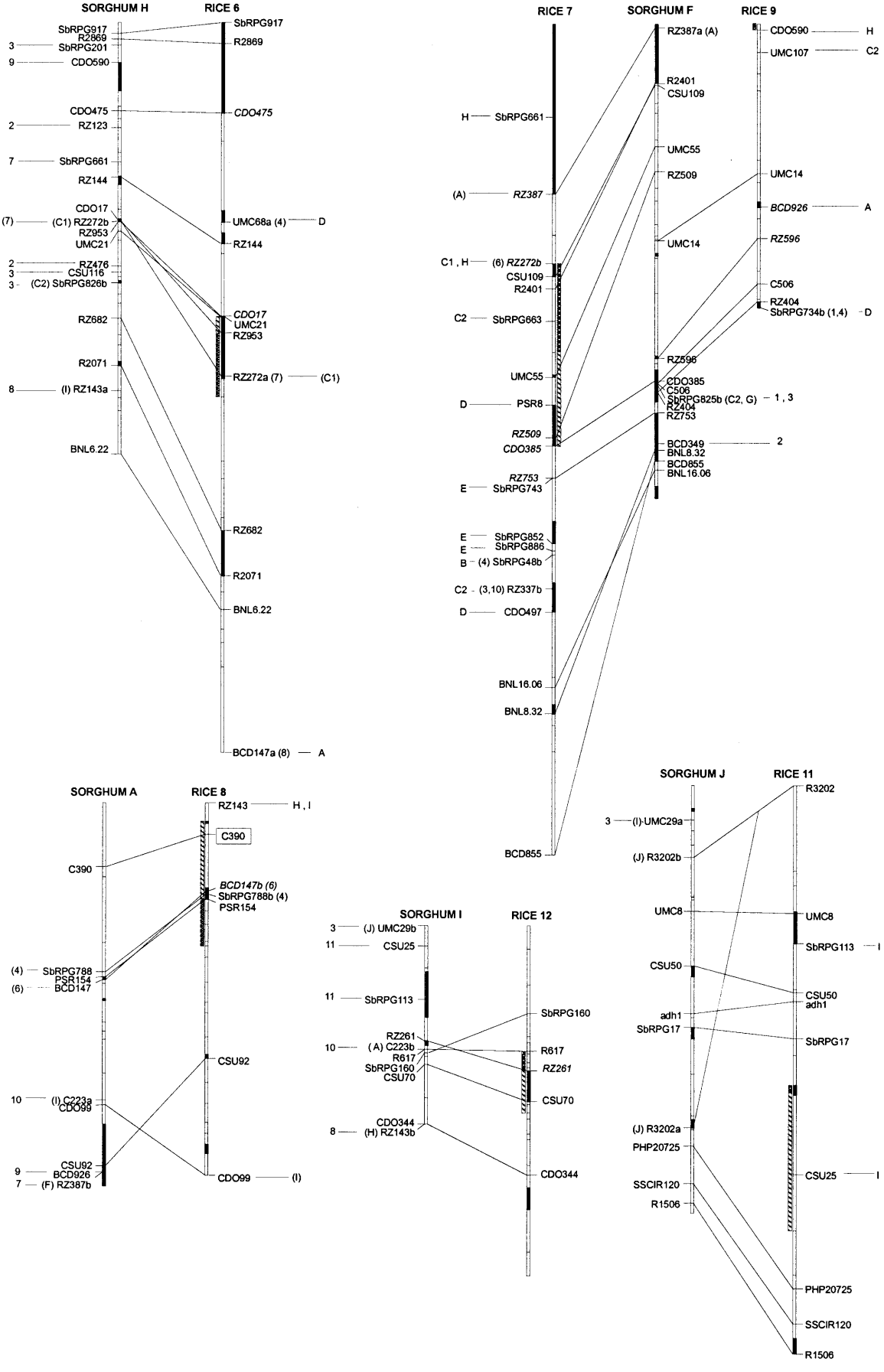
SORGHUM H
RICE 6
SbRPG917
RZ869
SbRPG201
CDO590
CDO475
RZ123
SbRPG661
RZ144
CDO17
(C1) RZ272b
RZ953
UMC21
RZ476
CSU116
(C2) SbRPG826b
RZ682
R2071
(I) RZ143a
BNL6.22
R2869
CDO475
UMC68a (4)
D
RZ144
CDO17
UMC21
RZ953
RZ272a (7)
(C1)
RZ682
R2071
BNL6.22
BCD147a (8)
A
RICE 7
SORGHUM F
RICE 9
H
SbRPG661
(A)
RZ387
C1 , H
(6) RZ272b
CSU109
R2401
C2
SbRPG663
UMC55
D
PSR8
RZ509
CDO385
RZ753
E
SbRPG743
E
SbRPG852
E
SbRPG886
B
(4) SbRPG48b
C2
(3,10) RZ337b
D
CDO497
BNL16.06
BNL8.32
BCD855
RZ387a (A)
R2401
CSU109
UMC55
RZ509
UMC14
RZ596
CDO385
C506
SbRPG825b (C2, G)
RZ404
RZ753
BCD349
BNL8.32
BCD855
BNL16.06
2
CDO590
H
UMC107
C2
UMC14
BCD926
A
RZ596
C506
RZ404
SbRPG734b (1,4)
D
1 , 3
SORGHUM A
RICE 8
C390
BCD147b (6)
SbRPG788b (4)
PSR154
(4) SbRPG788
PSR154
(6) BCD147
CSU92
10 (I) C223a
CDO99
9 CSU92
BCD926
7 (F) RZ387b
RZ143
H , I
C390
BCD147b (6)
SbRPG788b (4)
PSR154
CSU92
CDO99
(I)
SORGHUM I
RICE 12
3 (J) UMC29b
11 CSU25
11 SbRPG113
RZ261
10 (A) C223b
R617
SbRPG160
CSU70
CDO344
8 (H) RZ143b
SbRPG160
R617
RZ261
CSU70
CDO344
SORGHUM J
RICE 11
3 (I) UMC29a
(J) R3202b
UMC8
CSU50
adh1
SbRPG17
(J) R3202a
PHP20725
SSCIR120
R1506
R3202
UMC8
SbRPG113
I
CSU50
adh1
SbRPG17
CSU25
I
PHP20725
SSCIR120
R1506

