STUDIES ON CROSSING OVER IN HOMOZYGOUS AND HETEROZYGOUS CHROMOSOME REARRANGEMENTS IN ZEA MAYS

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ABSTRACT

The nature and behavior of chromosome inversions and translocations are discussed and the literature reviewed. Their uses in cytogenetic and biochemical studies are also outlined and applications are cited.

Linkage data are presented for the genetic positions of sixteen translocations in chromosome 9 with reference to the marker genes C, sh_1, and wx. Data are also presented for the map positions of fourteen translocations in chromosome 2, with reference to the genes lg_1, gl_2, B, sk_1, and v_4. The uses of duplicate-deficient gametes and pollen grains in cytogenetic investigations are outlined and their applications to these studies are described. Techniques for the classification and transmission of unbalanced chromosome complements are presented and the phenotypic effects of certain gene dosages are described. Available information on each of the thirty translocations mentioned above is summarized and its bearing on previous information regarding chromosomes 2 and 9 is discussed.

Studies are also reported in which the lg_1-gl_2 and C-wx regions are moved to different positions in the chromosome complement. Changes of position were brought about by using chromosome rearrangements. In each case, the crossover value is measured in the homozygous rearrangement and is compared with the crossover value found when the region is in its standard position. In some cases recombination values from female and male transmission are also compared.

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PART I. INTRODUCTION.

Chromosome rearrangements, reciprocal translocations and inversions, have been of particular interest and value in maize because of the unique opportunities which they offer for correlating chromosome behavior with crossing over. The suitability of maize for such studies is due in large part to its excellence as material for the cytological observation of early meiotic stages, at which time the chromosomes appear as long, thin threads with homologous regions closely paired. In this condition the finer structure of the chromosome is clearly visible and each of the chromosomes may be differentiated by its characteristic features. The configurations resulting when rearranged chromosomes synapse with their normal homologues makes it possible to determine rather accurately the points at which chromosome rearrangement has occurred and permits the correlation of visible points on the chromosomes with loci on the linkage maps.

The usefulness of a combined cytological and genetic approach in maize has been amply demonstrated by such diverse studies as the correlation of cytological and genetic crossing over (Creighton and McClintock, 1931), studies on crossing over in trisomics (Rhoades, 1933a) and in maize-teosinte hybrids (Beadle, 1932a), investigation of the constitution and properties of a secondary trisomic (Rhoades, 1936), and analysis of the behavior of ring fragments (McClintock, 1932b, 1938a). More recently, cytogenetic evidence from a variety of sources was used by Anderson and Randolph (1945) as a basis for esti-

mating the positions of the centromeres on each of the linkage maps. Other recent applications of this dual approach have included McClintock's elaboration of the nature of chromosome and chromatid breakage-fusion-bridge cycles in maize (McClintock, 1938a and b, 1941, 1942a, and subsequent annual reports in Carnegie Yearbooks) and description of the behavior of dissociation loci (See McClintock, 1950 for references). Beginnings have also been made in the application of cytogenetic techniques to problems of economic importance. Burnham and Cartledge (1939) made use of reciprocal translocations in searching for genes for smut resistance in maize, and V. H. Rhoades (1935), using chromosomes deficiencies, succeeding in locating the factor for resistance to physiologic form 3 of Puccinia Sorghi.

In order that these, and similar techniques, may be used to maximum advantage, however, it is necessary that information on the linkage relations of genes and physical loci on the chromosome threads be improved and extended to permit adequate marking and controlling of all regions of the chromosome complement. Fortunately, an extensive collection of reciprocal translocations is now available and is admirably suited for this purpose.

A recognition of the need for a combined cytological and genetic study of an extensive series of chromosome rearrangements has led Dr. E. G. Anderson to assemble and maintain at the California Institute of Technology several hundred such stocks. Most of the older translocations and inversions were derived from X-ray treatment. The linkage relations of a large number of these have been investigated

extensively by Anderson, Burnham, Brink, and collaborators, as well as by others. More recent additions to the collection have consisted chiefly of rearrangements which occurred in progenies of maize seed exposed to radiations from atomic bombs. The cytological determinations of the interchange points of most of the rearrangements being maintained in stock have been made by Dr. Longley (1950, and Unpubl.).

The present study of chromosome rearrangements was undertaken at the suggestion of Dr. Anderson. Data reported here are primarily concerned with the linkage relations of a number of reciprocal translocations involving chromosomes 2 or 9, and with the effect upon crossing over relations in the $\underline{lg_1}$-$\underline{gl_2}$ region of chromosome 2 or the $\underline{C}$-$\underline{wx}$ region of chromosome 9, respectively, whenever the position of either of these regions with respect to the rest of the chromosome complement is changed.

