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Structure and evolution of the genomes of *Sorghum bicolor* and *Zea mays*

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Abstract. Cloned maize genes and random maize genomic fragments were used to construct a genetic map of sorghum and to compare the structure of the maize and sorghum genomes. Most (266/280) of the maize DNA fragments hybridized to sorghum DNA and 145 of them detected polymorphisms. The segregation of 111 markers was analyzed in 55 F_2 progeny. A genetic map was generated with 96 loci arranged in 15 linkage groups spanning 709 map units. Comparative genetic mapping of sorghum and maize is complicated by the fact that many loci are duplicated, often making the identification of orthologous sequences ambiguous. Relative map positions of probes which detect only a single locus in both species indicated that multiple rearrangements have occurred since their divergence, but that many chromosomal segments have conserved synteny. Some sorghum linkage groups were found to be composed of sequences that detect loci on two different maize chromosomes. The two maize chromosomes to which these loci mapped were generally those which commonly share duplicated sequences. Evolutionary models and implications are discussed.

Key words: Maize-Sorghum-Restriction fragment length polymorphism – Genetic maps – Inversion – Translocation – Duplication

Introduction

Sorghum (*Sorghum bicolor*) is an important crop plant that, after decades of genetic and breeding research, lacks a well-developed genetic map. Over 200 morphological and agronomically important markers have been identified, but only five linkage groups have been established. The biggest linkage group contains ten linked loci (Doggett 1988). Until recently, the development of genetic maps for plants was slow due to difficulties in constructing multiply marked lines. The development of restriction fragment length polymorphism (RFLP) technology has significantly eased this problem. This method has been used to construct detailed genetic maps of many plant species (Apuya et al. 1988; Beavis and Grant 1991; Bernatsky and Tanksley 1986; Burr et al. 1988; Chang et al. 1988; Coe et al. 1987; Ellis et al. 1992; Gebhardt et al. 1989; Helentjaris et al. 1986, 1988; Landry et al. 1987; McCouch et al. 1988; Nam et al. 1989; Slocum et al. 1990; Song et al. 1991) and has enabled geneticists to initiate the comparative mapping of related species that could lead to a better understanding of plant genome evolution (Binelli et al. 1992; Bonierbale et al. 1988; Gebhardt et al. 1991; Liu et al. 1992; McGrath and Quiros 1991).

Sorghum is a close relative of maize (*Zea mays*) and sugarcane (*Saccharum species*) (Springer et al. 1989). Of these three, maize is the best characterized and has a well-developed genetic map (Beavis and Grant 1991; Burr et al. 1988; Helentjaris et al. 1986, 1988). Sorghum and maize are members of the tribe Andropogonae in the family Gramineae (Smith 1977) and share the same basic chromosome number (n = 10). Maize, however, has at least 3 times more nuclear DNA than sorghum (Laurie and Bennett 1985; Michaelson et al. 1991). Mapped maize DNA probes are available, and restriction fragment length polymorphisms have been used to generate genetic maps (Beavis and Grant 1991; Burr et al. 1988; Coe et al. 1987; Helentjaris et al. 1986), to identify and position quantitative traits (Grant et al. 1989), and to estimate genetic distances between related species

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(Springer et al. 1989) and between various maize lines (Lee 1989; Livini et al. 1992). We have previously shown (Hulbert et al. 1990) that low copy number DNA fragments from maize generally hybridize well to sorghum DNA and can therefore be used to generate a genetic map of sorghum. In this paper, we present an expanded data set and make structural comparisons of the sorghum and maize genome based on the hybridization of maize probes to sorghum DNA.

Materials and methods

Genetic mapping population

An F_2 population was derived from a cross between sorghum cv 'Shanqui red' (a kaoliang cultivar from Northern China) and 'M91051' (a zera cultivar from East Africa). Field-grown F_1 and F_2 individuals were bagged prior to anthesis to prevent outcross contamination and allowed to self-fertilize.

DNA extraction and gel blot analysis

DNA from 30-day-old seedlings of pooled F_3 families was extracted, blotted and hybridized as described previously (Hulbert et al. 1990). Pooled F_3 families were generated to provide an "immortal" population for subsequent marker analyses and because higher quality DNA preparations can be derived from sorghum seedlings than from mature plants. Blots were washed at 65 °C with 0.5 × SSC, 0.1% SDS prior to autoradiography. Probes were screened for their ability to detect polymorphism by hybridization to gel blots carrying DNA of the two parental lines digested with each of seven enzymes: *Bam*HI, *Eco*RI, *Eco*RV, *Hin*dIII, *Xba*I, *Xho*I, and *Sac*I. If more than a single enzyme digest revealed polymorphisms between the parents, that with the most easily distinguished alleles was used to score the progeny.

