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Construction of a composite sorghum genome map and comparison with sugarcane, a related complex polyploid

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Abstract A sorghum composite linkage map was constructed with two recombinant inbred line populations using heterologous probes already mapped on maize and sugarcane. This map includes 199 loci revealed by 188 probes and distributed on 13 linkage groups. A comparison based on 84 common probes was performed between the sorghum composite map and a map of a sugarcane (*Saccharum* spp.) cultivar being developed and presently comprising 10 tentative linkage groups. A straight synteny was observed for 2 pairs of linkage groups; in two cases, 1 sorghum linkage group corresponded to 2 or 3 sugarcane linkage groups, respectively; in two cases 1 sugarcane linkage group corresponded to 2 separate sorghum linkage groups; for 2 sorghum linkage groups, no complete correspondance was found in the sugarcane genome. In most cases loci appeared to be colinear between homoeologous chromosomal segments in sorghum and sugarcane. These results are discussed in relation to published data on sorghum genomic maps, with specific reference to the genetic organization of sugarcane cultivars, and they, illustrate how investigations on relatively simple diploid genomes as sorghum will facilitate the mapping of related polyploid species such as sugarcane.

Key words Sorghum · RFLP map · Comparative mapping · Sugarcane

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Introduction

The construction of genetic maps using common sets of restriction fragment length polymorphism (RFLP) probes has recently enabled the arrangements of low-copy-number sequences along the genomes of various grass species to be compared. This led to the observation of an extensive conservation of gene order within homoeologous chromosomal segments (Moore 1995).

In the Andropogoneae tribe, attention was first focused on two important cereal crops, maize and sorghum, which have the same chromosome number, $2n = 20$. Comparative mapping between these species confirmed the duplicated nature of the maize genome, which is now interpreted to be a subsequent tetraploid phase (Moore et al. 1995). Most of the sorghum chromosomal segments were found to be colinear to pairs of duplicated regions in maize, although finer chromosomal rearrangements were demonstrated between the two genomes (Hulbert et al. 1990; Binelli et al. 1992; Whitkus et al. 1992; Melake-Berhan et al. 1993). In sorghum, RFLP maps revealed a few clusters of duplicated probes (Pereira et al. 1994; Chittenden et al. 1994; Xu et al. 1994; Lin et al. 1995).

Sugarcane is also an economically important tropical crop of the Andropogoneae tribe. Sugarcane cultivars have a complex genome organization. They are polyploid, aneuploid clones derived from interspecific hybridization between two species, *S. officinarum* ($2n = 80$) and *S. spontaneum* ($2n = 40$–128). Sugarcane was included in the Andropogoneae map comparison thanks to the identification of linkages between maize probes based on a progeny of a modern cultivar (D'Hont et al. 1994). Although the sugarcane linkage groups were non-ordered clusters of probes due to the small size of the progeny, they showed syntenic relationships to the duplicated regions of maize as did sorghum. Thus, the genomes of sugarcane and sorghum appeared to be more closely related to one another

with respect, to chromosome organization than either one with maize (Grivet et al. 1994). Using a new map, yet unsaturated, produced from the genome of a modern sugarcane cultivar of high agricultural interest ('R570') (Grivet et al. 1996), Dufour et al. (1996) recently confirmed this observation on a finer scale with a detailed comparison between duplicated segments of maize chromosomes 3 and 8 and homoeologous regions in sorghum and sugarcane. A complete colinearity was demonstrated between the sorghum and sugarcane linkage groups for this particular genome region.

In this paper we report the construction of a sorghum composite linkage map with heterologous probes based on two recombinant inbred line populations and the comparison of this map with that of sugarcane cultivar 'R570'.

Materials and methods

Construction of the sorghum composite map

Plant material

The two sorghum mapping populations were recombinant inbred line progenies (RIL) of 110 and 91 individuals, respectively. They were developed at INERA (Institut d'Etudes et de Recherches Agricoles) in Burkina Faso and had reached the fifth generation of selfing at the time of analysis. These populations were derived from two intraspecific crosses within *S. bicolor* ssp *bicolor* (IS2807 × 379 and IS2807 × 249). IS2807 (ICRISAT collection) used as the female parent in both crosses belongs to race caudatum. The male parents, 379 and 249 (CIRAD collection), belong to race guinea of the South African group and of the west African group, respectively (Chantereau et al. 1994).

Probes

Two hundred and fifty maize probes were used to test for hybridization and polymorphism on the sorghum parents of the two mapping populations. The BNL (Burr and Burr 1991), CSU (Gardiner et al. 1993), PHP (Beavis and Grant 1991) and UMC (Coe et al. 1990) maize probes were provided by the University of Missouri-Columbia, Columbia, Mo., USA. These probes were chosen to provide a uniform coverage of the maize genome.

Thirty probes (SsCIR prefix) were obtained from a sugarcane genomic library (Grivet et al. 1996). Probe CDSR29 is a sugarcane cDNA and was provided by Dr. J. da Silva (Copersucar, Brazil). They were selected for their ability to hybridize with sorghum DNA and to reveal polymorphism in the parental lines.

Four cloned genes, *Adh1* (Gerlach et al. 1982), *Pepc3* and *Pepc4* (Cretin et al. 1991) and *Pta71* (Gerlach and Bedbrook et al. 1979) and two morphological traits, colors of the leaves (gene *P*/*p*, Doggett 1988) and presence of a testa in the grain (gene *B2*/*b2*, Doggett 1988), were also mapped.

RFLP protocols and data analysis

RFLP protocols and data analysis were as described in Dufour et al. (1996). On average, nine restriction enzymes (*Bam*HI, *Bgl*II, *Dra*I, *Eco*RI, *Eco*RV, *Hin*dIII, *Sst*I, *Xba*I and *Xho*I) were screened for polymorphism.

