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Comparative genetic mapping between duplicated segments on maize chromosomes 3 and 8 and homoeologous regions in sorghum and sugarcane

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Abstract Comparative mapping within maize, sorghum and sugarcane has previously revealed the existence of syntenic regions between the crops. In the present study, mapping on the sorghum genome of a set of probes previously located on the maize and sugarcane maps allow a detailed analysis of the relationship between maize chromosomes 3 and 8 and sorghum and sugarcane homoeologous regions. Of 49 loci revealed by 46 (4 sugarcane and 42 maize) polymorphic probes in sorghum, 42 were linked and were assigned to linkage groups G (28), E (10) and I (4). On the basis of common probes, a complete co-linearity is observed between sorghum linkage group G and the two sugarcane linkage groups II and III. The comparison between the consensus sorghum/sugarcane map (G/II/III) and the maps of maize chromosomes 3 and 8 reveals a series of linkage blocks within which gene orders are conserved. These blocks are interspersed with non-homoeologous regions corresponding to the central part of the two maize chromosomes and have been reshuffled, resulting in several inversions in maize compared to sorghum and sugarcane. The results emphasize the fact that duplication will considerably complicate precise comparative mapping at the whole genome scale between maize and other Poaceae.

Key words Maize · Sorghum · Sugarcane · RFLP · Synteny

Introduction

Among the crops that are major sources of carbohydrates, maize, sugarcane and sorghum belong to the same botanical tribe of the Andropogoneae and may thus be expected to have marked similarities. Molecular mapping efforts were first focused on maize leading to the production of large libraries of mapped probes (Burr et al. 1988; Coe et al. 1988). One important conclusion of these works was the demonstration of the highly duplicated structure of the genome (Helentjaris et al. 1988). Subsequently, Hulbert et al. (1990) demonstrated the feasibility of heterologous hybridization between maize probes and sorghum DNA allowing the first comparison between the maize and sorghum genetic maps. It was shown that the 3.5-fold greater DNA content of the maize genome compared to the sorghum genome had no relevance to the gene content, and large stretches of co-linearity were observed (Hulbert et al. 1990; Binelli et al. 1992; Whitkus et al. 1992; Melake Berhan et al. 1993).

Similarly, maize genome probes were used to facilitate the mapping of the complex genome of sugarcane (octo- or deca-ploid) and revealed a large degree of synteny between maize and sugarcane, although a much lower recombination rate was observed in sugarcane (D'Hont et al. 1994). Grivet et al. (1994) were the first to attempt a three-way comparison of maize, sugarcane and sorghum. The syntenic regions between the three species appeared most often confined to chromosome arms in maize. Sugarcane and sorghum proved to be more closely related, relative to chromosome organization, than either was to maize. Generally, one sugarcane-sorghum synteny group showed homology with two or more different maize regions, which closely matched the duplication pattern in maize. Co-linearity between the three plant genomes could be documented in a particular region which was well resolved in sugarcane.

A new sugarcane map was recently constructed with a higher number of markers permitting the merging of homologous co-segregation groups and providing a tentative composite map composed of ten linkage groups (Grivet et al. 1996). In this study, the population size allowed the ordering of loci and thus facilitated a much more precise comparison of the sugarcane map

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with those of other plants. In the mean time we had undertaken the construction of a sorghum linkage map using maize and sugarcane probes.

In the present paper we analyse in more detail the relationship between maize chromosomes 3 and 8, which share large duplicated regions, and sorghum and sugarcane homoeologous linkage groups.

Materials and methods

Data used for maize and sugarcane

Genetic maps of maize (*Zea mays* L.) chromosomes 3 and 8 are as described in the UMC 1995 maize core map (Yerk-Davis et al. 1995), supplemented by information derived from the BNL maize map (Matz et al. 1994) or/and from the maize map of Chao et al. (1994).

Sugarcane (*Saccharum* spp.) mapping data were obtained from Grivet et al. (1996). The mapping population was a progeny of 77 individuals derived from the selfing of cultivar R570. Among the 120 RFLP loci placed on the composite map, 71 were obtained from maize probes. Among them, 16 were probes mapped on maize chromosome 3 or 8 and could be used in the present study.

