Mapping RFLP Loci in Maize Using B-A Translocations

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ABSTRACT

Plants hypoploid for specific segments of each of the maize (*Zea mays* L.) chromosomes were generated using 24 different B-A translocations. Plants carrying each of the B-A translocations were crossed as male parents to inbreds, and sibling progeny hypoploid or not hypoploid for specific chromosomal segments were recovered. Genomic DNAs from the parents, hypoploid progeny, and nonhypoploid (euploid or hyperploid) progeny for each of these B-A translocations were digested with restriction enzymes, electrophoresed in agarose gels, blotted onto reusable nylon membranes, and probed with nick-translated, cloned DNA fragments which had been mapped previously by restriction fragment length polymorphism (RFLP) analysis to the chromosome involved in the B-A translocation. The chromosomal segment on our RFLP map which was uncovered by each of the - B-A translocations was determined. This work unequivocally identified the short and long arms of each chromosome on this map, and it also identified the region on each chromosome which contains the centromere. Because the breakpoints of the B-A translocations were previously known on the cytological and the conventional genetic maps, this study also allowed this RFLP map to be more highly correlated with these maps.

CONSIDERABLE progress has been made by our group and other groups in constructing restriction fragment length polymorphism (RFLP) maps for maize. The high levels of polymorphism in the maize genome (BURR *et al.* 1983; RIVIN *et al.* 1983; HELENTJARIS *et al.* 1985; HELENTJARIS, WEBER and WRIGHT 1986) and the wealth of cytogenetic variants in maize (CARLSON 1977) have allowed this work to progress at a remarkably rapid rate. Currently, RFLP maps are being developed in maize by our group (HELENTJARIS, WEBER and WRIGHT 1986, 1988), and by B. BURR and F. BURR (BURR *et al.* 1988), D. HOISINGTON (HOISINGTON, COE and NEUFFER 1988), Agrigenetics (MURRAY *et al.* 1988), and Pioneer Hi-Bred Company (D. GRANT, personal communication). The establishment of linkage groups on RFLP maps is an exceedingly efficient process because most RFLP loci can be analyzed in a single segregating F_2 or testcross population. Furthermore, the chromosome associated with each linkage group can be efficiently determined utilizing monosomics (HELENTJARIS, WEBER and WRIGHT 1986). In fact, the number of RFLP loci mapped in maize by various groups now far exceeds the number of morphological and biochemical (isozymic) loci mapped on the conventional maize genetic map.

Unfortunately, RFLP maps in maize are poorly correlated with the conventional map at the present time. Certain maize loci, which were previously mapped on the conventional map, have been cloned by other investigators, and these cloned sequences have been used as probes and mapped on our RFLP map (HELENTJARIS, WRIGHT and WEBER 1986; WRIGHT, HELENTJARIS and KIKUCHI 1987). Also, certain morphological and isozymic loci have been mapped on our RFLP map by linkage analysis of segregating populations (HELENTJARIS, WRIGHT and WEBER 1986; HELENTJARIS, WEBER and WRIGHT 1988; M. EDWARDS, C. STUBER, T. HELENTJARIS and S. WRIGHT, unpublished results). Information from these experimental approaches has enabled us to correlate our RFLP map to a certain extent with the conventional maize genetic map. Other investigators have also taken advantage of cloned genes and isozymes to correlate their maps with the conventional linkage map.

Several different translocations between supernumerary (B) chromosomes and normal (A) chromosomes (B-A translocations) have been recovered in maize. These B-A translocations involve each of the maize A chromosomes, and in many cases, several different ones are available which have breakpoints at different positions on the same A chromosome. The breakpoints of many of these B-A translocations have been determined on both the cytological and conventional genetic maps (BECKETT 1978; HOISINGTON 1985).