A composite sorghum linkage map was constructed based on the two progenies using the software JOINMAP V1.4 (Stam 1993). The multipoint analyses were performed using a minimum LOD score of 4, and the results were checked with the marker order obtained for each population using MAPMAKER software (Lander et al. 1987). Genetic distances were estimated with the Haldane mapping function. The composite sorghum linkage groups were named on the basis of their homology with the linkage groups defined by Pereira et al. (1994).

Origin of the sugarcane map

The sugarcane map used is that in development for cv 'R570' (Grivet et al. 1996). This map was built using 128 maize and sugarcane probes. The study of linkages in coupling between the segregating alleles enabled 408 of these alleles to be assembled into 96 cosegregation groups (i.e. individual chromosomes or pieces of chromosomes). The cosegregation groups were assembled into 10 tentative basic linkage groups (i.e. homology groups) based on common probes and were designated LG I to LG X. The cosegregation groups that could not be assigned to any LG were designated "u" (for "unassigned").

Arguing the fact that recombination seems possible between *S. officinarum* and *S. spontaneum* inherited chromosomes, a composite map was then tentatively constructed for each basic linkage group. No significant difference of loci order was detected between *S. officinarum* and *S. spontaneum* inherited cosegregation groups in the 'R570' map. Nevertheless, due to probable differences in the basic chromosome number of the two ancestral species (D'Hont et al. 1996), chromosomal rearrangements must exist and the bispecific origin of the cultivars has to be kept in mind, as will be discussed later. Composite sugarcane groups were those actually used for the comparison with sorghum linkage groups.

Results

Sorghum linkage map

Among the 285 probes tested for polymorphism between the parents of the two progenies, 217 were unique copies (a single band revealed by hybridization with restricted DNA for most of the restriction enzyme tested), 55 were low-copy probes (2 or 3 bands revealed for all restriction enzyme tested) and 13 were multicopy probes (more than 3 bands revealed) (Table 1). In the first population (IS2807 × 379) 151 polymorphic probes were used for mapping, and in the second population (IS2807 × 249) 127 were used.

IS2807 × 379 genetic linkage map

The linkage study placed 155 loci on 13 linkage groups (LG) spanning a genetic length of 977 cM. Four probes mapped 2 loci, namely UMC50 and UMC124 on LGs E and G, UMC29 on LGs I and J and BNL12.09 on LGs B and D. Nine loci showed significant deviations from the expected 1 : 1 Mendelian segregation ratio at the 1% level. There was an excess of male alleles for 8 loci, of which 7 mapped on LG F. The ninth locus

Table 1 Characteristics of probes tested for mapping in sorghum. An average of nine restriction enzymes (*Bam*HI, *Bgl*II, *Dra*I, *Eco*RI, *Eco*RV, *Hin*dIII, *Sst*I, *Xba*I and *Xho*I) were screened for polymorphism

Typical number of bands revealed by hybridization with sorghum DNA	Types of probes				Total
	Cloned genes	cDNA maize	Genomic		
			Maize	Sugarcane	
1 band	2	25	165	25	217
2 to 3 bands	2	9	38	6	55
up to 3 bands	0	0	13	0	13
Total	4	34	216	31	285

revealed by probe BNL15.45 (LG J) displayed a deviation in favor of the female allele.

IS2807 × 249 genetic linkage map

The 129 segregating loci fell into 12 linkage groups spanning a genetic distance of 878 cM. In this population, 2 probes mapped duplicated loci, namely CSU94 on LGs E and H and SsCIR209 on LG J. As was observed in the first map, significant deviations from a Mendelian segregation ratio were mostly in favor of the alleles inherited from the male guinea parent. This was the case for 29 loci that mapped predominantly on LGs F and G. A selection in favor of female alleles was noted for 2 loci on LG I (PHP20075 and BNL3.04).

Composite sorghum linkage map

The two maps had 85 loci in common, which showed a complete conservation of loci order. This permitted the construction of a composite map of 199 loci revealed by 188 probes spanning a genetic distance of 1095 cM (Fig. 1). The loci were distributed on 13 linkage groups, although the basic chromosome number of sorghum is x = 10. Ninety-four loci shared with other published sorghum maps showed complete congruence. On the basis of information obtained from those maps it was possible to merge LGs K and C: loci revealed by BNL5.09 and BNL12.06 are linked to UMC27 in the map of Pereira et al. (1994); BNL5.09, BNL14.28 and CSU59 are linked to UMC83, UMC166, UMC27, UMC140, BNL8.29 and UMC84 in the maps of Lin et al. (1995) and Paterson et al. (1995). Similarly, LGs D and L are probably borne by a unique chromosome: LG D of Pereira et al. (1994) includes PHP20608 and BNL5.40, both corresponding both to single-copy probes in the sorghum genome.

Of the 188 probes used for the construction of the composite map 140 were single-copy probes, 41 were low-copy probes and 7 were multicopy probes. For 39 low-copy or multicopy probes, only a single locus could be mapped even though two mapping populations were used. These loci were distributed all over the genome with an excess on LGs E, F, G and J. Only 9 probes enabled the mapping of two loci (4 with RIL379, 2 with RIL249 and 3 (CSU16, UMC1 and UMC22) with both populations. Among these, 3 were duplicated on LGs E and G (UMC50, UMC124 and CSU16). When we included the mapping data from the map of Lin et al. (1995) it was possible to identify 4 additional duplicated loci between LGs E and G (CDO109, CDO1160, UMC60, pSB333).