Construction of the sorghum map

Plant material. The segregation analyses were performed on two populations of 110 and 91 recombinant inbred lines. These populations were derived from two intraspecific crosses, within *Sorghum bicolor* (L.) Moench ssp. *bicolor*, between an accession of the race caudatum (IS 2807 in the ICRISAT collection) and two accessions of the race guinea (Nbs 249 and 379 in the CIRAD collection). They were developed at I.N.E.R.A (Institut d'Etudes et de Recherches Agricoles) in Burkina Faso and had reached the fifth generation of selfing at the time of analysis.

Choice of probes. Fourty four maize probes and four sugarcane probes were used in this study (see Table 1). The BNL maize probes were provided by Brookhaven National Laboratory (Burr and Burr 1991) and UMC; CSU probes were provided by the University of Missouri-Columbia (Coe et al. 1990 ; Gardiner et al. 1993). They covered maize chromosomes 3 and 8 and were selected for their ability to hybridize with sorghum DNA. Twenty seven revealed a unique locus in maize, 17 of which were specific to chromosome 3, and ten were specific to chromosome 8. Fifteen probes revealed two loci; in seven cases these loci were located on both maize chromosomes 3 and 8. Two probes revealed more than two loci located on maize chromosomes 3 or/and 8 plus 1, 2 or 9 . The sugarcane probes (SsCIR library) were obtained from a library constructed in our laboratory. They were selected for this study because they are linked on our sugarcane map with maize probes that reveal loci on chromosomes 3 and 8. In order to maximize the number of probes simultaneously mapped in maize, sugarcane and sorghum, up to 12 restriction enzymes were used to screen for polymorphism between the sorghum parental accessions.

RFLP protocols. Total DNA was extracted from freeze-dried leaf tissues according to the protocol of Saghai-Maroof et al. (1984) modified by Hoisington (1992). Blots were prepared using 5 µg of total DNA for each plant after digestion with one restriction enzyme. The restriction fragments were separated by electrophoresis on 0.8% agarose gels in TAE buffer (0.1 M Tris, 1 mM EDTA, pH 8). DNA was transferred onto nylon membranes (Hybond N+, Amersham). Probes were labelled with ^{32}P-αdCTP using the Amersham Megaprime commercial kit. Pre-hybridization, hybridization and washes were performed according to the protocols of Hoisington (1992). Blots were washed rapidly in 2 SSC, 0.5% SDS at room temperature and then for 30 min, two times in 0.5 SSC, 0.1% SDS at 65 °C, and two more times in 0.1 SSC, 0.1% SDS at 65 °C.

Data analysis. For each population, the first segregation analysis was carried out using MAPMAKER 2.0 software (Lander et al. 1987). The multipoint analyses were performed using a minimum LOD score of 4 with a maximum recombination value of 0.30, and three-point and n-point analyses were performed to determine the most likely order of the markers. Then, composite sorghum linkage groups were constructed using JOINMAP V1.4 software (Stam 1993). The following rules were applied for typing anchor loci mapped in both populations : when a probe revealed a single hybridization signal on the sorghum accessions of the polymorphism survey for at least one enzyme, it was considered as a single copy and the corresponding locus was named similarly in the two populations; when a probe revealed two or more bands for all enzymes, suggesting the existence of a multiple copy, the loci that are homologous in the two populations were identified with the allelic information of the common parent (IS 2807) and were further tested on the basis of their position in the respective linkage groups obtained with Mapmaker. The multipoint analyses were performed using a minimum LOD score of 4 and the results were checked with the marker order obtained using Mapmaker. Genetic distances were estimated with the Haldane mapping function. The sorghum linkage groups were named on the basis of their homology with the linkage groups of Pereira et al. (1994).

Results

Linkage groups formed in sorghum and sugarcane

The number of bands revealed in sorghum and the clustering of corresponding loci in the sorghum and sugarcane linkage groups are given in Table 1. In sorghum, the four sugarcane probes and 42 of the 44 maize probes revealed polymorphism. Two maize probes remained monomorphic, although up to 12 restriction enzymes were used. Of the 46 probes polymorphic in sorghum, 14 displayed patterns typical of multiple-copy probes. Eleven of them, however, revealed a single polymorphic locus whereas three revealed two polymorphic loci. Twenty eight, ten, and four loci were linked in sorghum, leading to linkage groups G, E and I respectively (Fig.1). Seven maize probes remained unlinked. The distribution of the multicopy probes appeared concentrated on one side of linkage group G and on a large part of linkage group E. The three probes that revealed two polymorphic loci each mapped to both G and E linkage groups.