The centromeres of B chromosomes often undergo nondisjunction at the second male gametophyte division (the second postmeiotic mitosis during pollen
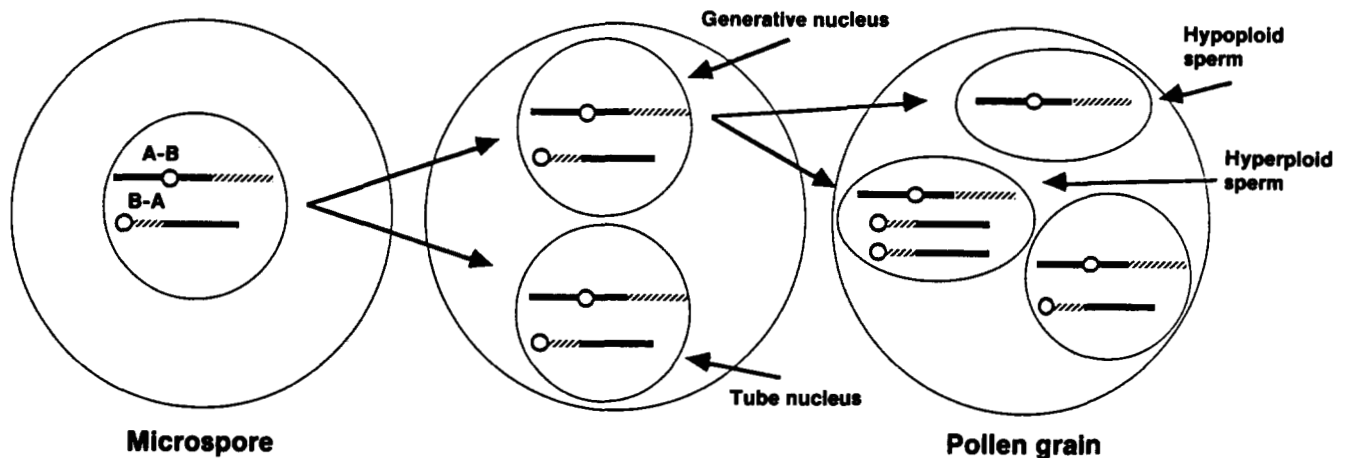
FIGURE 1.—Development of a pollen grain containing a B-A translocation. An A chromosome (shown as a solid line) was translocated with a B chromosome (shown as a slashed line) to produce an A-B chromosome (which contains the centromere of the A chromosome) and a B-A chromosome (which contains the B centromere). The B centromere frequently undergoes nondisjunction during the second male gametophyte division to produce a mature pollen grain containing an euploid tube nucleus, a hypoploid sperm, and a hyperploid sperm (modified from ROMAN 1947).

grain formation in which the generative nucleus divides to produce two sperm). An A chromosome segment translocated onto a B chromosome (a B-A chromosome) will be present in zero and two copies in the two sperm nuclei of a pollen grain in which the B centromere nondisjoined at this division (Figure 1). When haploid eggs produced by a diploid plant are fertilized by pollen grains of this type, kernels are produced containing embryos which are hypoploid or hyperploid for the translocated segment of the A chromosome. These embryos are accompanied by hyperploid and hypoploid endosperms, respectively. Kernels with euploid embryos and endosperms also are produced when normal disjunction of the B-A chromosome takes place. B-A translocations have been used extensively in maize to locate genes to chromosome arms and specific segments of arms (ROMAN and ULLSTRUP 1951; BECKETT 1978).

NEWTON and SCHWARTZ (1980), EVOLA, BURR and BURR (1986), and BURR et al. (1988) have demonstrated the usefulness of B-A translocations in mapping both isozymic and RFLP loci in maize. In the current study, the breakpoints of 24 different B-A translocations (involving 18 of the 20 chromosome arms) were determined on our RFLP map. The results (1) identify the short and long arms of each chromosome on the RFLP map, (2) identify the chromosomal regions which contain the centromeres on the RFLP map, and (3) allow a greater correlation of this RFLP map with the cytological and conventional genetic maps.

MATERIALS AND METHODS

Stocks: Inbreds Mo17, B14, B73 and B57 were obtained from the USDA Plant Introduction Center, Ames, Iowa. Stocks containing the B-A translocations analyzed in this study, and tester lines used to confirm each B-A translocation were generously provided by J. KERMICLE, University

TABLE 1

B-A translocations and testers

Translocation	Breakpoint(s)	Source	Tester
TB-1Sb	1S.05	PATTERSON	vp5
TB-1Sb-2L4464	1S.05–.53, 2L.28	PATTERSON	v4
TB-1La	1L.20	Stock center	bm2
TB-1La-4L4692	1L.20–.46, 4L.15	PATTERSON	c2
TB-3La	3L.10	PATTERSON	a1
TB-3La-2S6270	3L.10–.60, 2S.46	Stock center	lg1
TB-3Sb	3S.50	Stock center	h1
TB-4Sa	4S.25	PATTERSON	su1
TB-5Sc	5S.30	PATTERSON	a2
TB-5La	5L.10	Stock center	pr1
TB-6Sa	6S.50	Stock center	l11
TB-6Lc	6L.12	Stock center	py1
TB-6Lb	6L.65	PATTERSON	y1
TB-7Lb	7L.30	PATTERSON	gl1
TB-7Lb-4L4698	7L.30–.74, 4L.08	Stock center	c2
TB-8La	8L.70	PATTERSON	fl3
TB-9Sb	9S.40	PATTERSON	c1
TB-9Sb-4L6504	9S.40–.68, 4L.09	Stock center	c2
TB-9Sd	9S.08	Stock center	c1
TB-9Lc	9L.10	PATTERSON	v1
TB-9La	9L.40	Stock center	bm4
TB-10Sc	10S.30 or closer	PATTERSON	oy1
TB-10L19	10L.03	KERMICLE	r1
TB-10L36	10L distal to 0.03	KERMICLE	r1

of Wisconsin, Madison; E. PATTERSON, University of Illinois, Urbana; and the Maize Genetics Cooperation Stock Center, Urbana, Illinois. The source of each B-A translocation utilized in this study is indicated in Table 1.