Comparison between sorghum and sugarcane maps

For comparison, the approximate position of loci revealed by 12 probes mapped in sugarcane were added to our sorghum composite map on the basis of other published sorghum maps (Whitkus et al. 1992; Melake-Berhan et al. 1993; Lin et al. 1995; Paterson et al. 1995). Finally, the comparison between sorghum and sugarcane maps was based on 84 common probes (Fig. 2). The following correspondances could be noted:

- straight synteny and colinearity were observed for 2 pairs of linkage groups, sorghum LG E and sugarcane LG IV, sorghum LG H and sugarcane LG IX,
- in two cases, 1 sorghum linkage group was colinear to either 2 or 3 sugarcane linkage groups, respectively; sorghum LG G with sugarcane LGs II and III; sorghum LG C with sugarcane LGs I, V and VI,
- in two cases, 1 sugarcane linkage group was colinear to 2 sorghum linkage groups: sugarcane LG VIII with sorghum LGs B and J; sugarcane LG X with sorghum LGs F and I,
- for 2 sorghum linkage groups very few common loci were available in the sugarcane map. Sorghum LG D shared 3 probes with the small sugarcane LG VII, but a large length of the sorghum group remained without any counterpart in sugarcane. Sorghum LG A shared 1 locus with sugarcane cosegregation groups u1 and 2 loci with u9.

The order of mapped probes was most often similar between homoeologous chromosomal segments in sorghum and sugarcane. In a few cases, however, inversions of loci order were noted. These can be due to

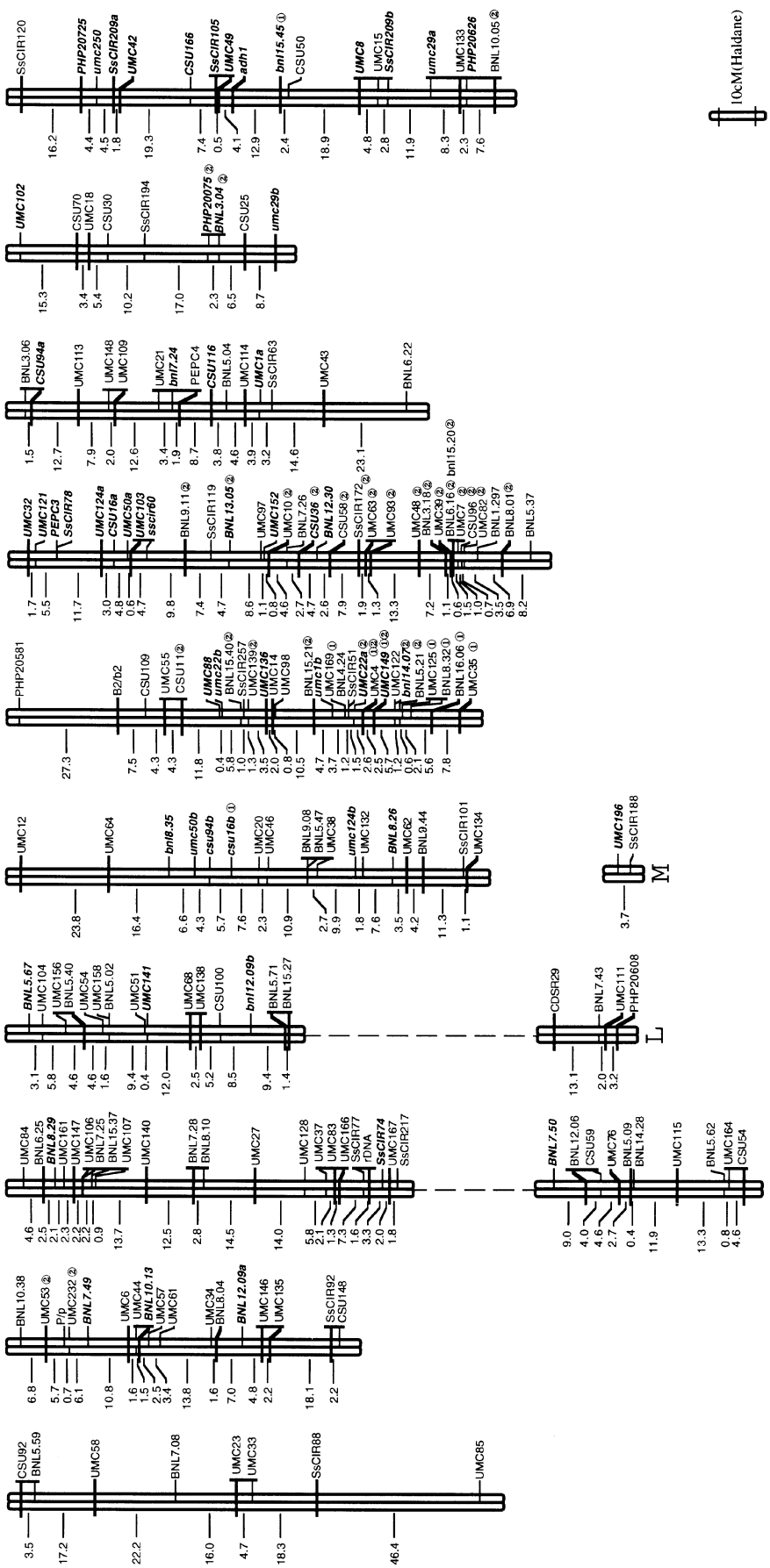

Fig. 1 Composite linkage map of sorghum genome obtained from analyses of two RIL populations. *Horizontal bars* show loci mapped in the IS2807 × 249 (*left*) and IS2807 × 379 (*right*) populations. *Bold horizontal bars* indicate loci common to the two maps. *Vertical lines* to the *left* of markers close to each other indicate that alternate orders cannot be ruled out at LOD = 2 with MAPMAKER analysis. Markers in *bold face italics* are low or multi-copy. Loci showing segregation distorsion ($P < 0.01$) are indicated by the symbol ① for the RIL IS2807 × 379 population, and ② for the RIL IS2807 × 249 population. *Lowercase letters* distinguish loci corresponding to a minor RFLP band