Segregation analysis

Results for DNA samples representing 55 F_2 progeny were analyzed with the Linkage-1 program (Suiter et al. 1983) as described previously (Hulbert et al. 1990).

DNA probes

Plasmids containing maize RFLP probes were generously supplied by D. Hoisington, University of Missouri, Columbia (BNL, UMC) and D. Grant, Pioneer Hi-Bred International (NPI, PIO). Clones of characterized maize genes, beyond those previously described (Hulbert et al. 1990) were kindly provided by A.L. Kriz, University of Illinois-Urbana (clones of chitinase and B-1,3-glucanase cDNAs); J.C. Walker, University of Missouri-Columbia [a 2.7-kb *Eco*RI/*Eco*RV fragment of a protein kinase cDNA (Walker and Zhang 1990)]; K. Cone, University of Missouri-Columbia (a 250-bp *Hin*dIII/*Eco*RI genomic fragment specific to *C1*, a 1.1-kb *Hin*dIII/*Eco*RI genomic fragment specific to *Pl*, and a 1.5-kb *Eco*RI cDNA fragment for *trpB synthase*); P. Chourey, University of Florida-Gainseville (a 2.5-kb *Eco*RI fragment of a *sucrose synthase*-2 (*Su2*) cDNA (Gupta et al. 1988)); R.J. Schmidt, University of California-San Diego [a 285-bp *Pst*I/*Sal*I cDNA clone of *O2* (Schmidt et al. 1990)]; B. Burr, Brookhaven National Laboratory (a 1.5-kb *Hin*dIII/*Eco*RI cDNA fragment of *phy1*); S. Hake, University of California-Berkeley [a *Kn1* genomic clone (Hake et al. 1989)]; and E. Groetwald/T. Peterson, Cold Spring Harbor Laboratory (a chalcone flavanone isomerase cDNA clone).

Table 1. The number and distribution of RFLP probes used to characterize sorghum

Chromosome	Number used	Number polymorphic	Polymorphic/Nonpolymorphic	
			L-arm	S-arm
1	42	22	12/11	10/9
2	27	16	9/5	7/6
3	33	21	15/6	6/6
4	16	5	4/7	1/4
5	32	14	6/8	8/10
6	23	13	11/6	2/4
7	26	18	14/8	4/0
8	22	9	6/10	3/3
9	24	18	8/5	10/1
10	18	9	5/3	4/6

Clones KSU3, H^+ATPase (the maize plasma-membrane proton ATPase), PBS4.0, and PBS5.5 are maize DNA fragments that we have isolated in our laboratories. Clones representing two sorghum gene families were also utilized in our studies: the genes that encode phosphoenol pyruvate carboxylase (PEPC) (Cretin et al. 1990a) and malate dehydrogenase (MDH) (Cretin et al. 1990b), kindly provided by C. Cretin, Laboratoire Physiologie Vegetale Moleculaire, Universite Paris-Sud.

The genomic distribution, in maize, of the probes employed is presented in Table 1, as are the levels of polymorphism detected between the two parental lines for these probes.

Results

Hybridization of maize probes to sorghum DNA

Most of the maize probes that we employed were found to efficiently hybridize with DNA from the two sorghum lines examined. Of 280 probes used, only 14 did not hybridize detectably to sorghum. Of those that did hybridize, 145 detected polymorphism when hybridized to DNA of the two parental lines. Of the seven restriction enzymes employed, the most successful in identifying polymorphisms between these parents were *Hin*dIII (13.8%), *Eco*RI (11.2%), *Eco*RV (9.0%), and *Xba*I (9.0%). These four enzymes accounted for 70.5% of the polymorphisms detected. The enzyme least effective in detecting polymorphism was *Xho*I (3.7%).