Crosses: Plants containing 22 of the B-A translocations (all except TB-5Sc and TB-9Sd) were crossed as male parents to various lines by the individuals who provided them, and progeny of these crosses were the starting material for this study. Fifteen sibling progeny of crosses with each of these B-A translocations were planted as a family in a winter nursery in 1985–1986. Five nonhypoploid plants in each family were identified and crossed as male parents to plants carrying a recessive mutation located distal to the breakpoint of the B-A translocation in the A chromosome (between the

breakpoint and the end of the A chromosome arm). Progeny of these crosses were analyzed to (1) establish that the B-A translocation was correct and (2) to identify plants that were heterozygous for the complete B-A translocation. These same plants were also crossed as male parents to three genetically distinct inbreds (Mo17, B14 or B73, and B57). Plants were identified which contained each of the 22 B-A translocations, and progeny of these plants crossed as male parents to each of the three inbreds were grown in a summer nursery in 1986. Plants with 50% or greater pollen abortion and a smaller stature and/or a distinctive abnormal morphology were identified as hypoploids. The hypoploid plants were compared with their sibling plants that were not hypoploid (euploids or hyperploids) in each family.

Also, a plant heterozygous for TB-5Sc which carried a2 on chromosome 5 and A2 on the B-A chromosome was crossed as a male parent by an inbred female parent that was a2. Kernels from this cross with colorless endosperm and a purple embryo contained hyperploid embryos and had 22 chromosomes while colored kernels contained hypoploid or euploid embryos. Both kernel types were grown, and plants from kernels of the latter type with 20 chromosomes (hypoploids) and were compared with sibling hyperploids and a2 tester plants which were siblings of the plant used as the female parent. Similarly, a plant heterozygous for TB-9Sd which carried c1 on chromosome 9 and C1 on the B-A chromosome was crossed as a male parent by an inbred female that was c1. Kernels from this cross with colorless endosperm and a purple embryo were hyperploid and contained 22 chromosomes. Sibling colored kernels with 20 chromosomes were hypoploids. Hyperploids, hypoploids, and siblings of the c1 plant used as the female parent were sampled and analyzed.

Sources of samples: leaf samples from each of the inbreds (Mo17, B14, B57 and B73) and from each B-A-containing plant crossed as a male parent were harvested. Hypoploid and nonhypoploid (euploid or hyperploid) sibling progeny from crosses of B-A translocation-containing plants by inbreds were also harvested. All leaf samples were freeze-dried soon after they were harvested and stored at −20° until analyzed. Plants for analysis of TB-5Sc and TB-9Sd were grown in a greenhouse in 1988.

Other methods: All other methods for the preparation of plant DNA, Southern blots, and hybridization (aqueous with 5× SSC at 60°) and wash (0.25× SSC at 60°) conditions were as described previously (HELENTJARIS et al. 1985; 1986).

RESULTS AND DISCUSSION

Plants with each of the 24 B-A translocations were crossed as male parents to inbreds, and F$_1$ sibling hypoploid and nonhypoploid (euploid or hyperploid) progeny produced by these crosses were selected. DNAs were prepared from freeze-dried leaves of the parents and their hypoploid and nonhypoploid sibling progeny. These DNAs were analyzed by restriction fragment length analysis to determine the breakpoints of each of the B-A translocations on our RFLP map.