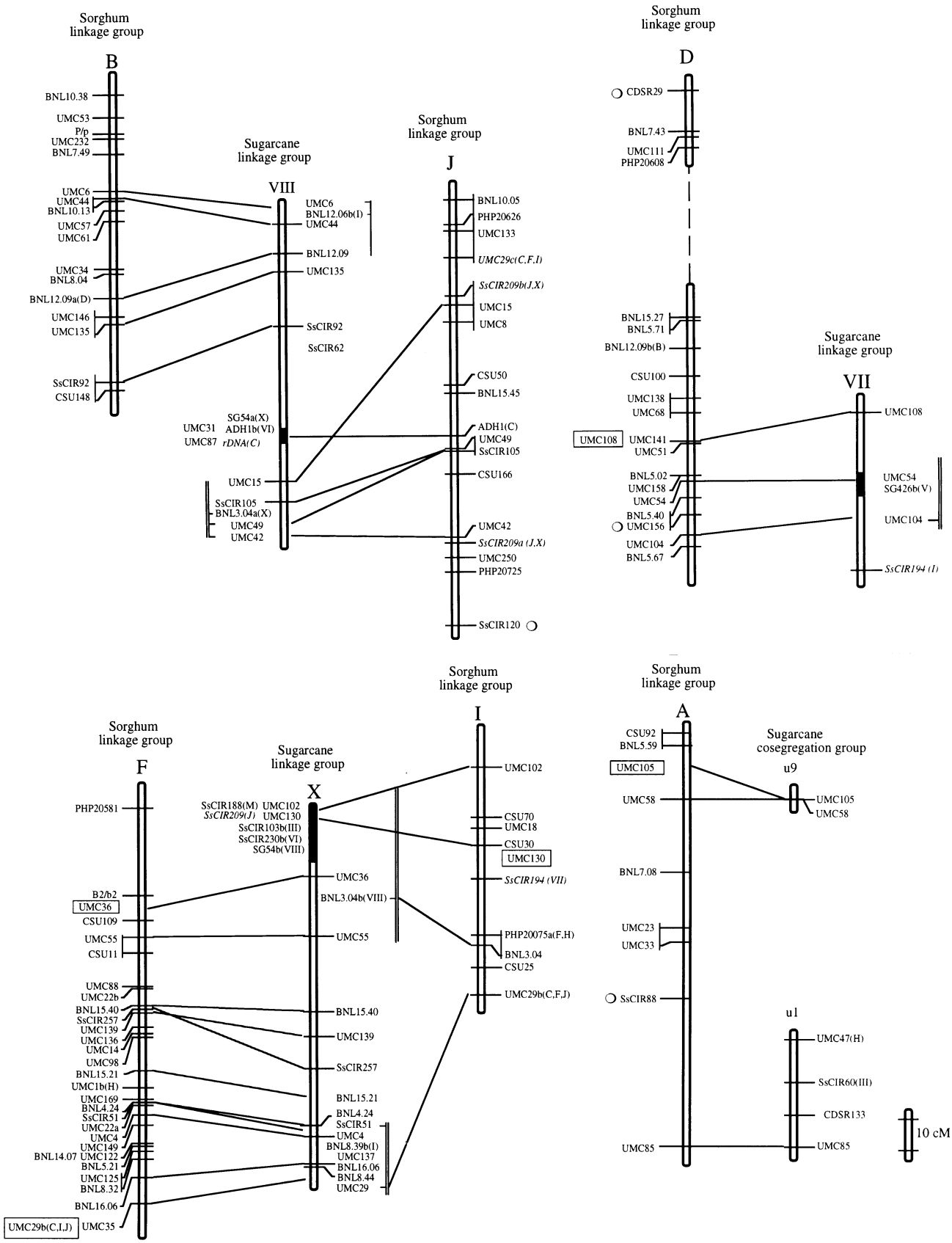

Fig. 2 See page 415 for legend

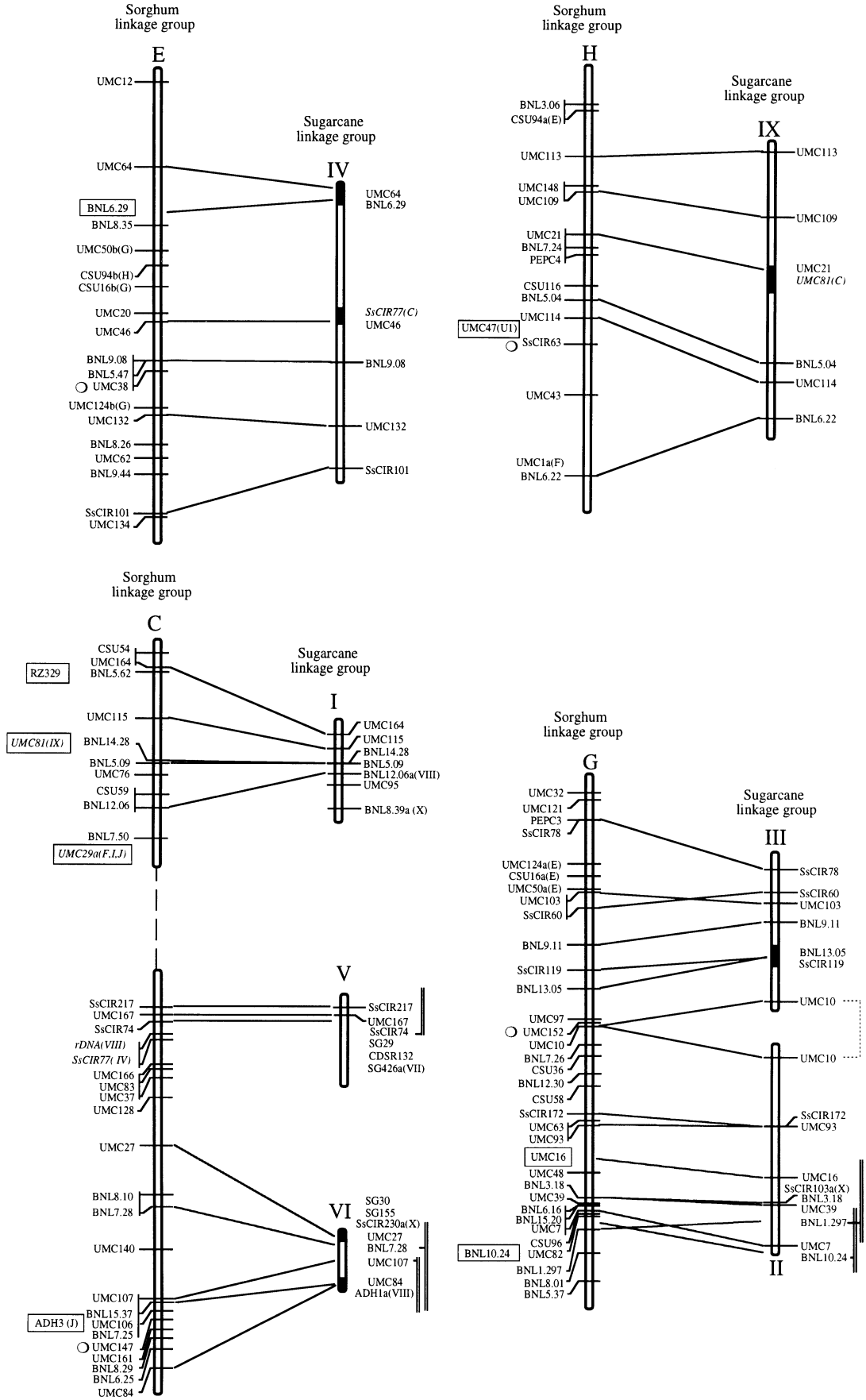

Fig. 2 See page 415 for legend

uncertainty in determining the loci order on the two composite maps. It is certainly the case for ADH1 and UMC15 on sorghum LG J and sugarcane LG VIII, SsCIR60 and UMC103 on sorghum LG G and sugarcane LG III and SsCIR257 and UMC139 on sorghum LG F and sugarcane LG X.

Five loci were mapped on non-homoeologous linkage groups; UMC81 was located on sorghum LG C and sugarcane LG IX; SsCIR77 was on sorghum LG C and sugarcane LG IV; rDNA was on sorghum LG C and sugarcane LG VIII; SsCIR194 was on sorghum LG I and sugarcane LG VII; SsCIR209 was on sorghum LG J and sugarcane LG X.

Eight markers yet unlinked in sugarcane were mapped on sorghum. These are distributed on 7 sorghum linkage groups. Three of them (SsCIR88, SsCIR120 and CDSR29) are located in sorghum genome regions without clear homoeology yet in the sugarcane map. No further conclusion can be drawn at this time for the other 5, which are probably located on cosegregation groups uncovered by other markers in the sugarcane map. Indeed, in polyploids, the segregating alleles amenable to linkage analysis are not always appropriate to detect all linkages.

Discussion

Sorghum linkage maps

In the present study, a composite sorghum genome map was constructed on the basis of two RIL populations using maize and sugarcane heterologous probes.

In order to have sufficient molecular polymorphism, we used progenies derived from interracial crosses involving distinct varietal clusters, as suggested by earlier diversity studies (Deu et al. 1994; Chantereau et al. 1994). The dynamics of race differentiation in sorghum remains to be studied in detail, particularly with respect to the specific selection pressure affecting distant hybrids. In the case of our two cross combinations, the segregation distortions