In sugarcane, 19 of the 48 probes considered here have already been mapped, and corresponding loci are distributed in linkage groups II (9), III (6), IV (2), VIII (2), and X(1) (Table 1). One of them (UMC10) mapped in both groups II and III of sugarcane.

Comparison of linkage-group organization between sorghum and sugarcane

The comparison between the sorghum and sugarcane linkage groups is summarized in Fig. 1. On the basis of common probes, a complete co-linearity was observed between the sorghum linkage group G and the two sugarcane linkage groups II and III. Gene order is conserved and the recombination rates are comparable in both crops. The sorghum group E and the sugarcane group IV share two probes (BNL 9.08 and SsCIR 101)

Table 1 Linkage group locations on sorghum, sugarcane and maize of DNA fragments that hybridized to maize and sugarcane probes

Probes	Chromosomal or group location			Number of bands in the sorghum polymorphism survey
	Maize	Sorghum	Sugarcane	
UMC32	3S, 8S	G		2
UMC121	3S	G		2
SsCIR78		G	III	2,3
UMC124	8L	G/E[a]		>3
CSU16	3S	G/E[a]		2
UMC50	3S	G/E[a]		>3
UMC103	3L,8S	G	III	>3
BNL9.11	8S	G	III	1
SsCIR119		G	III	1
BNL13.05	3S,8S	G	III	2
UMC97	3S	G		1
UMC10	3S	G	II, III	1
BNL7.26	3L	G		1
BNL12.30	3L,8L	G		2
CSU58	3L	G		1
SsCIR172		G	II	1
UMC63	3L	G		1
UMC93	8L	G	II	1
UMC16	3L	(c)	II	1
UMC48	8L	G		1
BNL3.18	3L	G	II	1
UMC39	3L,8L	G	II	1
BNL6.16	3L	G		1
UMC7	8L	G	II	1
CSU96	3L,8L	G		1
UMC82	3L,8L,1L,9S	G		1
BNL1.297	3L	G	II	1
BNL10.24	3L,8L	(c)	II	1
BNL8.01	3L	G		1
BNL5.37	3L	G		1
UMC12	8L	E		1
BNL8.35	3S	E[b]		>3
BNL9.08	8L	E	IV	1
BNL5.47	6L,8L	E		2
BNL8.26	8L	E		>3
BNL9.44	8L	E		1
SsCIR101		E	IV	1
UMC102	3L	I	X	2
UMC18	3L,10L	I		1
CSU30	3L	I		1
CSU25	3L,10L	I		1
BNL10.38	1S,2S,8L	Unlinked		1
UMC53	2S,8L	Unlinked		1
BNL7.08	8L	Unlinked		1
UMC4	2L,8L	Unlinked		1
UMC15	3L,4L	Unlinked	VIII	1
UMC42	3S,4	Unlinked	VIII	2
UMC161	1L,3S	Unlinked		1

[a] G"strong"/ E"weak"bands
[b] "Weak" band mapped in sorghum
[c] Monomorphic band in sorghum

and could be homoeologous. The probes found unlinked or located in linkage groups other than G and E for sorghum were also located in sugarcane groups other than II or III. For example, UMC102 belongs to sorghum group I and to sugarcane group X; UMC 42 and UMC 15 are unlinked in sorghum and mapped on sugarcane group VIII.

Comparison between sorghum/sugarcane data and homoeologous maize chromosomes

Relying on the perfect co-linearity and the comparable genetic distances among "bridge-loci" shared by the sorghum and sugarcane homoeologous linkage groups G, II and III, we performed a single comparison with maize chromosomes 3 and 8, using the map of sorghum with the addition of probe UMC16, whose position was derived from the sugarcane map.

The consensus map (G/II/III) is presented in the center part of Fig. 2 and compared with the maps of maize chromosomes 3 and 8. It can be divided in two segments (S1 and S2), in which gene content is conserved with homoeologous and duplicated maize segments. The first segment S1, delimited by probes UMC32 and UMC10, corresponds to the small arm of maize chromosomes 3 and 8. Gene order is globally conserved between this segment and maize chromosome arm 3S.

