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Genetics

Genetic mapping and characterization of sorghum and related crops by means of maize DNA probes

(genome structure/DNA duplication/genetic variation/chromosomal rearrangements/millet)

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ABSTRACT **Cloned DNA fragments from 14 characterized maize genes and 91 random fragments used for genetic mapping in maize were tested for their ability to hybridize and detect restriction fragment length polymorphisms in sorghum and other related crop species. Most DNA fragments tested hybridized strongly to DNA from sorghum, foxtail millet, Johnsongrass, and sugarcane. Hybridization to pearl millet DNA was generally weaker, and only a few probes hybridized to barley DNA under the conditions used. Patterns of hybridization of low-copy sequences to maize and sorghum DNA indicated that the two genomes are very similar. Most probes detected two loci in maize; these usually detected two loci in sorghum. Probes that detected one locus in maize generally detected a single locus in sorghum. However, maize repetitive DNA sequences present on some of the genomic clones did not hybridize to sorghum DNA. Most of the probes tested detected polymorphisms among a group of seven diverse sorghum lines tested; over one-third of the probes detected polymorphism in a single F_2 population from two of these lines. Cosegregation analysis of 55 F_2 individuals enabled several linkage groups to be constructed and compared with the linkage relationships of the same loci in maize. The linkage relationships of the polymorphic loci in the two species were usually conserved, but several rearrangements were detected.**

The tribe Andropogonae of the Gramineae contains several important crop species of which maize (*Zea mays*) is the best characterized genetically. Cloned maize DNA fragments that detect polymorphism and have been genetically mapped are available to the public (1–3). These probes have been used to generate a genetic map (1), to estimate evolutionary relationships between related species (4), and to estimate the genetic distance between various maize populations. Other crops of this group, such as sorghum (*Sorghum bicolor*) and sugarcane (*Saccharum* species), are less well characterized genetically despite their economic importance and decades of genetic and breeding research. Over 200 Mendelian characters have been identified in sorghum, but only a few small linkage groups have been established (5). Few genes have been molecularly characterized, and the genetic control of many relatively simple traits is not well understood.

If most maize restriction fragment length polymorphism (RFLP) probes hybridize sufficiently well to sorghum DNA, then it is possible to construct a genetic map of sorghum that can be directly compared to that of maize. Cloned DNA fragments that hybridize to single sites in the genomes of both species can be assumed to have arisen from a single sequence in a common ancestor. The genomic position of such orthologous (6) loci in each of the two species can be compared to outline the chromosomal rearrangements that have occurred during species divergence. Sorghum and maize have the same chromosome number ($n = 10$), but the nuclear DNA content of maize is over 3 times that of sorghum (7).

The utility of genetic mapping in related species with common RFLP probes has been demonstrated in some of the solanaceous crops (6, 8). Tomato (*Lycopersicon esculentum*), garden pepper (*Capsicum annuum*), and potato (*Solanum tuberosum*) all have the same basic chromosome number ($n = 12$) and the nucleotide sequences of most genes are conserved well enough to permit heterologous hybridization. While few differences were found between the tomato and potato genomes, numerous rearrangements characterized the linkage map of pepper.

The present study was undertaken to determine the feasibility of genetic mapping in sorghum with the use of maize RFLP probes, to initiate the construction of a detailed genetic map in sorghum, and to make comparisons between the maize and sorghum genomes wherever sufficient polymorphisms could be identified. These genomic comparisons are an important step in applying the rapidly advancing genetic technology of maize to sorghum.

MATERIALS AND METHODS

Plant Material. An F_2 population was derived from a cross between the sorghum cultivars Shanqui Red (a kaoliang cultivar from North Central China) and M91051 (a zera 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. Fifteen to twenty F_3 seedlings from each F_2 individual were pooled for DNA isolation.

Other sorghum lines used for RFLP analysis were P954114 (a zera zera cultivar of the durra-caudatum type), Arcola 27 (a broomcorn cultivar of the bicolor type), and the cultivars Framida (a kafir), Msumbite (a guinea type from southern Tanzania), and IS11167 (a durra type from Ethiopia). The representative maize line used was the inbred R168. Other species that were tested for hybridization to maize probes were *Setaria indica* (foxtail millet), *Pennisetum glaucum* (pearl millet), *Sorghum halepense* (Johnsongrass), and *Hordeum vulgare* (barley, cultivar Pike). Also tested was the sugarcane cultivar CP 70–321 (4).