observed were limited in intensity and confined to LG F in both progenies and LG G in the progeny involving the west African guinea male parent (249). While this deserves further investigation, in particular with respect to the adaptive gene content in these regions, it can be considered to have little or no impact in the scope of our mapping study.

Our composite map is unsaturated, it consists of 13 linkages groups and spans 1095 cM. On the basis of common maize probes, it can be integrated into some of the published sorghum maps (Whitkus et al. 1992; Melake-Berhan et al. 1993; Pereira et al. 1994; Lin et al. 1995; Paterson et al. 1995). The comparison along all of the homologous segments showed a consistent linear order of markers and, moreover, it indicated that our composite map represents about 90% of saturated map of Pereira et al. (1994) and consequently covers a very significant part of the sorghum genome. The alignment of the different molecular maps will serve to increase the number of available RFLP markers to sorghum researchers. It should facilitate efforts to map characters of agronomic importance and compare the locations of quantitative trait loci (QTL) between progenies and environments.

The rate of multiple-copy probes is 23%, which is consistent with those observed in previous sorghum studies – 11–41% duplicate patterns (Whitkus et al. 1992; Chittenden et al. 1994; Pereira et al. 1994). The number of mapped duplicated loci of each sorghum map is low. However, some linkage groups share several duplicated probes, thus appearing as duplicated segments. The present study as well as that of Lin et al. (1995) suggest the existence of a large duplication between sorghum LGs E and G. Without information on the location of the other multicopy probes, it is not possible to draw a definitive conclusion on the occurrence of complete chromosomal or segmental duplication in sorghum.