Generation of a sorghum genetic map

Co-segregation of 111 RFLP probes was analyzed on the Linkage-1 program (Suiter et al. 1983). From this analysis, we were able to link 96 markers into 15 linkage groups containing from 2 to 20 linked loci each, spanning a total of 709 map units (Fig. 1). The largest of these linkage groups encompasses 138 map units. Fifteen RFLP loci were not significantly linked to any other markers. Only loci which were estimated to map within 26 recombination units of each other were considered to

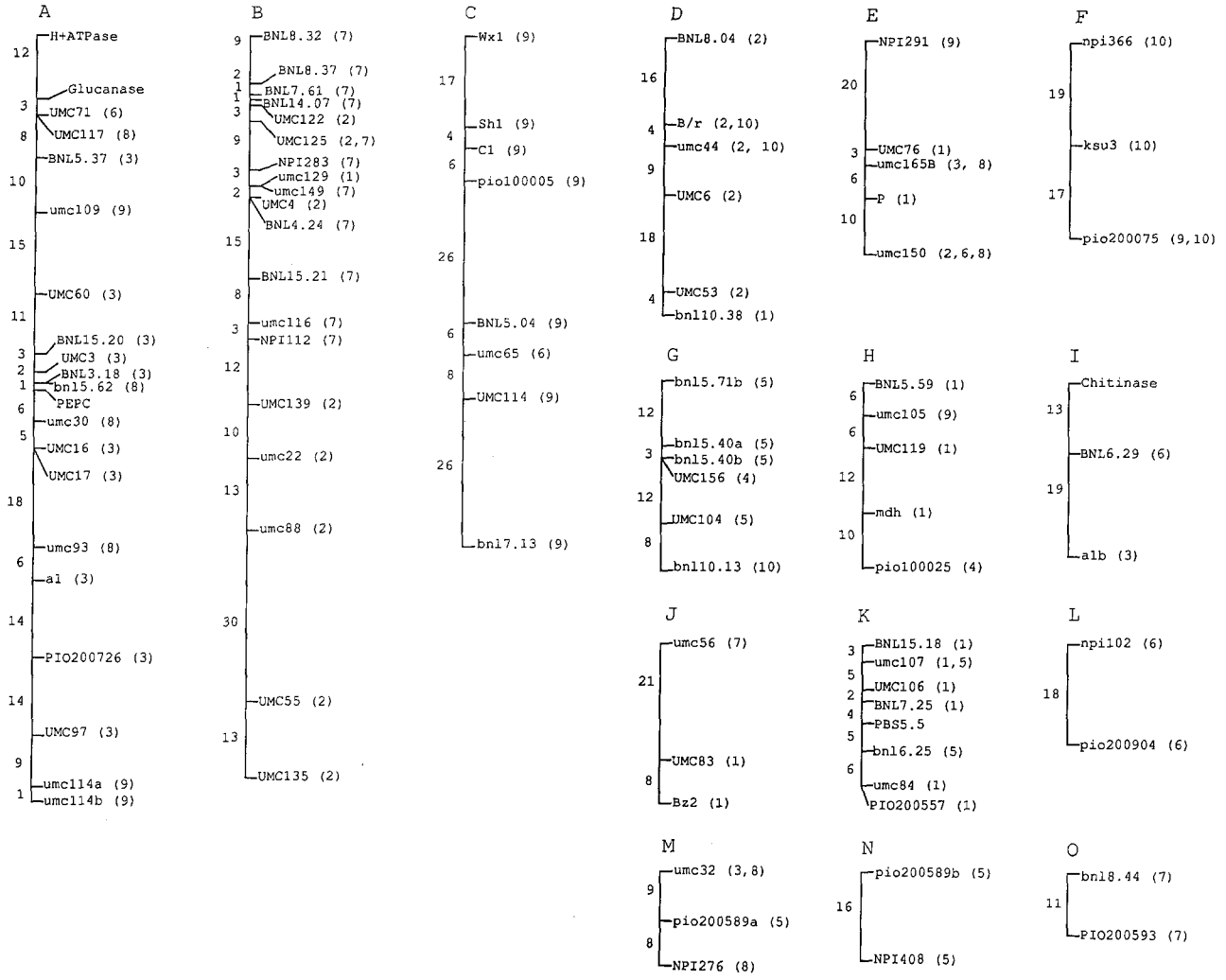

Fig. 1. Linkage relationships of sorghum loci identified by maize DNA probes. *Vertical lines* represent groups of linked loci. *Numbers* to the *left* lines are estimates of recombination distance. *Characters* to the *right* of the lines represent the maize (or sorghum) probes used to identify sorghum RFLP loci. *Lowercase letters* in the BNL, KSU, NPI, PIO, or UMC prefixes are used when the orthology of the locus to the mapped maize locus was not certain (see text and Hulbert et al. 1990). *Numbers in parentheses* to the *right* of the locus designations indicate the maize chromosome(s) to which this maize probe was mapped

be linked. The probability of 2 linked genes exhibiting this level of linkage was very low ($P<0.002$). In one case (markers umc88 and UMC55 in linkage group B), a linkage of 30 map units was presented ($P<0.017$) because this gene order agreed with the gene order in maize.