DNA Isolation, Digestion, and Gel Blot Hybridization. DNA was prepared from 30-day-old seedlings from F_3 families by a procedure similar to that used by Saghai-Maroof *et al.* (9). Restriction enzymes were purchased from Bethesda Research Laboratories, New England Biolabs, or Boehringer Mannheim and used in a 5-fold excess under conditions specified by the supplier. Genomic DNAs (6–8 μg per lane) were digested with the appropriate restriction enzymes and

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Abbreviations: RFLP, restriction fragment length polymorphism; cM, centimorgan(s).

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fractionated in 0.8% agarose gels. The DNA was transferred to MSI blotting membrane and hybridized as described (10). Cloned maize DNA fragments were purified by agarose gel electrophoresis and labeled by random primer extension. Membranes were washed four times (30 min each) with 0.5× SSC/0.2% SDS (1× SSC = 0.15 M sodium chloride/0.015 M sodium citrate, pH 7.0) at 65°C prior to autoradiography.

Detection of Polymorphisms and Segregation Analysis. Cloned maize DNA fragments were hybridized to genomic blots containing DNA from the two parental sorghum varieties (Shanqui Red and M91051) independently digested with each of seven restriction enzymes (*Bam*HI, *Eco*RI, *Eco*RV, *Hin*dIII, *Xba* I, *Xho* I, and *Sac* I). Many of the clones that detected polymorphism were then used in a segregation analysis on 55 F_2 individuals derived from these two parental cultivars. To obtain DNA representative of each F_2 individual in a nondestructive manner, 15–20 F_3 seedlings from each F_2 individual were pooled. The resulting DNA samples were equivalent to that of the individual F_2 parent and also constituted a more permanent population. χ^2 goodness-of-fit values for segregation and independent assortment and maximum likelihood estimates of recombination frequency were calculated on an IBM XT personal computer with the LINKAGE-1 program (11). Recombination values and their standard errors were obtained for all possible pairs of loci. The linkage groups were deduced as the best fit to these values.

Probes Used for RFLP Analysis. Cloned maize DNA fragments that were used as probes consisted of either random, low-copy-number genomic fragments or clones of characterized genes. Cloned random genomic fragments were obtained from D. Hoisington, University of Missouri, Columbia. These clones are designated either UMC (University of Missouri, Columbia) or BNL (Brookhaven National Laboratory). Clones of characterized genes were obtained from various suppliers: H. Saedler provided a 4.3-kilobase (kb) *Eco*RI–*Hin*dIII genomic fragment of the *A1* locus (12), a 1-kb *Eco*RI fragment carrying part of the *C1* structural gene (13), and a 1.6-kb cDNA clone of the *C2* locus (14). A 3-kb genomic fragment carrying a maize actin clone was obtained from R. Meagher (15). The *Adh1* probe used was a 1.5-kb *Pst* I fragment of a cDNA clone provided by W. Gerlach and W. J. Peacock (16). A 0.8-kb *Pst* I genomic fragment of the *Bz1* locus (17) was provided by D. Furtek and O. Nelson. P. Starlinger and R. Kunze provided a 3-kb *Bgl* II genomic fragment of the *Bz2* gene (18) and a 16.3-kb *Bam*HI genomic fragment containing the *Sh1* locus (19). S. Wessler provided a cDNA clone carrying a 2.5-kb *Eco*RI fragment of the *Lc* component of the *R* locus (20) and a 10.8-kb *Eco*RI fragment carrying the *Wx* gene (21). A 0.4-kb *Sal* I–*Sac* I genomic fragment of the *P* locus was obtained from T. Peterson, Cold Spring Harbor Laboratories. The rDNA hybridization probe was provided by I. Rubenstein (22). A 0.6-kb cDNA clone (pZ19.1) of a gene encoding a 19-kDa zein was provided by B. Larkins (23). A 0.8-kb *Pst* I fragment of the *B* locus was provided by V. Chandler (24).

RESULTS

Conservation of DNA Sequence and Similarities in Gene Duplications in Maize and Sorghum. Nearly all of the maize clones tested hybridized to genomic blots of sorghum DNA under the hybridization conditions employed (see *Materials and Methods*). Of 105 clones tested, only 1 did not hybridize; 15–20 other probes hybridized ≈10 times more strongly to maize DNA than to sorghum DNA. Most of the remaining fragments (approximately two-thirds) hybridized as strongly, or nearly as strongly, to sorghum DNA as they did to maize DNA. Highly repetitive DNA present on some maize clones did not cross-hybridize with sorghum DNA (Fig. 1*D*).