Comparison of the sorghum and sugarcane maps

The first comparisons between the sorghum and sugarcane maps were mostly indirect, in which maize was used as an intermediate, but they gave a hint of a large degree of synteny between the genomes of the two species (D'Hont et al. 1994; Grivet et al. 1994). The present results reinforce this and argue for a good general colinearity between the two genomes. There is a fine and straight colinearity between 2 pairs of sorghum and sugarcane linkage groups (LGs E-IV and LGs H-IX). Large arrays of colinear probes with sugarcane were also observed along the other sorghum linkage groups. However, the exact extent of colinearity is probably underestimated due to a comparison between maps that are not saturated, especially for sugarcane. In several cases the physical link between linkage groups appearing to be independent in the map of 'R570' can be anticipated from linkages detected in

Fig. 2 Comparative mapping between sorghum and sugarcane. Sugarcane tentative linkage groups are designated with *Roman numerals*. Additional cosegregation groups that could not be assigned to any linkage group in the map of R570 are designated with a "*u*". *Vertical lines* near the markers and *black areas* indicate an uncertain relative position of markers, with alternate orders that cannot be ruled out at LOD = 1 for sugarcane and LOD = 2 for sorghum with MAPMAKER analyses. Thirteen loci (in *boxes*) mapped in sorghum by Whitkus et al. (1992); Melake-Berhan et al. (1993); Lin et al. (1995) and Paterson et al. (1995) were additionally placed on the composite linkage groups. Markers which were independent or not assigned to a composite linkage group in sugarcane are noted with an *open circle* (○). Duplications are noted in *brackets* to the *right* of the markers. Markers in *italics* designate non-syntenic loci, and the location of the linkage group location is in *parentheses*

a map of *S. spontaneum* (da Silva et al. 1995). Sorghum LG C is colinear to sugarcane LGs I, V and VI. Linkage of probes SG29, CDSR132 (LG V) and SG155 (LG VI) in *S. spontaneum* indicates that LGs V and VI are probably parts of a single basic chromosome. To a lesser extent, linkage of probe RZ329 (part of sorghum LG C homoeologous to sugarcane LG I) and CDSR132 (sugarcane LG V) could be in favor of a linkage between sugarcane LGs V and I. It is thus possible to anticipate the existence of a complete homoeologous counterpart of LG C in sugarcane. A similar prediction can be made for sorghum LG G and sugarcane LGs II and III as has already been discussed by Dufour et al. (1996).

In two cases, 2 different sorghum linkage groups have adjacent homoeologous counterparts on a single sugarcane linkage group (sugarcane LGs VIII and X). This can be related to the genetic organization of modern sugarcane cultivars, which are derived from ancient