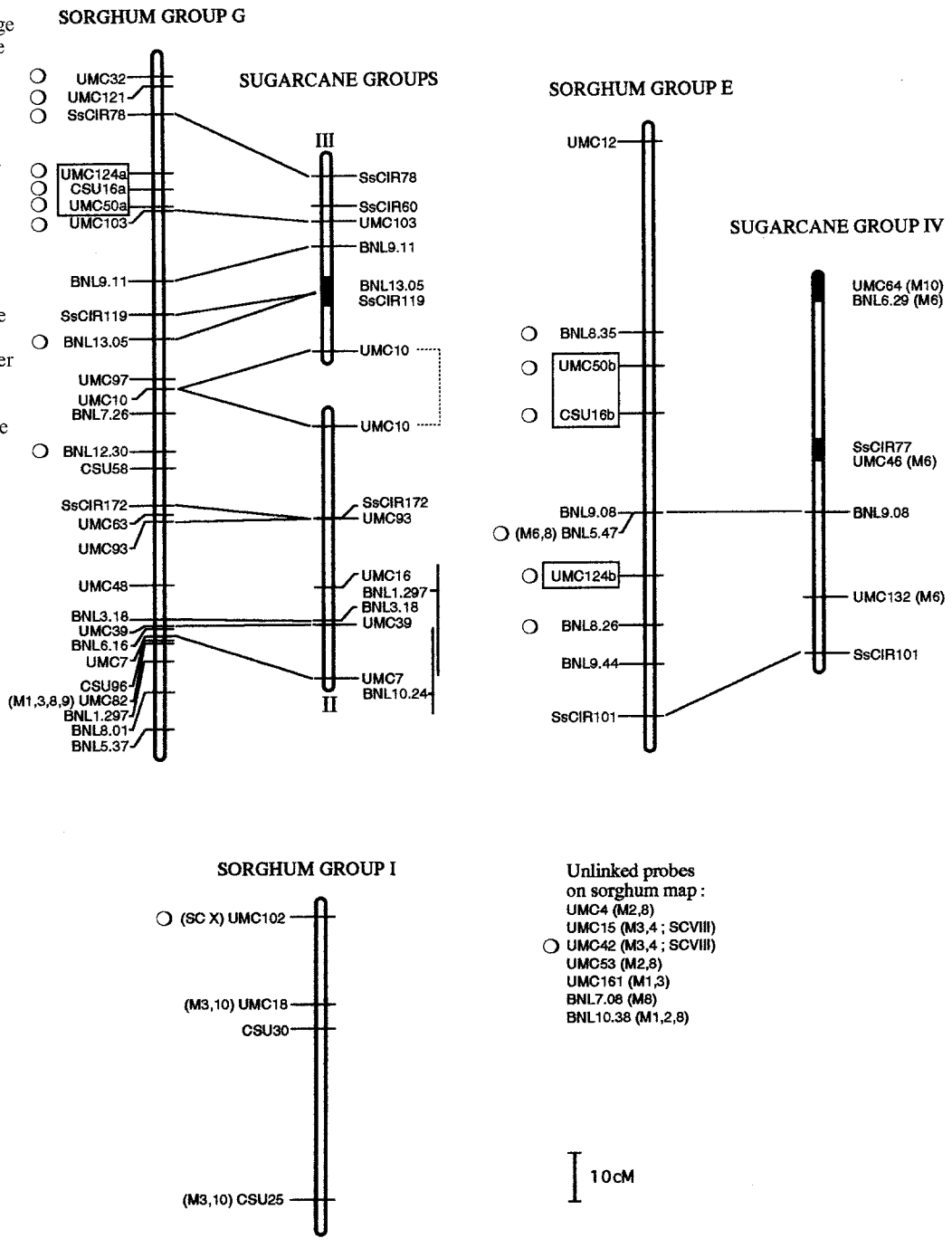

Fig. 1 Comparative map of sorghum and sugarcane linkage groups constructed with maize and sugarcane probes. The sorghum linkage groups were named on the basis of their homology with the complete map from Pereira et al. (1994). Markers in *boxes* correspond to duplicated loci. Markers displaying patterns typical of multiple-copy probes in the polymorphism survey are preceded by a *circle*. The sugarcane linkage groups were obtained from Grivet et al. (1996). Areas of uncertain order are represented by a *bold line* for clustered markers or by a "*T*" *bar* on the right of the co-segregation group for a single marker. *M* indicates maize chromosomes and *SC* sugarcane linkage groups