Of all the probes that detected polymorphism between our two parental lines, only 24 RFLP probes identified single loci (i.e., single hybridizational bands in a homozygous individual) in both sorghum and maize. As observed previously (Hulbert et al. 1990), the majority of DNA probes that gave two or more bands in maize also gave two or more bands in sorghum. Our expanded data set confirms that the sorghum genome, like that of maize (Helentjaris et al. 1988; Wendel et al. 1986), is duplicated for most RFLP probes.

Comparison of the maize and sorghum genetic maps

Comparative analysis of gene arrangement in maize and sorghum is complicated by the presence of duplicated sequences. When a single RFLP probe detects 2 loci either in maize or sorghum, it is difficult to determine whether the locus segregating in the sorghum population is orthologous to the locus that was mapped in maize. Both copies of some of the loci that are duplicated in maize have been mapped, but this was rarely possible in sorghum since both loci were not often polymorphic in this single population. Most of the RFLP loci that identify a single locus in maize, however, also identified a single locus in sorghum. These loci were useful in making genomic comparisons and are represented by uppercase

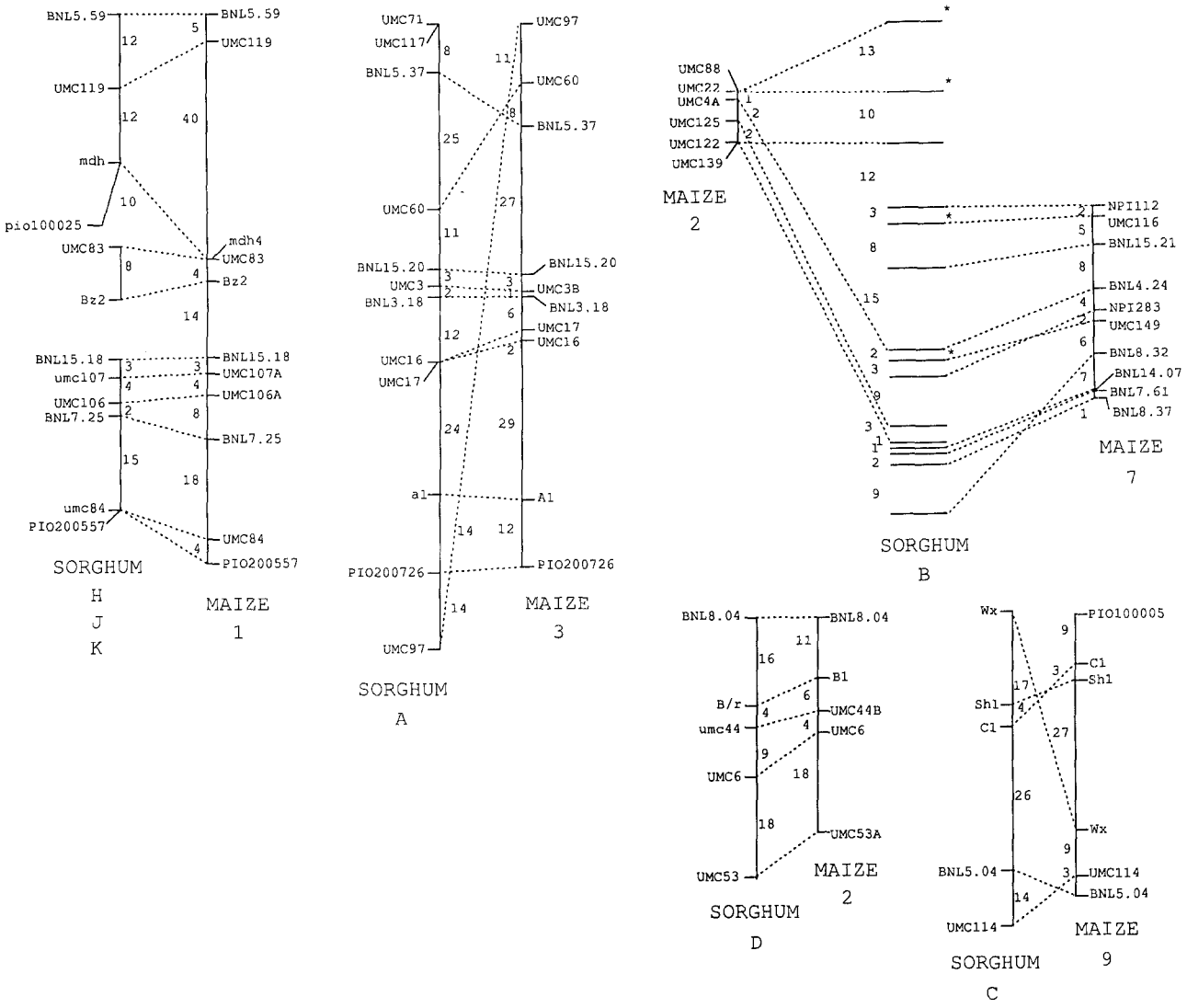

Fig. 2. Comparative map of maize and sorghum linkage groups constructed with maize DNA probes. *Vertical lines* represent linked loci in each species; *dotted lines* connect homeologous loci in maize and sorghum. *Numbers between* the vertical lines are estimates of recombination distances for the sorghum linkage groups and map distances (cM) for the maize map. The sorghum linkage groups are identified by A, B, C, D, H, J, or K, indicating their designation in Fig. 1. Each maize linkage group is identified by chromosome number; 1, 2, 3, 7, or 9. *Lowercase letters* in BNL, NPI, PIO, and UMC prefixes are used in sorghum when the orthology of the locus to the maize locus mapped was not certain (see text). *Asterisks above* the line indicate a lack of clear orthology in the comparison between sorghum linkage group B and maize chromosomes 2 and 7

letters in the prefixes of their locus designations (BNL, NPI, PIO or UMC) in Figs. 1 and 2. Loci were also given uppercase designation if they hybridized much more intensely to a single band in maize and a single polymorphic band in sorghum than they did to one or more additional bands (Hulbert et al. 1990).