An example of such an analysis is shown in Figure 2. A plant containing TB-8La (which has its breakpoint at 0.70 in the long arm of chromosome 8) was crossed as a male parent to inbred Mo17. The parents, hypoploid progeny, and hyperploid progeny from this cross were analyzed. DNAs from each of these plant
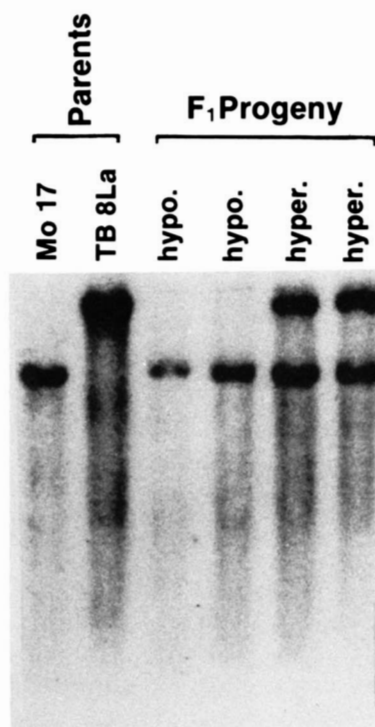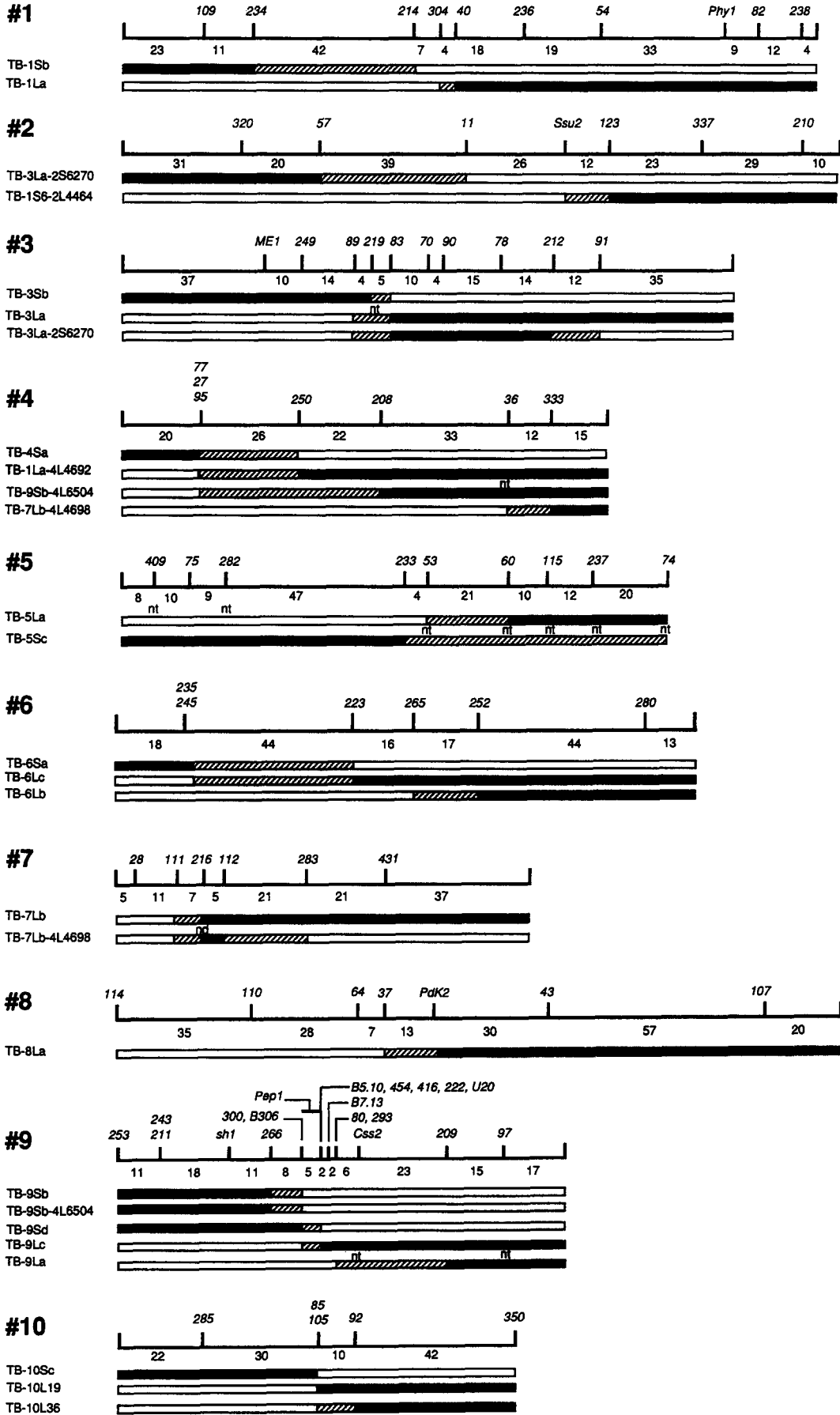

FIGURE 2.—Analysis of a clone with a B-A translocation. A plant containing TB-8La was crossed as a male parent to an inbred female parent, Mo17, and the sibling hypoploid and hyperploid progeny were identified. DNAs from these plants were digested with the restriction enzyme, SstI and analyzed on a Southern blot using clone #107. The two parents contain different RFLP alleles, and hyperploid progeny contain both alleles while hypoploid progeny only contain the allele from the female parent. Clearly, this locus is "uncovered" by TB-8La.