Most of the probes detected more than one locus (Table 1) as indicated by the presence of more than one band in every enzyme digest. Generally one locus hybridized more strongly than the other, resulting in bands 2–10 times more intense (Fig. 1*C*). Probes that detected two loci in sorghum always detected two or more loci in maize. As in sorghum, one maize locus usually hybridized more strongly.

The detection of two loci with a single probe presents a problem in comparative gene mapping between the two species. Of the 48 probes that detected polymorphism and were mapped, only 11 identified a single locus in both maize and sorghum (Table 1, Fig. 1*B*). Unless a single locus is detected in each species by a given probe, it cannot be assumed that a locus mapped in one species is orthologous to one mapped in the other species. In most cases, only one of the two loci was polymorphic in our parental lines and, therefore, could be mapped in sorghum. Similarly, only one locus was usually mapped in maize, generally the locus that hybridized most strongly to the probe. When a probe hybridizes to one locus much more strongly than the other in both species, it is likely that the two loci that are more homologous to the probe are orthologous. Therefore, a RFLP mapped with a probe that detects either a single locus or a single strongly hybridizing locus in both species is designated by an uppercase prefix (UMC or BNL) in Fig. 2.

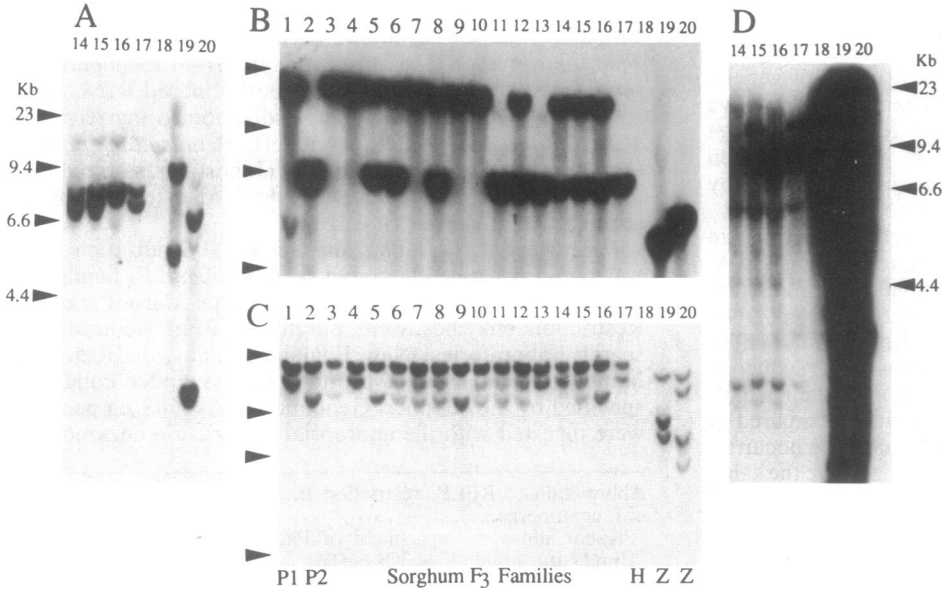

FIG. 1. Hybridization of several maize RFLP probes to maize and sorghum DNA. Each panel is an autoradiograph of a gel blot hybridized with a different maize RFLP probe: *Sh1* (*A*), UMC139 (*B*), UMC105 (*C*), and UMC107 (*D*). Lanes 1 and 2, DNA from the two parental sorghum lines; lanes 3–17, DNA from pooled seedlings from individual F_3 families; lanes 18, barley DNA; lanes 19 and 20, maize DNA. DNA in lanes 19 was digested with *Eco*RI; DNA in lanes 20, with *Hin*dIII; and DNA in lanes 1–18, with *Eco*RI (*A* and *B*), *Hin*dIII (*C*), or *Eco*RV (*D*).