Fig. 1

Table 1 Global correspondence between rice and sorghum chromosomes. The nomenclature used to designate the sorghum linkage groups is the same as Pereira et al. (1994). The number of loci mapping on a given rice chromosome and syntenic on sorghum is indicated. The corresponding percentage is in brackets

Rice chrom.	Sorghum chrom.	Syntenic loci
1	G	12/17 (71%)
2	D	7/13 (54%)
3	C	14/19 (82%)
4	B	10/13 (77%)
5	E	5/5 (100%)
6	H	11/13 (85%)
7	F	10/20 (50%)
8	A	6/7 (86%)
9	F	4/8 (50%)
10	C	3/7 (43%)
11	J	8/10 (80%)
12	I	5/5 (100%)

Wilson et al. (1999) and could have their origin in the early events that led to the differentiation between Panicoids and Oryzoids.

Synteny conservation

Regarding the synteny conservation, a mean of 69% of loci which mapped on a given rice chromosome also map to the expected homoeologous chromosome in sorghum. This percentage ranges from 43 to 100% depending on the chromosomes involved. Non-syntenic loci of any given rice chromosome are generally scattered on several different sorghum chromosomes and vice versa. In five cases, however, three loci or more were mapped on the same chromosome, as distinct from the expected homoeologous one. This concerns chromosome pairs (1, E), (2, B), (3, H), (7, C) and (7, E). Loci are either closely linked as in pair (7, E) or are dispersed along the whole chromosome as in pairs (1, E) and (7, C). In the first case a single translocation event is very likely, but in the second case either several such events or a single one followed by rearrangements might have taken place. Pair (1, E) is of particular interest because it involves four loci, whereas the homoeology between chromosomes 5 and E, was assessed based on five loci. This suggests a possible composite organization of rice chromosome 1 and/or sorghum chromosome E. More data are needed to reveal its actual extent. Those data are indices of the lability of genomes through evolution. Even if the ancestral foundation structure left a durable matrix for modern grass genomes, the fine-chromosome evolutionary scheme may prove to be more complex as additional data become available.

Colinearity conservation

Regarding colinearity conservation, 84% of loci appear in the same order on both maps when syntenic loci are considered and when uncertain local orders (blackened segments on Fig. 1) are removed from the comparison. A few situations where a concerted change involved several adjacent loci were taken as indicative of cytological rearrangements between the two homoeologous chromosomes: two cases of inversion were observed, one at the end of chromosomes 1 and G, which was already noticed by Paterson et al. (1995), and one at the end of chromosomes 8 and A, based only on a single pair of markers. Situations where a single probe shows a change in map position within a general colinear scheme are less informative regarding the underlying phenomenon involved. They can derive from various phenomena as yet to be clearly understood. One or two such cases are observed on almost every chromosome.

Centromere locations

The results of Singh et al. (1996) were used to locate centromeres on the composite map developed here. The localization involves a ‘certainty’ zone (stripped boxes on Fig. 1), which includes the closest external markers to the centromere that are common to BC and our composite map, and a more delimited ‘high-probability’ zone corresponding to a proportionate projection of the centromere zone defined by Singh et al. (1996) on the composite map (core black area inside stripped boxes). The positions of centromeres on the rice chromosomes give a first indication of their position on sorghum chromosomes. In the two cases where one sorghum chromosome was homoeologous to two nested rice chromosomes, the projections of the two rice centromeres on the sorghum chromosome were close to one another, at least with the precision allowed by our data.

Conclusion

The present study involves the numerous genome comparison studies in grasses based on linkage maps. Its main virtue is to provide information that directly and reliably relates two simple diploid species that serve as references for more complex crops using probes that can be employed with a wide range of other species. Moreover, DH and RIL are immortalised population types that will enable us to feed maps with information for loci (either major genes or QTLs) involved in the variation of useful agronomic traits. However, more detailed comparisons are obviously needed to differentiate the various modes of genome evolution. High-density linkage maps with expressed sequenced tags (ESTs) performed on wide crosses are being produced in rice (Harushima et al. 1998), sorghum (Bowers et al. 2000) and probably other grasses. They should enable one to refine alignment by an *in silico* sequence comparison of ESTs. The complete sequencing of the rice genome will result in a further improvement, permitting more comprehensive comparisons with higher ordering precision than a physical map will allow.

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