types were cut with the restriction enzyme, SstI, and analyzed using clone #107, which had been previously mapped by monosomic and linkage analysis on chromosome 8. This clone hybridizes with a slowly migrating restriction fragment in the parent carrying the B-A translocation and a more rapidly migrating fragment in the inbred, Mo17. Hyperploid F$_1$ progeny display both fragments while sibling hypoploid F$_1$ progeny (which lack the chromosomal segment from the male parent distal to the breakpoint in the long arm of chromosome 8) only display the fragment which was present in the female parent. Because the fragment from the male parent is not present in hypoploid progeny, the DNA sequence homologous to this probe must be located distal to the breakpoint in the long arm of chromosome 8. If it had been located proximal to this breakpoint on the long arm (between the breakpoint and the centromere), in the other arm of this chromosome, or in any other chromosome, the fragment from the male parent would have been present in both hypoploid and nonhypoploid progeny. To be consistent with descriptions used for morphological loci, we will indicate that this locus was "uncovered" by this B-A translocation because the

#1

109   234   214 304 40   236   54   Phy1 82 238

23   11   42   7 4 18   19   33   9 12 4

TB-1Sb
TB-1La

#2

320   57   11   Ssu2 123   337   210

31   20   39   26   12   23   29   10

TB-3La-2S6270
TB-1S6-2L4464

#3

ME1 249   89 219 83   70 90   78   212   91

37   10   14   4 5   10   4   15   14   12   35

TB-3Sb
TB-3La   nt
TB-3La-2S6270

#4

77
27
95   250   208   36   333

20   26   22   33   12   15

TB-4Sa
TB-1La-4L4692
TB-9Sb-4L6504   nt
TB-7Lb-4L4698

#5

409   75   282   233 53   60   115   237   74

8   10   9   47   4   21   10   12   20

TB-5La   nt   nt
TB-5Sc   nt   nt   nt   nt   nt

#6

235
245   223   265   252   280

18   44   16   17   44   13

TB-6Sa
TB-6Lc
TB-6Lb

#7

28   111 216 112   283   431

5   11   7 5   21   21   37

TB-7Lb
TB-7Lb-4L4698   nd

#8

114   110   64 37   PdK2   43   107

35   28   7 13   30   57   20

TB-8La

#9

B5.10, 454, 416, 222, U20
Pep1   B7.13
300, B306   80, 293
243   sh1   266   Css2   209   97
253 211

11   18   11   8   5 2 2 6   23   15   17

TB-9Sb
TB-9Sb-4L6504
TB-9Sd
TB-9Lc
TB-9La   nt   nt

#10

85
285   105   92   350

22   30   10   42

TB-10Sc
TB-10L19
TB-10L36

allele from the male parent is absent in plants hypoploid for this B-A translocation.

Analyses of this type were carried out using 87 RFLP probes and 24 B-A translocations. Nineteen of the B-A translocations analyzed in this study were simple B-A translocations and five were compound B-A translocations (TB-3La-2S6270, TB-1Sb-2L4464, TB-1La-4L4692, TB-7Lb-4L4698, and TB-9Sb-4L-6504). A simple B-A translocation is produced by an exchange between an A and a B chromosome while a compound B-A translocation is produced by crossing an appropriate reciprocal translocation (between two A chromosomes) with a B-A translocation and selecting a crossover derivative (RAKHA and ROBERTSON 1970). A plant hypoploid for a compound B-A translocation is hypoploid for segments of two different A chromosomes; it is hypoploid for the region between the two breakpoints on the chromosome arm in the original B-A translocation and also hypoploid for the region distal to the breakpoint in the translocated A chromosome. For example, TB-3La-2S6270 produces plants that are hypoploid for a segment of the long arm of chromosome 3 from 0.10 to 0.60 and also hypoploid for a segment of the short arm of chromosome 2 from 0.46 to the end of the arm. Data for these compound B-A translocations are also included in this study.

Figure 3 shows the loci on our RFLP map which were analyzed using each of the B-A translocations. All tested adjacent loci at one end of a linkage group were uncovered in the A chromosome translocated in each simple B-A translocation while those at the other end were not uncovered. This result is expected if the linear order of RFLP loci on the chromosome is correct. Clearly, the uncovered loci are located distal to the breakpoint in the A chromosome. Compound B-A translocations, as expected, uncovered loci on two different chromosomes. For example, TB-3La-2S6270 uncovered loci in the middle of chromosome 3 but not at either end, and it also uncovered loci at one end of chromosome 2.

Each B-A translocation uncovered RFLP loci on the linkage group that we had originally associated with that B-A translocation; this confirmed that the linkage groups on our RFLP map were assigned correctly. The current study also identified the long and short arms of each chromosome on our RFLP map. The chromosome arm involved in each of these B-A translocations was previously known, and each B-A trans-

location indeed uncovered RFLP loci at only one end of the RFLP linkage group associated with that chromosome. Clearly, the uncovered loci identify the chromosome arm that was involved in the B-A translocation. In our current map (Figure 4), the short arms of each linkage group are shown to the left and the long arms to the right.