Table 1. Patterns of hybridization of the maize RFLP probes mapped in sorghum

Hybridization to one locus in both maize and sorghum:
UMC4, UMC6, UMC94, UMC114, UMC117, UMC122, UMC139, BNL5.04, BNL5.59, BNL7.25, BNL15.21
Two loci in both maize and sorghum; one locus hybridized less strongly (10–50%) than the other:
UMC3, UMC22, UMC30,* UMC32, UMC53,§ UMC76, UMC83, UMC84,* UMC93,* UMC102,§ UMC103, UC129,§ UMC154, BNL5.62,† BNL15.20, *P*,* UMC105,† UMC107,† UMC125, *C1*‡
One sorghum locus and two maize loci; one of the maize loci hybridized less strongly:
UMC16, UMC60, UMC106, UMC116,* UMC119, UMC32
Two or more loci in both maize and sorghum; one maize band more intense, sorghum bands similar in intensity:
UMC81,* UMC97, *A1*,* *B*, *R*
Extensive hybridization to maize DNA, one or more loci in sorghum:
UMC55, UMC136, BNL7.61, *Bz2*, *Sh1*, *Wx*

*Hybridization to sorghum DNA was <25% as strong as that to maize DNA.

†Hybridization intensity of the maize loci appeared nearly equal in some digests. UMC105 probably detected more than two loci in maize (Fig. 1*C*).

‡Hybridization to multiple bands (>15) in maize and sorghum, but one band was more intense in both species.

§Probably more than two loci in maize and sorghum.

Linkage Mapping in Sorghum. Polymorphism was frequently detected between the two parental sorghum cultivars. About half (52/105) of the maize clones tested identified polymorphisms in at least one of seven enzyme digests. The frequency in which a given locus was polymorphic was about 30%, however, as most probes identified more than one locus, but only rarely was more than one locus polymorphic.

The level of polymorphism detected in sorghum was sufficient to establish several clusters or pairs of linked loci (Fig. 2) and permit the gene orders of these areas of the genome to be compared with that of maize. RFLP loci found to be linked in sorghum were generally also linked in maize, and clusters of linked genes were usually colinear with the maize linkage groups. RFLPs that were identified by probes that hybridized to more than one locus, however, frequently did not map to their expected position, particularly when more weakly hybridizing bands were mapped. For example, the probes UMC22, UMC102, UMC105, and UMC129 identified two loci each: an invariant, strongly hybridizing locus and a less strongly hybridizing polymorphic locus. In all four cases, the polymorphic locus did not cosegregate with the RFLP probes that identified closely linked loci in maize. We expect that the more strongly hybridizing locus that was invariant in the sorghum cross is orthologous to the locus mapped in maize. Following this result, only polymorphisms that were among the most strongly hybridizing bands were mapped. Of four RFLP probes that gave multiple bands in every digest of sorghum DNA (UMC95, UMC29, *C1*, and *C2*), only the *C1* polymorphism was mapped, as it was the only case where the most strongly hybridizing bands were polymorphic.

Fig. 2 shows the groups of linked genes established by cosegregation analysis. Most of the probes used to generate linkage groups a, b, c, and d identified loci on chromosome I of maize. The only exception was UMC105, which identified a locus on chromosome IX in maize. As mentioned above, this probe identified more than one locus and the locus mapped in maize is probably not orthologous to the one mapped herein. The gene order of the cluster of loci identified by UMC107, UMC106, BNL7.25, and UMC84 was completely conserved. Similarly, loci identified by UMC83 and a *Bz2* clone were tightly linked, as were UMC76 and a *P*-locus clone. The *Bz2*