PART II. GENERAL DISCUSSION OF CHROMOSOME REARRANGEMENTS

The evidence so far obtained suggests that most chromosome rearrangements can be explained on the assumption that broken ends of chromosomes tend to unite two-by-two. When, through natural causes or by artificial means, a chromosome becomes broken at any one place, two broken ends are produced. If, in addition, a similar break occurs at some other point in the chromosome complement, two more broken ends may be present in the same cell simultaneously. According to current theory, these broken ends tend to unite two-by-two, the types of chromosomes which result being entirely dependent upon the positions of the breaks and the manner of reunion. If each of the breaks is in a different chromosome, and reunion occurs in such a manner that portions of two chromosome arms become reciprocally transposed, the result is termed a reciprocal translocation, or chromosome interchange. If, on the other hand, both breaks occur in the same chromosome, reunion of broken ends may occur in such manner that an internal region of a chromosome becomes inverted with respect to its standard, or normal, relation in the chromosome. Such a rearrangement is termed a chromosome inversion. Other possible ways of reunion of the broken ends may produce deleted, dicentric, or ring chromosomes as well as acentric fragments. All of these latter types are variously lacking in chromatin and are either non-transmissible or are recognizable by suitable means. Of course, if broken ends which were previously joined should reunite, the constitution and sequence of parts

of the original chromosomes is re-established. The available information indicates that only broken ends reunite, and that terminal inversions and so-called "simple" translocations do not occur. Each of the latter types would require the union of a broken end with an unbroken, terminal end of a chromosome.

Inversions

Changes in pairing homology as a result of the presence of an inversion produce a pachytene loop configuration, whose extremities indicate the two points of interchange. The cytological positions of the points of breakage in an inverted chromosome may be determined in the heterozygote by cytological analysis of the early meiotic prophase chromosomes. Heterozygous inversions also form loop configurations in the salivary gland chromosomes of Drosophila.

Muller (1940) proposed that inversions including the centromere be termed pericentric and those confined to a single chromosome arm be called paracentric. Heterozygous inversions of both types produce loop configurations in meiotic prophase or in the salivary gland chromosomes. Single crossover chromatids arising from exchanges within the bounds of a heterozygous paracentric inversion are dicentric and form a chromatin bridge at meiotic anaphase or are acentric and become lost in succeeding mitoses (McClintock, 1933). These dicentric and acentric crossover chromatids carry genetic duplications and deficiencies. Single crossover chromatids arising from exchanges within heterozygous pericentric inversions also carry duplications and deficiencies but

each chromatid has a single centromere and hence no chromatin bridges are produced. Double crossover chromatids arising from multiple exchanges within the limits of either type of heterozygous inversion carry neither duplications nor deficiencies and are recovered in viable progeny. Duplicate deficient chromatids usually cause abortion of the gametophyte generations of plants. In animals, on the other hand, aneuploid gametes carrying duplicate deficient chromatids are functional but ordinarily give rise to zygotic or embryonic lethals. Heterozygous inversions have been found to result in a great reduction in genetic recombination within inverted regions in Drosophila melanogaster (Sturtevant, 1926, 1931; Sturtevant and Beadle, 1936) and in D. pseudoobscura (Dobzhansky and Epling, 1948). Duplicate-deficient crossover chromatids are excluded from functional egg nuclei in Drosophila and Sciara (Sturtevant and Beadle, 1936; Carson, 1946), resulting in eggs carrying only non-crossover chromatids. Normal sperm are produced by Drosophila males heterozygous for inversions because of the absence of crossing over.

Darlington and LaCour (1941) found that in plants dicentric chromatids are excluded from terminal megaspores in megasporogenesis, but are included in aneuploid microspores, usually non-functional. Thus, in plants heterozygous paracentric inversions may give rise to pollen abortion but little or no ovule abortion.