The unique exception observed is the locus revealed by probe UMC103, which is located on maize chromosome arm 3L. Contrastingly, an inversion of this segment is observed between the consensus group and the maize chromosome arm 8S. Peculiarly, probe BNL13.05 reveals a single locus on the consensus group as well as on maize chromosome 3S, but reveals two loci on maize chromosome arm 8S. Taking into account the general inversion noted above, co-linearity would be respected with locus BNL13.05a.

The second segment S2, delimited by BNL7.26 and BNL5.37, is completely inverted to a large fragment of maize chromosome arm 3L, with the exception of loci BNL12.30b and BNL1.297. The counterpart of S2 in the maize chromosome 8L can be divided into two subregions, one that is co-linear, delimited by loci BNL 12.30a and UMC48, and the other that is inverted, delimited by loci UMC71b and UMC39b.

Segments S1 and S2 are contiguous in the consensus sorghum-sugarcane group but are separated in each maize chromosome by a portion homoeologous to another sorghum linkage group. The central portion of maize chromosome 3 displays three loci that are homoeologous to group I; in addition, a probe that maps to the distal part of maize chromosome 3L also maps in the same sorghum linkage group I. Likewise,

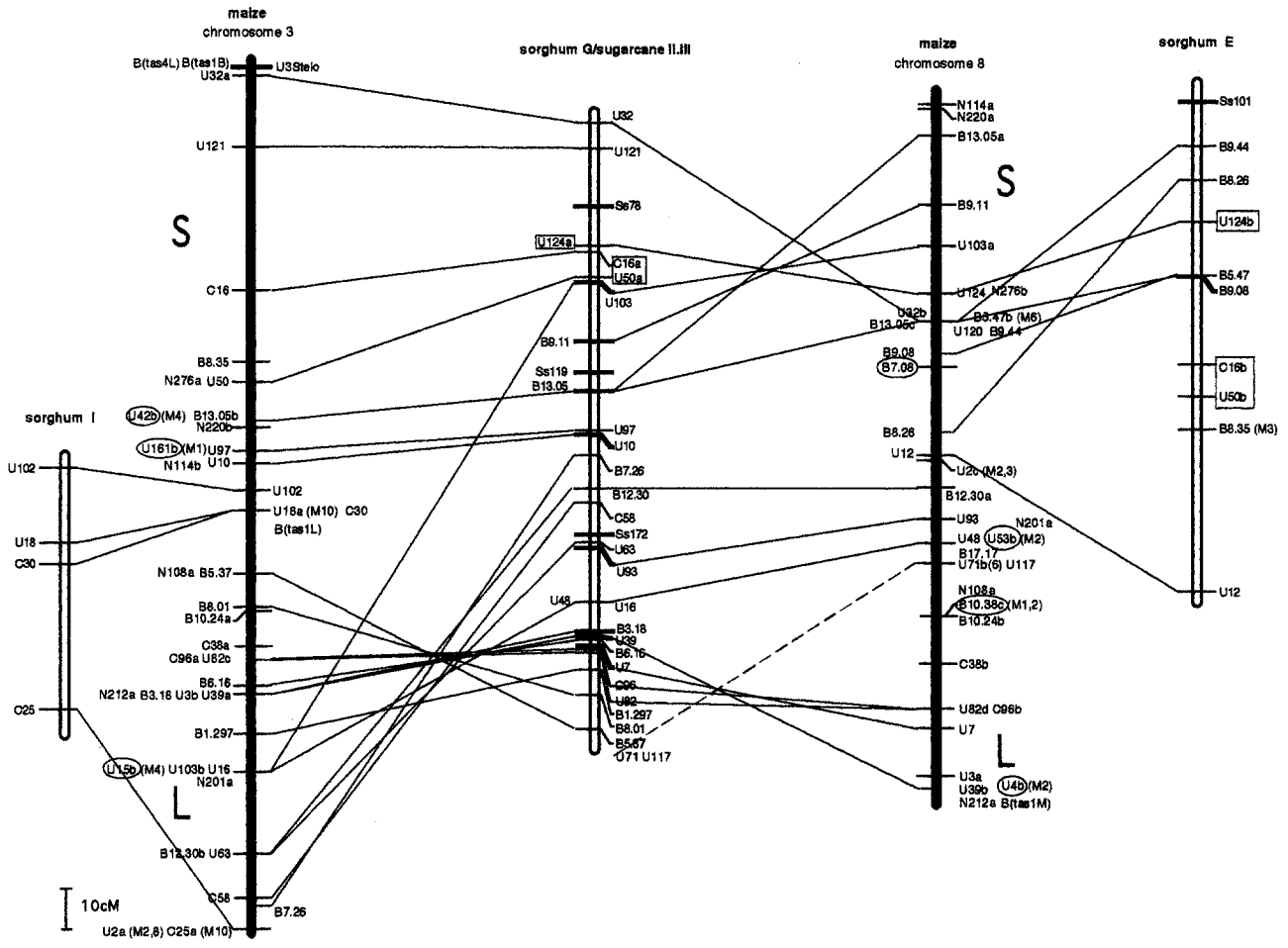

Fig. 2 Comparison of the loci order between sorghum, sugarcane and maize chromosomes 3 and 8. On the synteny sorghum/sugarcane group G/II/III, the 13 *bold lines* identify the probes that show co-linearity (Fig.1). Duplicated probes in sorghum are in *boxes*. Unlinked probes in sorghum are shown on maize chromosomes in *ovals*. In order to facilitate this comparison, we have located probes not mapped in this study, either duplicated on maize chromosomes 3 and 8, mapped in homoeologous sorghum linkage group in previous studies (UMC71/UMC117) (Whitkus et al. 1992; Melake-Berhan et al. 1993), or corresponding to telomeric sequences. Probe abbreviations are as follows: for the maize probes B = BNL, C = CSU, N = NPI, U = UMC, and for the sugarcane probes : Ss = SsCIR