When the map positions of such loci in sorghum were compared to their map positions in maize, regions of gene synteny were usually observed. For instance, linkage groups K, D, and most of A appeared to be fully collinear with chromosome arms IL, 2S, and 3L of maize, respectively (Fig. 2). In rare cases, only a single probe conflicted with a collinear gene arrangement between maize and sorghum. In three previous cases we have seen these conflicts removed by improvements in the maize map. For this reason, and because the large numbers of clones involved can lead to trivial handling and storage errors, we did not seriously evaluate apparent rearrangements based on the results with a single probe. For instance, UMC97 maps at the opposite ends of a long (about 100 map unit) stretch of collinear loci between chromosome arm 3L of maize and our linkage group A (Figs. 1, 3). Although a number of models could explain these data, the placement of UMC96 in maize at the position we find UMC97 in sorghum suggested a likely trivial explanation.

Some rearrangements of the sorghum genome relative to maize were obvious. For example, the linkage group (C) that mostly contained loci from maize chromosome 9 exhibited an inversion in the short arm and possible rearrangement of the long arm (Figs. 1, 2). In other linkage groups, comparison of the gene order revealed a number of probable rearrangements, including a few translocations. For instance, the different linkage groups of sorghum (H, J, K) mostly identified by probes from maize chromosome 1 (Fig. 2) demonstrated collinearity between the two species in those regions. However, *Mdh4* and UMC83 are very tightly linked in maize, while the *mdh* and UMC83 RFLP probes were not found to be linked in sorghum. This might be due to the fact that we mapped a sorghum MDH gene clone (Cretin et al. 1990b) that was not mapped in maize and, therefore, we are not certain if these two genes are orthologous. More likely, however, a translocation has occurred with a breakpoint between this MDH gene and UMC83. Another apparent chromosomal rearrangement between maize and sorghum was a probable translocation (and possible adjacent inversion) that differentiates our linkage group A (which terminated with a probe mapping to chromosome 6) and maize chromosome arm 3L (Fig. 2).

Linkage group B (Figs. 1, 2) was detected by a number of probes from maize chromosomes 2 and 7. However, within this linkage group, linear arrangement of the majority of loci in both chromosome 2 and 7 was the same in sorghum as in maize. These probes all come from the long arms of the respective maize chromosomes.