The breakpoints of each of the B-A translocations tested are also shown in Figure 3. The region from the distal-most locus uncovered by each B-A translocation to the end of each chromosome is indicated with a solid line, and the region between that locus and the next closest locus which was not uncovered is indicated with a slashed line. The breakpoint of each B-A translocation, therefore, is within the region identified by the slashed line.

This type of analysis turned out to be quite helpful in clarifying certain aspects of our RFLP linkage map. For example, the order of RFLP loci on chromosome 3 near the centromere had previously been determined to be "...-249-219-89-83..." (HELENTJARIS, WEBER and WRIGHT 1988). However, because TB-3Sb uncovers 249 and 89 but not 219, there appears to have been a mistake in interpreting the recombinational data or the Southern blot data may have been misread. It is possible that the stock containing TB-3Sb and the RFLP mapping population differ by a small inversion; however, this is probably not the case because there is very little inversion polymorphism in maize. Clearly, 89 must be distal to 219, and this information is reflected in the current map. This type of mistake is not surprising because relatively small segregating populations are used to develop RFLP linkage maps, and data from four different segregating populations were used to assemble this map. Linkage data for closely linked clones are far less reliable than linkage data for more distantly located clones because recombinants between closely linked clones are infrequent. Data from B-A translocations are more reliable than recombinational data because B-A data are qualitative while recombinational data are quantitative in nature.

Another example of this type involves analysis of several RFLP loci which mapped near the centromere of chromosome 9. We had previously been unable to unambiguously determine the order or spatial relationship of these loci using only recombinational analyses for the reasons mentioned above. We found that TB-9Sb uncovered loci 253, 211, 343, sh1, and 266;

FIGURE 3.—B-A translocational analysis of RFLP loci in maize. Horizontal lines denote the chromosomes, and RFLP loci analyzed in this study are represented above the lines by numerical designations. Loci in Figures 3 and 4 which were detected with probes from B. BURR, Brookhaven National Laboratory, and D. HOISINGTON, University of Missouri, are designated with prefixes of "B" and "U" respectively. Numbers below the lines are distances between loci in map units. Bars below each chromosome present the results obtained with each B-A translocation analyzed. The solid segment of each bar includes all RFLP loci tested which were uncovered by a particular B-A translocation, the open segment includes the RFLP loci which were not uncovered, and the slashed segment is the segment between the most proximal locus uncovered and next closest tested locus which was not uncovered. "nt" indicates that this locus was not tested with this B-A translocation.
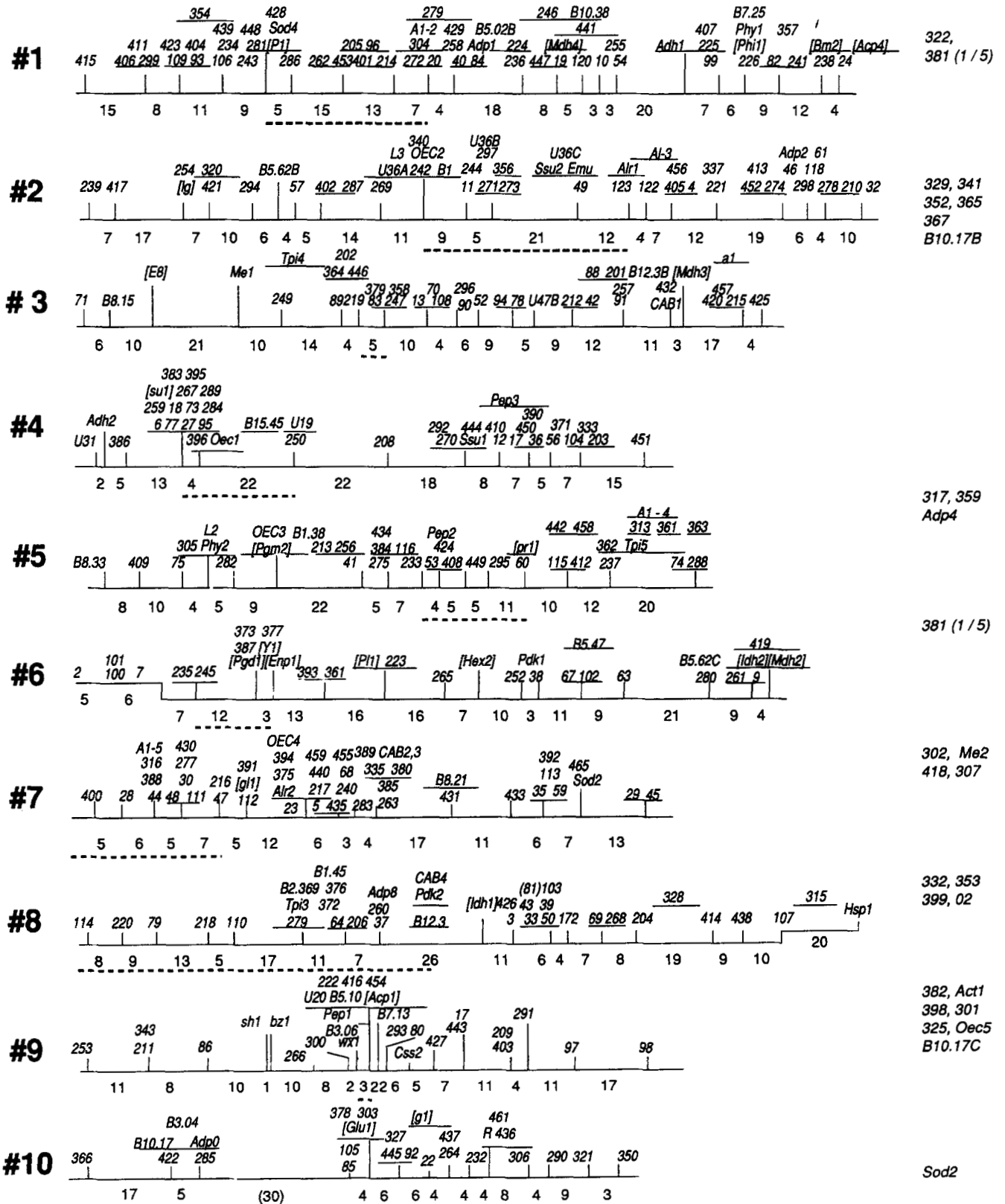
FIGURE 4.—Our current maize RFLP linkage map. Horizontal lines denote the chromosomes, and numbers above the lines represent RFLP loci. Where the exact location of a locus is unknown, this ambiguity is denoted as an underlined segment. Loci along the right side of the figure have been assigned to chromosomes by monosomic analysis, but linkage data are not available. Loci in brackets were detected as morphological markers or isozymes, while all other loci were detected by RFLP analysis. The region which must include the centromere of each chromosome is indicated with a dashed line.