The cytological behavior of inversions in maize has been reported by McClintock (1931, 1933, 1938b) and a cytogenetic study was recently

made by Morgan (1950). The latter used pollen abortion frequency as a measure of the minimum genetic length of an inversion. The break points of an inversion may be considered as two loci bounding the inverted segment with the products of recombination measured as aborted pollen grains. Each single or three-strand double exchange within the inversion gives rise to two normal and two aborted pollen grains. Each four-strand double exchange produces four aborted pollen grains, while each two-strand double exchange gives rise only to normal pollen and hence remains undetected. The percentage of pollen abortion will therefore equal one-half the single and three-strand double chiasma frequencies plus the four-strand double chiasma frequency. The percentage of pollen abortion is thus a measure of the minimum genetic length of the inversion, since it represents a fairly accurate approximation of one-half the total chiasma frequency. By observing the amount of aborted pollen in normal sister plants, appropriate corrections may be made for the small amount of pollen abortion due to causes other than aneuploidy. Due to suppression of crossing over by asynapsis and non-homologous pairing (McClintock, 1933), the calculated genetic length of an inversion may be expected to be less than the genetic length of the same sector in either its normal arrangement or in the homozygous inversion. Morgan (1950), in studying paracentric inversion 4a, found a striking difference between pollen abortion (25 percent) and ovule abortion (4 percent). Since Eyster (1922) found no significant difference in crossing over in male and female

flowers for the su-Tu region of chromosome 4, it appears that in maize, as in Drosophila, single crossover chromatids from heterozygous paracentric inversions are not ordinarily included in functional eggs. By contrast, plants heterozygous for pericentric inversion 2b showed an average pollen abortion of 19.1 percent and an average ovule abortion of 20.1 percent. These results are consistent with previous observations that crossover chromatids from heterozygous pericentric inversions are not excluded from megaspores.

The only inversion (inversion 2a) included in the data reported in this paper was studied exclusively in the homozygous state. It is expected that under these conditions there would be no suppression of crossing over or production of duplicate-deficient spores and that pairing of homologous regions should be complete. Unless specifically noted, therefore, all further references to duplicate-deficient spores and aneuploidy which appear in the discussion and references to the data in the text will be concerned with aneuploid types encountered in studies of heterozygous chromosome interchanges.

Chromosome Interchanges

Chromosomal interchanges, or reciprocal translocations, in maize arise by a mutual exchange of parts of non-homologous chromosomes. Cells containing such interchanged chromosomes have all chromosome material represented in the normal amount but are characterized by an altered sequence of certain chromosome regions. The changed sequence is also attended by altered linkage relations of genetic and cytological

markers carried on the regions shifted.

The positions within chromosomes at which an interchange has occurred may be determined fairly accurately by cytological observation of the configurations assumed by the meiotic prophase chromosomes in microsporocytes of plants heterozygous for the interchange. The synaptic pairing of the interchanged chromosomes with their normally-arranged homologues leads typically to a cross-shaped configuration whose point of intersection indicates the points of interchange in the two chromosomes. In some instances, the position of an interchange may be placed with reference to conspicuous markers such as knobs or other stable morphological features of a chromosome. Non-homologous pairing in some translocation complexes sometimes causes considerable difficulty in determining the points of interchange. Usually such non-homologous associations can be detected when several figures are compared because of the variable position of the cross in the configuration (Longley, 1950). The positions of interchange can be determined quite accurately in certain favorable instances by observing the homozygous translocations. If, as a result of translocation, chromosome regions of markedly different appearance are joined, the precise point of union may be apparent. This has been true particularly in those instances where a heavily-staining chromosome region has become attached to a lightly-staining one.

The genetic behavior of interchanges has been clearly described by Anderson (1935). Semisterile-1 (now designated T_{1-2a}) is found to

be typical. Originally reported by Brink (1927), it has been studied by Brink and Burnham (1929), Brink and Cooper (1931, 1932a) and Cooper and Brink (1931). Later it was used by Anderson and Clokey (1934) and Anderson (1935) for identification of unplaced translocations by analysis of diakinesis figures. Plants heterozygous for the interchange produce empty (starch-free) aborted pollen grains and normal pollen grains in approximately equal numbers. When such semisterile plants are selfed, their progeny consists of fifty percent semisterile plants and fifty percent normals. The normals are, however, of two types. One-half are ordinary normals and have their chromosomes in standard sequence. These yield only fully-fertile plants when outcrossed to normal stocks. The remaining half (originally termed X-normals) are homozygous for the interchanged chromosomes and give only semisterile plants in outcrosses to standard stocks. Homozygous interchange plants are not phenotypically different from ordinary normals and are fully fertile.