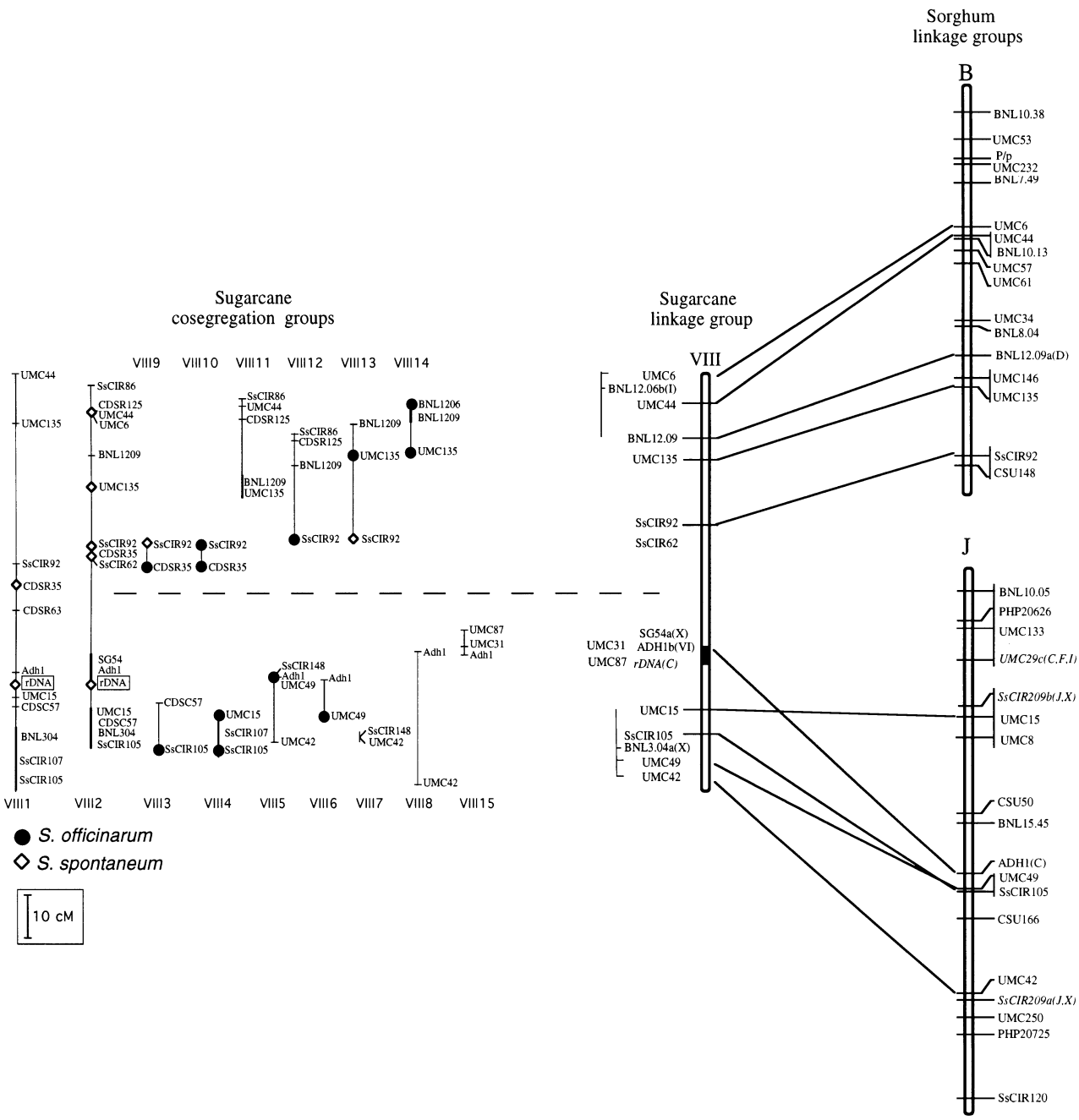

Fig. 3 Comparative mapping between sorghum linkage groups B and J and composite sugarcane linkage group VIII, confirming a probable genome rearrangement during the evolution of *S. officinarum* and *S. spontaneum*. When it is known, the specific origin of markers in the sugarcane cosegregation groups is indicated by a *black circle* for *S. officinarum* and a *white lozenge* for *S. spontaneum*. The *dashed line* highlights the discontuinity between *S. officinarum* cosegregation groups

interspecific hybridization between the sugar-producing species *S. officinarum* and the wild species *S. spontaneum*. A cultivar composite map thus encompasses cosegregation groups originated from both species. Recently, the physical location of the rDNA loci (D'Hont et al. 1996) has reinforced previous suggestions (review by Sreenivasan et al. 1987) on the occurrence of a basic chromosome number of 10 for the species *S. officinarum* and of 8 for the species *S. spontaneum*. Thus, structural differences between the chromosomes of the two species are expected. Indeed, for sugarcane LG VIII, the genetic mapping data (Grivet et al. 1996) and the different physical location of the rDNA loci, terminal for *S. officinarum* and interstitial for *S. spontaneum*, suggest that 1 *S. spontaneum* linkage group corresponds to 2 non-overlaping *S. officinarum* linkage groups (Fig. 3). A simple explanation can be a Robertsonian fusion or fission that occurred after the differentiation of the two species. The comparison between the sugarcane map and our composite sorghum map reinforces this hypothesis. It argues in favor of a fusion that would have occurred in *S. spontaneum* since the duality of sugarcane LG VIII is also recognized in the two corresponding sorghum LGs B and J. A similar development could have occurred for LG X also, although it is supported by less conclusive data. A comparison of more saturated maps will help us to understand the complete set of chromosomal rearrangements that have occurred during evolution between *Saccharum* species and between *Saccharum* and *Sorghum* genus. Integration in the comparison of *S. spontaneum* and *S. officinarum* maps will also be of great help in this way.

Future applications

The advantages of comparative genome analyses for crop improvement have been widely reviewed, particularly in the Poaceae family (Bennetzen and Freeling 1993; Moore et al. 1993; Devos et al. 1995; Moore 1995). The usefulness of diploid relatives for mapping in polyploids has been emphasized. In the Andropogoneae tribe, the extensive colinearity of the sugarcane gerome with the sorghum genome will facilitate mapping of the former since linked loci can be predicted based on their location on the sorghum map. For example, well-chosen probes on sorghum LG A should certainly lead to the identification of its homoeologous composite linkage group on sugarcane. Colinearity could also be used to help in tagging homologous genes of agronomic interest in sugarcane thanks to the expected orthology with sorghum. Mapping efforts in sugarcane could thus be concentrated, revealing all of the segregating alleles in specific important genome regions.

The global pattern of probe duplications in the sorghum genome has not yet been unraveled. Nevertheless, in contrast with genomes of polyploid sugarcane and ancient tetraploid maize, the apparent simple organization of the sorghum genome suggests that this crop stands central in the Andropogoneae tribe with respect to comparative mapping. The resolution of comparative mapping between sorghum and maize should be refined thanks to the co-alignment of published sorghum maps from a common set of maize markers. This co-alignment should endole a more precise investigation of the sorghum-maize synteny on the whole genome scale and confirm accurately the nature of extensive rearrangements of the maize genome. Simirlarly, one can expect that the sorghum genome could be a good model to bridge comparative genome analyses between Andropogoneae and, perhaps, Paniceae and other Poaceae. A first comparison between sorghum and rice (Paterson et al. 1995) and indirect comparisons taking maize as an intermediate (Ahn and Tanksley 1993; Moore 1995) permit us to expect an important synteny between the two species.

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References

Ahn S, Tanksley SD (1993) Comparative linkage maps of the rice and maize genomes. Proc Natl Acad Sci USA 90:7980–7984

Beavis WD, Grant D (1991) A linkage map based on information from four F_2 populations of maize (*Zea mays* L.). Theor Appl Genet 82:636–644

Bennetzen JL, Freeling M (1993) Grasses as a single genetic system: genome composition, collinearity and compatibility. Trends Genet 9:259–261

Binelli G, Gianfranceschi L, Pé ME, Taramino G, Busso C, Stenhouse J, Ottaviano E (1992) Similarity of maize and sorghum genomes as revealed by maize RFLP probes. Theor Appl Genet 84:10–16

Burr B, Burr FA (1991) Recombinant inbreds for molecular mapping in maize: theoretical and practical considerations. Trends Genet 7:55–60

Chantereau J, Deu M, Glaszmann JC, Degremont I, Gonzalez-De-Leon D, Hamon P (1994) RFLP diversity in cultivated sorghum in relation to racial differentiation and heterosis in hybrids. In: Witcombe JR, Duncan RR (eds) Use of molecular markers in sorghum and pearl millet breeding for developing countries. (Proc ODA Plant Sci Res Programme Conf. Norwich, UK), pp 38–45. Published by Overseas Development Administration (ODA), UK

Chittenden LM, Schertz KF, Lin YR, Wing RA, Paterson AH (1994) A detailed RFLP map of *Sorghum bicolor* × *S. propinquum*, suitable for high-density mapping, suggests ancestral duplication of sorghum chromosomes or chromosomal segments. Theor Appl Genet 87:925–933