Discussion

Analysis of the sorghum genome with maize DNA probes identified similarities in the two chromosome sets. Despite having a three- to fourfold smaller genome than maize (Laurie and Bennett 1985; Michaelson et al. 1991), sorghum has sequences homologous to the large majority of maize RFLP and gene probes. Hence, the DNA sequences missing from sorghum, relative to maize, are not the low copy number DNAs that comprised the probes used in this study.

Genes and other probes commonly detected 2 loci in both maize and sorghum, although one often hybridized less strongly than the other. Loci that are duplicated in maize were more likely to be duplicated in sorghum, while those that exist in only a single copy in maize generally also did so in sorghum. The map positions of duplications in maize imply that large segments of the genome were duplicated together; different duplicated loci are often tightly clustered in two areas of the genome. The segments that share duplicated sequences may reflect what were once homeologous chromosomes following duplication of the whole genome by a polyploidization event.

There are two interesting anomalies in our general mapping results: first, the number (15 out of 111) of polymorphic probes that are unlinked to any other marker and, second, the number (8 out of 20) of maize chromosome arms that are unrepresented in the 15 linkage groups in sorghum. Studies with even fewer probes and smaller populations than those we have employed were able to generate maps that covered most of the genome of maize (Helentjaris et al. 1986). By contrast, we found no homeologous linkage group in sorghum (of any size) that included maize probes from chromosome 4 or arms 3S, 5S, 7S, 8L, 9L, and 10L. Moreover, in no case were we able to unambiguously link markers on opposite sides of any centromere, assuming that centromeres are placed in homologous positions in the two species. This was particularly surprising because we made use of the developed maize map to specifically select probes that would provide broad genomic coverage and, later in the study, to fill in identified gaps in the sorghum map. It is not clear whether our lack of success in linking together much of the sorghum genome indicates a very large genetic size for the sorghum genome, an exceptional degree of as-yet-undetected genetic rearrangement in maize as compared to sorghum, the conservative nature of our linkage assignments, or a combination of these factors. Although some chromosome arms (e.g., 4S and 6S) exhibited a lower percentage of probes that detected polymorphism than did others (e.g., 3L, 6L, and 9S), this cannot fully account for our map deficiencies.

At an absolute minimum, the 15 unlinked markers in our study indicate the existence of at least 400 cM of sorghum DNA that we have not linked to any other markers. Most probably, we have covered less than one-half of the sorghum genetic map, and our linkage groups of 709 map units would suggest that the sorghum genome will contain at least 1400 cM of chromosomal DNA. This is in general agreement with the genetic size of many higher plants, including maize.

Comparision of the maize and sorghum genomes is complicated by the presence of duplicated loci, which often make the determination of orthologous loci ambiguous. Probes which identify single loci in both species, however, are most likely orthologous. Comparative mapping of such loci identified large genomic segments that appear to be conserved in gene order within the two species. Simple inversions and translocations were detected, but these have been relatively rare to this point in our analysis. Sorghum and maize differ by more genetic rearrangements than do tomato and potato (Bonierbale et al. 1988), but fewer differences are seen than those between tomato and pepper (Tanksley et al. 1988). Different levels of detected rearrangements could be due to differences in the time since divergence and/or to differ-

ent rates of genetic rearrangement in these species. One maize/sorghum change, the inversion on the short arm of chromosome 9, apparently differentiates maize from an even more closely related species, *Zea mexicana* (Ting 1958). Since the teosinte *Z. mexicana* and *S. bicolor* appear to have the same 9S structure, this inversion probably occurred uniquely and recently in the evolution of *Zea mays*. Similar analyses of chromosome organization amongst the Andropogonae, using common maize probes, should allow further delineation of the timing, source, and direction of the chromosomal rearrangements that have punctuated the descent of the current Andropogonae species.

Certain areas of the sorghum genome that (at first glance) appear scrambled when compared to maize were found to be composed of RFLP loci that mapped to only two different maize chromosomes. For example, linkage group B was composed of loci from maize chromosomes two and seven. Interestingly, these linkage groups often reflect the patterns by which genome duplications occur in the maize genome. Chromosomes two and seven commonly share duplicated sequences in maize (Helentjaris et al. 1988). It is not clear why these chromosomes should reflect the patterns of genomic duplication in maize. This might be expected if a common ancestor underwent an amphidiploidization and if translocations between the two homeologous or partially homeologous chromosomes were common during the evolution of the two modern genomes. Translocations between homeologous chromosomes may be more common than other translocations if ectopic recombination between related DNA sequences were involved. An alternative explanation that does not require numerous translocations between homeologous chromosomes is also possible. After progenitor chromosomes were duplicated, two copies of every gene would probably not always be required. Hence, one of the copies would be free to mutate. The nonfunctional copy could then acquire sequence changes or deletions until it was no longer detectable by gel blot hybridization analysis. Since this evolutionary "decay" of one of the two copies of many genes in the post-polyploid era would presumably have been a random event, either gene might have been lost after the species separated. Two such modern genes might map to chromosomes two and seven in maize but still be linked in sorghum if the two copies that were lost in sorghum were both from the same duplicated chromosome.