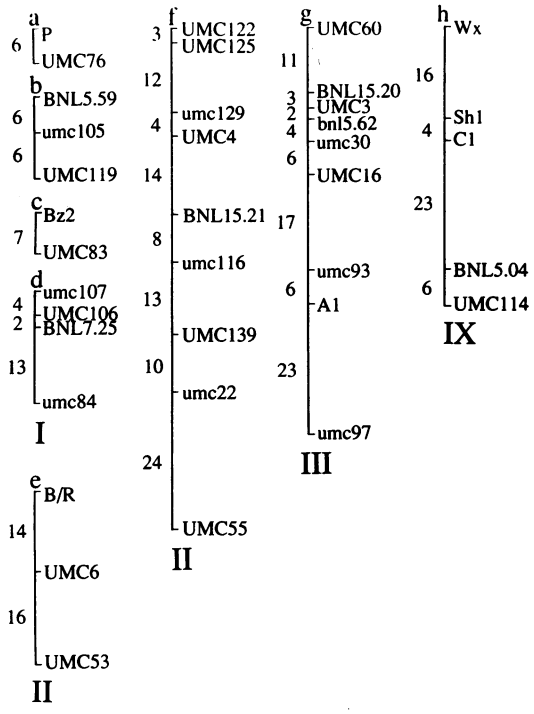

FIG. 2. Linkage relationships of sorghum loci identified by maize DNA probes. Vertical lines represent groups of linked loci (linkage groups a–h). Numbers to the left of the lines are estimates of recombination distance. Character to the right of the lines represent the maize probes used to identify loci. Lowercase letters in BNL or UMC prefixes of probe designations are used when the probe detected more than one locus with similar hybridization intensities in either maize or sorghum (umc97, umc105, umc107, bnl5.62), when more than one maize locus was observed but hybridization to sorghum was <25% the intensity of that to maize DNA (umc30, umc84, umc93, umc116), or when the more weakly hybridizing of two sorghum loci was mapped (umc22, umc129). Loci mapped with the *A1*-, *B*-, and *R*-locus clones also may not be orthologous to those loci in maize as these probes detected two or more loci in sorghum, all of which hybridized with similar intensities. The *B* and *R* loci do cross-hybridize in maize (24). Roman numerals indicate the maize chromosome to which most of the RFLP probes on the above sorghum linkage group have been mapped; they are not meant to imply associations of the sorghum linkage groups with sorghum chromosomes of any previous designation.

and *P* loci have not been formally placed on the RFLP maps of maize, but their positions on the classical genetic maps of maize predict them to be situated near these RFLP loci.

Maize loci homologous to UMC60, UMC3, UMC16, BNL15.20, and the *A1* locus belong on the long arm of chromosome III in maize. These loci constitute a nearly colinear linkage group in sorghum (Fig. 2, group g). The gene order of UMC3 and BNL15.20 may be inverted with respect to that in maize. The two markers are also very closely linked in maize [1 centimorgan (cM)], however, and the gene order of very closely linked markers is often difficult to determine unequivocally. Also included in this sorghum linkage group are loci homologous to UMC30, UMC93, and BNL5.62. The locus mapped in maize that is homologous to BNL5.62 is near the end of the short arm of chromosome I. Loci homologous to UMC30 and UMC93 in maize are on the long arm of chromosome VIII and are separated by about 10 map units. It is likely that the loci mapped in maize with these three probes are not orthologous to those mapped in sorghum; all three of these probes identified two or more loci in both species. In each case, the locus that was mapped in sorghum corresponded to the most strongly hybridizing bands. The UMC30 and UMC93 probes, however, hybridized much more strongly to maize DNA than to sorghum DNA, and the

sorghum bands they identified were similar in intensity to the weakly hybridizing bands in maize. The BNL5.62 probe hybridized strongly to sorghum DNA, but the two loci detected in maize were similar in hybridization intensity. Another locus, identified by UMC97, mapped 24 map units from the *A1* probe locus. In maize, this probe has identified a locus on the opposite side of this linkage group on the short arm of chromosome III. This result can again be explained by the fact that probe UMC97 identified two (or possibly three) loci of similar intensity, and the locus mapped herein may not be orthologous to the locus mapped in maize.

Another linkage group that is conserved, at least partially, between maize and sorghum was identified by the probes UMC114 and BNL5.04 and the cloned *Wx*, *Sh1*, and *C1* genes. All of these are found on chromosome IX in maize. The two RFLP probes were closely linked in maize (3 cM) as they were in sorghum and BNL5.04 mapped about 20 map units from *Wx*. The *Sh1* and *C1* genes also mapped close together in both species (3 cM in maize). In maize, however, these two loci mapped on the opposite side of *Wx* from UMC114 and BNL5.04, while in sorghum they mapped between *Wx* and the two RFLP loci (Fig. 2, linkage group h). The difference between the two species is most easily explained by postulating a paracentic inversion with one of the breakpoints between the *Wx–Sh1–C1* group and BNL5.04 and the other breakpoint distal to these three genes. The only other available probes that identified loci on chromosome IX of maize and detected polymorphism on our parental lines were UMC81, UMC94, and UMC105. As previously mentioned, the polymorphic locus detected by UMC105 in this sorghum cross is probably not orthologous to the gene mapped in maize. UMC94 mapped between *Wx* and *Sh1* in maize, and UMC81 mapped between *Wx* and BNL5.04. The UMC81 locus is probably not orthologous to the one mapped in maize, as the probe identified several bands of similar hybridization intensity of which only one was polymorphic. UMC94, however, detected only a single, strongly hybridizing locus in both maize and sorghum. The lack of cosegregation between UMC94 and *Wx* or *Sh1*, therefore, may represent another rearrangement in this area of the genome.