Coe EH, Hoisington DA, Neuffer MG (1990) Linkage map of corn (maize) (*Zea mays* L.). In: O'Brien SJ (ed) Genetic maps. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, NY, pp 39–67

Cretin C, Santi S, Keryer E, Lepiniec L, Tagu D, Vidal J, Gadal P (1991) The phosphoenolpyruvate carboxylase gene family of Sorghum: promoter structures, aminoacid sequences and expression of genes. Genes 99:87–94

Deu M, Gonzalez-de-Leon D, Glaszmann JC, Degremont I, Chantereau J, Lanaud C, Hamon P (1994) RFLP diversity in cultivated sorghum in relation to racial differentiation. Theor Appl Genet 88 : 838–844

Devos K, Moore G, Gale MD (1995) Conservation of marker synteny during evolution. Euphytica 85 : 367–372

D'Hont A, Lu YH, Gonzalez-de-Leon D, Grivet L, Feldmann P, Lanaud C, Glaszmann JC (1994) A molecular approach to unravelling the genetics of sugarcane, a complex polyploid of the Andropogoneae tribe. Genome 37 : 222–230

D'Hont A, Grivet L, Feldmann P, Rao PS, Berding N, Glaszmann JC (1996) Characterization of the double genomic structure of modern sugarcane cultivars, *Saccharum spp*, by molecular cytogenetics. Mol Gen Genet 250 : 405–413

da Silva J, Honeycutt RJ, Burnquist W, Al-Janabi SM, Sorrells ME, Tanksley SD, Sobral BWS (1995) *Saccharum spontaneum* L. 'SES 208' genetic linkage map containing RFLP and PCR based markers. Mol Breed 1 : 165–179

Dogget H (1988) Sorghum. John Wiley & Sons, New York

Dufour P, Grivet L, D'Hont A, Deu M, Trouche G, Glaszmann JC, Hamon P (1996) Comparative genetic mapping between duplicated segments on maize chromosomes 3 and 8 and homoeologous regions in sorghum and sugarcane. Theor Appl Genet 92 : 1024–1030

Gardiner JM, Coe EH, Melia-Hancock S, Hoisington DA, Chao S (1993) Development of a core RFLP map in maize using an immortalized F2 population. Genetics 134 : 917–930

Gerlach WL, Bedbrook JR (1979) Cloning and characterization of ribosomal RNA genes from wheat and barley. Nucleic Acids Res 7 : 1869–1885

Gerlach WL, Pryor AJ, Dennis ES, Ferl RJ, Sachs MM, Peacock WJ (1982) cDNA cloning and induction of the alcohol dehydrogenase gene (*Adh1*) of maize. Proc Natl Acad Sci USA 79 : 2981–2985

Grivet L, D'Hont A, Dufour P, Hamon P, Roques D, Glaszmann JC (1994) Comparative genome mapping of sugar cane with other species within the Andropogoneae tribe. Heredity 73 : 500–508

Grivet L, D'Hont A, Roques D, Feldmann P, Lanaud C, Glaszmann JC (1996) RFLP mapping in cultivated sugarcane (*Saccharum spp.*): genome organization in a highly polyploid and aneuploid interspecific hybrid. Genetics 142 : 987–1000

Hulbert SH, Richter TE, Axtell JD, Bennetzen JL (1990) Genetic mapping and characterization of sorghum and related crops by means of maize DNA probes. Proc Natl Acad Sci USA 87 : 4251–4255

Lander ES, Green P, Abrahamson J, Barlow A, Daly MJ, Lincoln SE, Newburg L (1987) MAPMAKER: an interactive computer package for constucting primary genetic linkage maps of experimental and natural populations. Genomics 1 : 174–181

Lin YR, Schertz KF, Paterson AH (1995) Comparative analysis of QTLs affecting plant height and maturity across the Poaceae, in reference to an interspecific sorghum population. Genetics 141 : 391–411

Melake-Berhan A, Hulbert SH, Butler LG, Bennetzen JL (1993) Structure and evolution of the genomes of *Sorghum bicolor* and *Zea mays*. Theor Appl Genet 86 : 598–604

Moore G (1995) Cereal genome evolution: pastoral pursuits with "lego" genomes. Curr Biol 5 : 717–724

Moore G, Gale MD, Kurata N, Flavell RB (1993) Molecular analysis of small cereal genomes – current status and prospects. Bio/technology 11 : 584–589

Moore G, Foote T, Helentjaris T, Devos K, Kurata N, Gale M (1995) Was there a single ancestral cereal chromosome? Trends Genet 11 : 81–82

Paterson AH, Lin YR, Li Z, Schertz KF, Doebley JF, Pinson SRM, Liu SC, Stansel JW, Irvine JE (1995) Convergent domestication of cereal crops by independent mutations at corresponding genetic loci. Science 269 : 1714–1718

Pereira MG, Lee M, Bramel CP, Woodman W, Doebley J, Whitkus R (1994) Construction of an RFLP map in sorghum and comparative mapping in maize. Genome 37 : 236–243

Sreenivasan TV, Ahloowalia BS, Heinz DJ (1987) Cytogenetics. In: Heinz DJ (ed) Sugarcane improvement throught breeding. Elsevier, Amsterdam, pp 221–253

Stam P (1993) Contruction of integrated genetic linkage maps by means of a new computer package: JOIN MAP. Plant J 3 : 739–744

Whitkus R, Doebley J, Lee M (1992) Comparative genome mapping of sorghum and maize. Genetics 132 : 1119–1130

Xu GW, Magill CW, Schertz KF, Hart GE (1994) A RFLP linkage map of *Sorghum bicolor* L. Moench. Theor Appl Genet 89 : 139–145