thus, these loci must be located distal to the breakpoint of this B-A translocation on the short arm. TB-9Sd, which has its breakpoint more proximal than TB-9Sb, also uncovers loci *B3.06* and *300*; thus, these loci are also in the short arm and proximal to loci *253*, *211*, *343*, *sh1*, and *266*. Another group was uncovered by TB-9Lc (*B5.10*, *B7.13*, *454*, *416*, *222*, *Css2*, *U20*, *80*, *293*, *97*); therefore, these loci are located on the long arm distal to the breakpoint of this B-A translocation. Locus *Pep1* was not uncovered by any of these B-A translocations and must be located between the breakpoints of TB-9Sd and TB-9Lc near the centromere. Thus, B-A translocational analysis provided additional information about the order of loci tightly clustered around the centromeric region of chromosome *9*. Subsequent recombinational analysis of all of these loci in the same F_2 population confirmed this general order. It was previously known that TB-9Sb, TB-9Sd, and TB-9Lc uncover *sh1*, *wx1*, and *Css2* respectively, and *B3.06* was found to be distal to *wx1* by recombinational analysis (HOISINGTON 1985; BURR *et al.* 1988). The results obtained in the current study confirmed and extended these observations.

This study also provides information about the locations of centromeres on this RFLP map. Each centromere must be located between the most proximal RFLP locus uncovered in each arm by B-A translocations. The region on each chromosome which must include the centromere is indicated in Figure 4 by a dashed line. In some cases, additional information is available which allows more precise placement of the centromeres on the map. For example, because the *y* locus is uncovered by TB-6Lc (see HOISINGTON, COE and NEUFFER 1988), the centromere must be located proximal to this locus on our RFLP map. Similarly, because the *P1*, *B1*, and *wx* loci on chromosomes *1*, *2*, and *9* are uncovered by TB-1Sb, TB-3La-2S6270, and TB-9Sd (see HOISINGTON, COE and NEUFFER 1988), the centromeres on each of these chromosomes must be located proximal to these loci. This information is reflected in this figure. In certain cases, centromeres are very precisely defined on our RFLP map. For example, on chromosome *10*, loci *105* and *85* map very close to each other; however, TB-10Sc uncovers *105* and TB-10L19 uncovers *85*. Clearly, the centromere must lie between these two closely-linked RFLP loci.