the central portion of maize chromosome 8 displays several loci that have their homoeologous counterparts not in the consensus group (G/II/III) but in sorghum linkage group E. Linkage group E of sorghum thus shows homology with segment S1 and with a specific portion of maize chromosome 8. The gene order, however, is not conserved.

The synteny is also disrupted occasionally, with probes on maize chromosome 3 (UMC42b, UMC161b, UMC15b) or on chromosome 8 (UMC53b, BNL10.38c and UMC4b) which map out of sorghum linkage groups G, E and I and sugarcane linkage groups II, III and IV. It is noteworthy that all these probes also map to chromosomes other than 3 and 8 in maize.

Discussion

The present study was undertaken to compare three species of the same botanical tribe, thus expected to show closely related genome organization. Maize was taken as a starting point by sampling probes located on two chromosomes supposed to be strongly related by extensive duplication. This study permitted the identification of particular genome rearrangements, essentially specific to the maize genome, and highlighted various sources of complexity in comparative genome analysis.

The first noteworthy feature is the existence of large co-linear regions among the three crop species. The genomes of sugarcane and sorghum show simple mutual relationships on the basis of the full co-linearity between sorghum linkage group G and sugarcane linkage groups II and III. Given the difficulties specific to the mapping of a highly polyploid crop such as sugarcane (Grivet et al. 1996), it is possible that some linkages would be left unidentified and, in particular, that sugarcane groups II and III are actually two parts of a single linkage group. This is supported by the presence of a UMC10 locus on the end of both these groups and the clustering by Da Silva et al. (1993) of probes CDSC52 (group II) and SG99 (group III) into the same linkage group using the

progeny of a wild sugarcane genotype. The comparison between the consensus sorghum-sugarcane linkage group (G/II/III) and maize chromosomes 3 and 8 reveals a series of linkage blocks, within which gene orders are conserved. However, these blocks are interspersed with non-homoeologous regions and have been reshuffled, resulting in several inversions. The apparent relatedness between chromosomes 3 and 8 in maize is therefore most probably incidental.