Sorghum linkage groups e and f (Fig. 2) showed evidence of several genomic rearrangements when compared with the maize map. Most of the probes used to construct these linkage groups identified loci on the long arm of chromosome II in maize. They occur in the following order, starting with the most distal: UMC22, UMC4, UMC122, UMC125, UMC139, UMC6, and UMC55. UMC53 mapped ≈140 map units from UMC55, on the short arm of maize chromosome II. In sorghum, UMC53 mapped only 16 map units from UMC6 (Fig. 2, linkage group e) and these segregated independently of the other maize chromosome II probes. A polymorphism detected by the *B*-locus clone also mapped to this linkage group. While the *B* locus mapped to chromosome II of maize, the *B*-locus clone identified more than one locus in sorghum (as it does in maize). This same locus, and others in sorghum, was detected by the *R*-locus probe.

UMC116 and BNL15.21 detected two linked loci on chromosome VII of maize but mapped in the middle of linkage group f in sorghum. This discrepancy between the two linkage groups may reflect a chromosomal rearrangement, as both probes detected only a single locus in sorghum (Table 1). It is possible that these loci are not orthologous, however, since the sorghum loci hybridized less strongly than the two maize loci. The UMC116 probe hybridized much less strongly to sorghum DNA (<20%), similar in intensity to a more weakly hybridizing, second maize locus. The BNL15.21 probe hybridized approximately 20–50% as strongly to sorghum DNA as to maize DNA. The loci marked by UMC129 and UMC22 also may not be orthologous to the loci mapped in maize using these probes, which mapped to maize chromosomes I and II, respectively; as mentioned above, they represent the segregation of the more weakly hybridizing band of two maize loci. Even if these probes do not mark orthologous loci in maize and sorghum, several rearrangements must be postulated to explain the differences in the linkage relationships of the remaining probes.

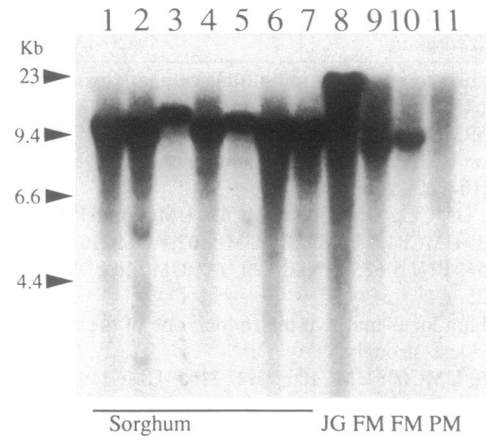

FIG. 3. Hybridization of a maize RFLP probe to DNA from related genera. Probe UMC130 was hybridized to *Eco*RI-digested DNA of seven sorghum lines (lanes 1–7), Johnsongrass (JG, lane 8), two foxtail millets (FM, lanes 9 and 10), and pearl millet (PM, lane 11). Sorghum lines in lanes 1–7 were two zera-zera types, a durra, a kafir, a guinea, a broomcorn, and a kaoliang type, respectively.

Diversity in Sorghum. Hybridization of 17 of the maize clones to several members of a diverse sorghum germ-plasm collection indicated that the high level of polymorphism that was detected between the two parental sorghum cultivars is representative of the diversity seen between some of the various types of sorghum (Fig. 3). Several probes that did not detect differences between the parental sorghum lines were tested on these other sorghum types and most of them detected polymorphisms. It was, however, possible to identify restriction fragments that were not polymorphic among any of the sorghum types tested.

Application of Maize RFLP Probes in Other Plant Species. The maize probes generally hybridized about as strongly to sugarcane and foxtail millet DNA as they did to sorghum DNA, but these probes generally hybridized less strongly to DNA from pearl millet and hybridized only occasionally to barley DNA (Fig. 3). With the exception of rDNA (4), none of the probes tested detected common restriction fragments between the sorghums, millets, or maize.