The presence of genomic segments with conserved gene synteny between maize and sorghum indicates that genetic mapping in sorghum using maize probes will be a good method of estimating whether genes controlling morphological traits in sorghum are orthologous to characterized maize genes. This would be most convincing for loci spanned by markers that are collinear in maize and sorghum. For example, if a locus controlling plant pigmentation in sorghum was found to be flanked by RFLP loci detected by the BNL8.04 and UMC6 probes, it is likely to be orthologous to the *B* locus of maize. Similarly, if a rust resistance locus was found to be flanked by KSU3 and PIO200075 in sorghum, it may be orthologous to the *Rp1* locus of maize.

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References

Apuya N, Keim GL, Roth P, Lark KG (1988) Restriction fragment length polymorphisms as genetic markers in soybean, *Glycine max* (L) Merrill. Theor Appl Genet 75:889–901

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

Bernatsky R, Tanksley SD (1986) Toward a saturated linkage map in tomato based on isozymes and random cDNA sequences. Genetics 112:887–898

Binelli G, Gianfranceschi L, Pe 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

Bonierbale MW, Plaisted RL, Tanksley SD (1988) RFLP maps based on a common set of clones reveal modes of chromosomal evolution in potato and tomato. Genetics 120:1095–1103

Burr B, Burr FA, Thompson KA, Albertson MC, Stuber CW (1988) Gene mapping with recombination inbreds in maize. Genetics 118:519–526

Chang C, Bowman JL, DeJohn AW, Lander ES, Meyerowitz EM (1988) Restriction fragment length polymorphism linkage map for *Arabidopsis thaliana*. Proc Natl Acad Sci USA 85:6856–6860

Coe EH Jr, Neuffer MG, Hoisington DA (1987) The Genetics of corn. In: Sprague GF, Dudley J (eds), Corn and corn improvement, 3rd edn. Am Soc Agron. Madison, Wis., pp 81–258

Cretin C, Keryer E, Tagu D, Lepiniec L, Vidal J, Gadal P (1990a) Complete cDNA sequences of *sorghum* phosphoenolpyruvate carboxylase involved in C4 photosynthesis. Nucleic Acids Res 18:658

Cretin C, Luchetta P, Joly C, Decottignies P, Lepiniec L, Gadal P, Sallantin M, Huet JC, Pernollet JC (1990b) Primary structure of sorghum malate dehydrogenase (NAPD) deduced from cDNA sequence: homology with malate dehydrogenases (NAD). Eur J Biochem 192:299–303

Doggett H (1988) Sorghum. Longman Singapore Publ, Singapore

Ellis THN, Turner L, Hellens RP, Lee D, Harker CL, Enard C, Domoney C, Davis RD (1992) Linkage maps in pea. Genetics 130:649–663

Gebhardt C, Ritter E, Debener T, Schachtschabel U, Walkemeier B, Uhrig H, Salamini F (1989) RFLP analysis and linkage mapping in *Solanum tuberosum*. Theor Appl Genet 78:65–75

Gebhardt C, Ritter E, Barone A, Debener T, Walkemeier B, Schachtschabel U, Kaufmann H, Thompson RD, Bonier-

bale MW, Ganal MW, Tanksley SD, Salamini F (1991) RFLP maps of potato and their alignment with the homoeologous tomato genome. Theor Appl Genet 83:49–57

Grant D, Nelson W, Blair D, Katt ML, Martich J, Smith JSC, Bowen SL, Tenborg RA, Fincher RR, Meier R, Beavis WD, Smith OS (1989) Identification and localization of loci affecting yield and other agronomic traits in maize. In: Helentjaris T, Burr B (eds) Development and application of molecular markers to problems in plant genetics. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, N.Y., pp 135–138

Gupta M, Chourey PS, Burr B, Still PE (1988) cDNAs of two non-allelic sucrose synthase genes in maize: cloning, expression, characterization and molecular mapping of the *sucrose synthase*-2 gene. Plant Mol Biol 10:215–224