Attempts to study structural differences between chromosomes 3 and 8 through multiple-copy probes do not provide a clear understanding of their structural relationships. Instead, the analysis of structural rearrangements may be simpler when using as a reference a map that describes both sorghum and sugarcane, and which may be closer to the common arrangement ancestral to the three crops. The regions that alter the general synteny are located in the central part of the two maize chromosomes. The centromeric region of maize chromosome 3 corresponds to sorghum linkage group I and seems to be duplicated on maize chromosome 1OS (locus CSU25b and UMC18b). The central region of maize chromosome 8 corresponds to sorghum/sugarcane linkage groups E/IV and seems to be duplicated on maize chromosome 6L.

These observations can be related to a global interpretation recently proposed for explaining the diversity of genome organization in various grasses (Moore et al. 1995). This rested on the identification of 19 linkage blocks conserved among grasses, designated Rn (n = 1–19) according to their position in the rice genome, and whose combination is specific in each species. In this scheme, maize chromosome 3 is made up of blocks R12a, R1a and R1b and maize chromosome 8 is made of blocks R1a, R5a, R5b and R1b. The first segment, S1, identified in the present study corresponds to block R1a, the second segment S2 to block R1b, the central segment in maize chromosome 3 to block R12a and the central portion of maize chromosome 8 to blocks R5a and R5b. Our results identify several inversions when comparing the various maps. Segment S1 reveals an inversion on maize chromosome arm 8S relative to sorghum, sugarcane and maize 3S. Segment S2 reveals an inversion on maize chromosome 3L relative to sorghum and sugarcane; this inversion may have occurred subsequent to the formation of the compound arrangement of blocks R1a-R12a-R1b and may have affected a segment of block R12a, as suggested by the terminal position of probe CSU25. This inversion is supported by the interstitial position of probe BNL(tas1L), which represents a telomeric sequence which most certainly originated from the terminal region of maize arm 3L. Segment S2 also reveals an internal partial inversion on maize chromosome 8L relative to the other maps. This inversion is supported by the particular location of probe BNL17.17, a repeated telomeric sequence, precisely at the location of the putative breakage site.

Other aspects of the results presented here illustrate more complex situations essentially related to duplication. The amount of duplication in the sorghum genome is expected to be low on the basis of most existing reports (Chittenden et al. 1994; Pereira et al. 1994). In the particular region under study, however, duplications seem common. The top part of linkage group G displays a majority of multiple-copy probes and those that could reveal two polymorphic loci suggest the existence of a significant segmental duplication with linkage group E. In a recent study, Lin et al. (1995) reported duplications between the central and bottom parts of linkage group G (LG A in their study) and linkage group E (LG G in their study). The fact that their study and ours highlight distinct zones showing duplications illustrates a difficulty when monitoring the impact of this phenomenon on the evolution of the genome. Nevertheless this provides additional evidence of important duplications between the two linkage groups. In addition to the regions duplicated with linkage group G, linkage group E encompasses a region homologous to the central part of maize chromosome 8, also corresponding to part of chromosome 6. Contrastingly, the respective putative homoeologous linkage groups in sugarcane did not show evidence of duplications; linkage group IV might be restricted to the region homoeologous to the maize chromosome 6 region. Alternately, it may be that the sugarcane map is not yet sufficiently populated and that priority has so far been given to probes yielding simpler banding patterns.

Duplications will considerably complicate comparative mapping, not only because of a non-equivocal correspondance between homoeologous regions across species, but also because of a possible faster molecular evolution allowed by functional complementation, which will mask the original duplication pattern. This was clearly discussed by Whitkus et al. (1992). Maize constitutes a good example. If it is accepted that maize has a tetraploid origin, it is paradoxical to have large numbers of maize genomic probes that cross hybridize with other species such as sorghum and sugarcane, and to have relatively fewer probes that reveal duplicate loci within maize. This may indicate that the ancestral genomes of maize were highly differentiated before polyploidization, or else that polyploidy allowed rapid molecular sequence evolution. Duplication can also result in local alterations to synteny between genomes. The ability of a duplicate genome to accumulate copies of gene sequences at non-syntenic locations as compared to a related diploid species, has yet been reported between rice and wheat (Devos et al. 1991; Kurata et al. 1994). This can be related in our study to the apparent insertion, within regions homoeologous to segments S1 and S2 in maize chromosomes 3 and 8, of loci which map in non-homoeologous regions in sorghum and sugarcane.

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