DISCUSSION

Several maize genomic clones that carried highly repeated sequences as well as low-copy sequences were used as hybridization probes. Such clones are not useful as RFLP probes in maize because of extensive hybridization to fragments from much of the genome. The repeated sequences did not hybridize with sorghum DNA, however, enabling single-copy sequences to be detected by the probes. This actually makes some maize DNA fragments easier to map in sorghum than in maize. This also suggests that the highly repeated sequences in the maize genome evolve at a higher rate than most lower-copy genomic sequences. A similar observation has been made for repetitive sequences of tomato (25).

The use of a single cross is the most efficient way to generate a genetic map, providing that a sufficiently polymorphic family can be generated. In very highly polymorphic species, such as maize, most RFLP loci can be mapped in a single intraspecific cross (3). In other species, such as tomato, interspecific crosses have been necessary to detect

sufficient polymorphism (2). The use of an intraspecific cross, when possible, should minimize the genetic distortion and error encountered (2, 8). Most of the loci analyzed in this study fit the expected 1:2:1 segregation ratio, and loci exhibiting small deviations were not consistently biased towards alleles of one parent. The parents used in this study were chosen on the basis of their morphological and geographical differences and provided acceptable levels of polymorphism for genetic mapping. A preliminary survey of a variety of sorghum cultivars indicated that similar, or possibly higher, levels of polymorphism could be obtained with other crosses between different sorghum races or types.

The presence of duplicated genes in maize has been observed for loci controlling morphological traits (26), isozyme loci (27), and RFLP loci (28, 29). The mechanism by which these duplications originated is not known, but mapping experiments with RFLP loci have indicated that they are usually duplicated on separate chromosomes and that large segments of different chromosomes sometimes contain these duplicated loci in the same linear order. We have found the frequency of duplicated DNA sequences in sorghum to be similar to that of maize. Nearly every RFLP probe that detected two loci in maize also detected two loci in sorghum. The exceptions, where only one sorghum locus was detected, were all cases where one of the maize loci hybridized more strongly than the other. These cases could be either due to the deletion of one of the copies or due to its sequence diverging until it no longer hybridized under the conditions employed. Maize lines in which sequences homologous to various RFLP probes have been deleted are rare, but several have been identified (30).

While many of the probes detected two loci in both species, only one of the loci was usually mapped in maize, and usually only one of the two loci was polymorphic in the sorghum lines assayed. In several cases, the locus mapped in sorghum did not cosegregate with the RFLP markers expected if it were orthologous to the locus mapped in maize and the genomes were colinear. In such cases, the locus mapped in sorghum is most likely orthologous to the unmapped duplicated sequence in maize. This conclusion is supported by the map positions of the RFLP loci, which did not map to their expected linkage groups in sorghum; they generally mapped to a position corresponding to a genomic area in maize that carries several duplicated loci in common with the area to which the maize polymorphism mapped. For example, a pair of loci on chromosome VIII in maize have been mapped with the probes UMC93 and UMC30, while these probes identified two sorghum loci in a cluster of loci detected by maize chromosome III probes. Similarly, two maize chromosome VII locus probes identified a pair of linked loci in a linkage group composed of mostly maize chromosome II probes. Chromosomes III and VIII of maize commonly share duplicated loci as do chromosomes II and VII (28, 29).

Several genetic maps of the maize genome have been independently developed by using RFLP probes (1–3, 29), many of which are available upon request. With approximately one-third of the corresponding sorghum RFLP loci polymorphic, it should be possible to cover most of the sorghum genome with markers by using these probes. Since the genomic position of these RFLP loci in the sorghum genome can often be predicted from their genomic positions in maize, it is possible to select clones for specific areas of the genome. There is bound to be a paucity of genetic markers in some areas of the genome, however, as even the maize genetic map has very few markers in certain regions.

While several of the linkage groups identified in sorghum were not completely colinear with those of maize, other clusters of genes retained the same linear order. The estimated linkage distances spanned by markers that appeared to be colinear in maize and sorghum and were precisely mapped in both species usually either were similar or were smaller in sorghum than in maize. The map distance spanned by these markers added up to 118 map units in maize and 71 map units in sorghum. If the area spanned by these probes is representative of the sorghum genome, then sorghum has a smaller genome than maize in terms of recombination as well as nuclear DNA content (7).

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