Hake S, Vollbrecht EV, Freeling M (1989) Cloning *Knotted*, the dominant morphological mutant in maize, using *Ds2* as a transposon tag. EMBO J 8:15–22

Helentjaris T, Slocum M, Wright S, Schaefer A, Nienhuis J (1986) Construction of genetic linkage maps in maize and tomato using restriction fragment length polymorphisms. Theor Appl Genet 72:761–769

Helentjaris T, Weber D, Wright S (1988) Identification of the genomic location of duplicate nucleotide sequences in maize by analysis of restriction fragment length polymorphisms. Genetics 118:353–363

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

Landry BS, Kesseli RV, Farrara B, Michelmore RW (1987) A genetic map of lettuce (*Lactuca sativa* L.) with restriction fragment length polymorphism, isozyme, disease resistance and morphological markers. Genetics 116:331–337

Laurie DA, Bennett MD (1985) Nuclear DNA content in the genera *Zea* and *Sorghum*. Intergeneric, interspecific and intraspecific variation. Heredity 55:307–313

Lee M (1989) Molecular genetic diversity among maize inbred lines: taxonomic and plant breeding implications. In: Helentjaris T, Burr B (eds) Development and application of molecular markers to problems in plant genetics. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, N.Y., pp 69–720

Liu CJ, Atkinson MD, Chinoy CN, Devos KM, Gale MD (1992) Nonhomoeologous translocations between group 4, 5 and 7 chromosomes within wheat and rye. Theor Appl Genet 83:305–312

Livini C, Ajmone-Marsan P, Melchinger AE, Messmer MM, Motto M (1992) Genetic diversity of maize inbred lines within and among heterotic groups revealed by RFLPs. Theor Appl Genet 84:17–25

McCouch SR, Kochert G, Yu ZH, Wang ZY, Kush GS, Coffman WR, Tanksley SD (1988) Molecular mapping of rice chromosomes. Theor Appl Genet 76:815–829

McGrath JM, Quiros CF (1991) Inheritance of isozyme and RFLP markers in *Brassica campestris* and comparison with *B. oleracea*. Theor Appl Genet 82:668–673

Michaelson MJ, Price HJ, Ellison JR, Johnston SJ (1991) Comparison of plant DNA contents determined by Feulgen microspectrophotometry and laser flow cytometry. Am J Bot 78:183–188

Nam HG, Giraudat J, Boer B den, Moonan F, Leos WDB, Hauge BM, Goodman HM (1989) Restriction fragment length polymorphism linkage map of *Arabidopsis thaliana*. Plant Cell 1:699–705

Schmidt RJ, Burr FA, Aukerman MJ, Burr B (1990) Maize regulatory gene opaque-2 encodes a protein with a "leucine-zipper" motif that binds to zein DNA. Proc Natl Acad Sci USA 87:46–50

Slocum MK, Figdore SS, Kennard WC, Suzuki JY, Osborn TC (1990) Linkage arrangement of restriction fragment length polymorphism loci in *Brassica oleracea*. Theor Appl Genet 80:57–64

Smith JR Jr (1977) Vascular plant families. Mad River Press. Eureka, Calif.

Song KM, Suzuki JY, Slocum KM, Williams PH, Osborn TC (1991) A linkage map of *Brassica rapa* (syn. *campestris*) based on restriction fragment length polymorphism loci. Theor Appl Genet 82:296–304

Springer PS, Zimmer EA, Bennetzen JL (1989) Genomic organization of the ribosomal DNA of sorghum and its close relatives. Theor Appl Genet 77:844–850

Suiter KA, Wendel JF, Case JS (1983) Linkage-1; a PASCAL computer program for the detection and analysis of genetic linkages. J Hered 74:203–204

Tanksley SD, Bernatzky R, Lapitan NL, Prince JP (1988) Conservation of gene repertoire but not gene order in pepper and tomato. Proc Natl Acad Sci USA 85:6419–6423

Ting YC (1958) Inversions and other characteristics of teosinte chromosomes. Cytologia 23:239–250

Walker JC, Zhang R (1990) Relationship of a putative receptor protein kinase from maize to the S-locus glycoproteins of *Brassica*. Nature 345:743–746

Wendel JF, Stuber CW, Edwards MD, Goodman MM (1986) Duplicated chromosome segments in maize (*Zea mays* L.): further evidence from hexokinase isozymes. Theor Appl Genet 72:178–185