The positions of the breakpoints on the cytological and conventional genetic map are also known for most of these B-A translocations (HOISINGTON, COE and NEUFFER 1988). The determination of the breakpoints on the RFLP map in the current study; therefore, allows these three types of maps (cytological, conventional, and RFLP maps) to be better correlated.

Clearly, B-A translocations are an exceedingly pow-

erful tool in RFLP mapping studies, and they have provided much additional information about this RFLP map. Certain probes analyzed in this study are being used by others as their RFLP maps are being constructed, and this will enable them to identify the short and long arms of their linkage groups. Analysis of additional loci and B-A translocations will provide still additional information regarding these maps.

LITERATURE CITED

BECKETT, J. B., 1978 B-A translocations in maize. I. Use in locating genes by chromosome arms. J. Hered. **69:** 27–36.

BURR, B., S. V. EVOLA, F. A. BURR and J. S. BECKMAN, 1983 The application of restriction fragment length polymorphism to plant breeding, pp 45–58 in *Genetic Engineering; Principles and Methods*, Vol. 5, edited by J. K. SETLOW and A. HOLLAENDER. Plenum, New York.

BURR, B., F. A. BURR, K. H. THOMPSON, M. C. ALBERTSEN and C. STUBER, 1988 Gene mapping with recombinant inbreds in maize. Genetics **118:** 519–526.

CARLSON, W. R., 1977 The cytogenetics of corn, pp 225–304 in *Corn and Corn Improvement*, edited by G. F. SPRAGUE. American Society of Agronomy, Madison, Wisc.

EVOLA, S. C., F. A. BURR and B. BURR, 1986 The suitability of restriction fragment length polymorphisms as genetic markers in maize. Theor. Appl. Genet. **71:** 765–771.

HELENTJARIS, T., D. F. WEBER and S. WRIGHT, 1986 Use of monosomics to map cloned DNA fragments in maize. Proc. Natl. Acad. Sci. USA **83:** 6035–6039.

HELENTJARIS, T., D. F. WEBER and S. WRIGHT, 1988 Identification of the genomic locations of duplicate nucleotide sequences in maize by analysis of restriction fragment length polymorphisms. Genetics **118:** 353–363.

HELENTJARIS, T., S. WRIGHT and D. F. WEBER, 1986 Construction of a genetic linkage map in maize using restriction fragment polymorphisms. Maize Genet. Coop. Newsl. **60:** 118–120.

HELENTJARIS, T., G. KING, M. SLOCUM, C. SIDENSTRANG and S. WEGMAN, 1985 Restriction fragment polymorphisms as probes for plant diversity and their development as tools for applied plant breeding. Plant Mol. Biol. **5:** 109–118.

HELENTJARIS, T., M. SLOCUM, S. WRIGHT, A. SCHAEFER and J. NIENHUIS, 1986 Construction of genetic linkage maps in maize and tomato using restriction fragment length polymorphisms. Theor. Appl. Genet. **72:** 761–769.

HOISINGTON, D., 1985 Compilation of B-A translocation data for maize. Maize Genet. Coop. News Lett. **59:** 159–167.

HOISINGTON, D., E. H. COE, JR., and M. G. NEUFFER, 1988 Genelist and linkage map of maize (*Zea mays* L.)—February 1988. Maize Genet. Coop. Newsl. **62:** 125–149.

MURRAY, M., J. CRAMER, Y. MA, D. WEST, J. ROMERO-SEVERSON, J. PITAS, S. DEMARS, L. VILBRANDT, J. KIRSHMAN, R. MC-LEESTER, J. SCHILZ and J. LOTZER, 1988 Agrigenetics maize RFLP linkage map. Maize Genet. Coop. Newsl. **62:** 89–91.

NEWTON, K. J., and D. SCHWARTZ, 1980 Genetic basis of the major malate dehydrogenase isozymes in maize. Genetics **96:** 424–442.

RAKHA, F. A., and D. S. ROBERTSON, 1970 A new technique for the production of A-B translocations and their use in genetic analysis. Genetics **65:** 223–240.

RIVIN, C. J., E. A. ZIMMER, C. A. CULLIS and V. WALBOT, 1983   Evaluation of genomic variability at the nucleic acid level. Plant Mol. Biol. Rep. 1: 9–16.

ROMAN, H., 1947   Mitotic nondisjunction in the case of interchanges involving the B-type chromosome in maize. Genetics 32: 391–409.

ROMAN, H., and A. J. ULLSTRUP, 1951   The use of A-B translocations to locate genes in maize. Agron. J. 43: 450–454.

WRIGHT, S., T. HELENTJARIS and Y. KIKUCHI, 1987   RFLP mapping of cloned genes in maize. Maize Genet. Coop. Newsl. 61: 89–90.