The typical semisterile nature of plants heterozygous for a chromosome interchange is occasioned by the manner of distribution of normal and interchanged chromosomes to the spores at meiosis. In the typical instance, the distribution of the interchange and normal chromosomes is such that one-fourth of the spores receive both interchange chromosomes, one-fourth receive both normal, and one-half a normal and an interchange chromosome. The first two classes have all chromosome regions present and are completely viable. Pollen grains

developed from spores of these types are filled with starch and normal in appearance and functioning. On the other hand, spores receiving a normal and an interchange chromosome are duplicated for a portion of one chromosome and deficient for part of the other. Pollen grains developed from them appear empty (starch-free) or abortive. Because of the fact that such unbalanced spores are not ordinarily functional, the complete interchange appears to be transmitted as a single unit. Since crossing over may occur between homologous regions of normal and interchange chromosomes, a translocation may be followed in linkage tests as if it were a dominant gene for partial pollen sterility located at the points of interchange in the linkage maps of both chromosomes.

In some translocations which have been studied, eggs of duplicate-deficient chromosome constitution may be functional. In these instances pollen of like constitution is usually partly or completely filled with starch, in some cases being indistinguishable from normal. The detection of unbalanced gametes and the genetic consequences of their functioning are elaborated in a later section.

Since chromosome interchanges in maize may be followed both genetically and cytologically, they afford an excellent means by which genetic and cytological maps may be closely correlated. As genetic markers they possess the advantages of being readily classifiable in combination with most genes and of having no pronounced detrimental physiological effects on plants carrying them. Except for the production of aborted spores, plants carrying translocations are not

distinguishable in appearance from normals.

It has been pointed out by Anderson and Randolph (1945) that the use of translocations in the measurement of map distances is somewhat unreliable because of their effect in suppressing crossing over. Also the sequence of translocations in a short region between two genes cannot at present be determined satisfactorily except in special instances. However, the order of genes and translocations on linkage maps can be ascertained reliably. Moreover, by making use of the homozygous translocation or the female transmission of duplicate-deficient gametes, it is often possible to determine the sequence of a translocation in a linkage map much more easily and accurately than would be possible in the case of a gene at the same locus. Translocations have been used in the mapping of the centromeres in maize by Anderson and Randolph (1945).

Anderson (1938) directed attention to the fact that chromosome interchanges provide excellent means of exploring regions of chromosomes where no genes are known. In most instances, one need simply cross any new or unplaced gene with a suitable translocation, then backcross to the new gene if recessive or to a normal stock if dominant. Classification of the progeny for the gene character and for pollen sterility affords a direct linkage test with a known point on a chromosome. This general technique was used by Burnham and Cartledge (1939) in searching for genes in maize conferring resistance to smut.

It was previously pointed out that the abortion of unbalanced, duplicate-deficient gametes in a plant heterozygous for a reciprocal translocation results in the translocation being transmitted as a unit. Stated in other words, the points of interchange in the two chromosomes are completely linked in inheritance. By choosing a translocation with interchange points in appropriate positions it is thus possible to bring about an artificial linkage of specified regions on two different chromosomes. The use of this very valuable technique will undoubtedly find important applications in physiological and developmental studies in the future. Its use in a study of developing maize endosperms was outlined recently by Anderson (1952 a,c). For a comparative biochemical assay of developing starchy and sugary kernels on the same ear, separation of the two classes at an early ontogenetic stage was required (Teas, et al, 1952). This separation, however, does not become apparent until near maturity. Yellow and white endosperm, on the other hand, can be separated at an early milk stage, about two weeks after pollination. The required separation was accomplished by means of translocation 4-6a, which artificially links the gene su on chromosome 4 and the gene Y on chromosome 6 with less than five percent crossing over.

In order to take full advantage of techniques involving chromosome interchanges, however, it is necessary to accumulate a considerable amount of information on the linkage relations of the various interchanges in order to correlate gene loci with positions in the observed chromosome threads.

PART III. A BRIEF OUTLINE OF THIS STUDY

Because of the presence of many very useful genes in the short arms of chromosomes 2 and 9, it was considered desirable that a study involving appropriate translocation stocks be undertaken in order to secure more exact information on the physical locations of the genes in these arms and concurrently to provide more effective means of marking and controlling desired portions of the two regions. The translocation stocks selected for this purpose were those which, on the basis of cytological determinations by Dr. Longley and others, were indicated in each case to have one interchange point in either the short arm of chromosome 2 or the short arm of chromosome 9. Several doubtful cases were also included, however, in which the pachytene configurations studied did not permit definite assignment of the positions of the interchange points with respect to the short or the long arms. In some cases the uncertainty was due to the proximity of the breakpoint to the centromere, while in other instances non-homologous chromosome associations within the pachytene translocation complex made determination of the interchange points difficult.

Translocations in chromosome 2 were placed with reference to some or all of the genes $\underline{lg_1}$, $\underline{gl_2}$, $\underline{B}$, $\underline{sk_1}$, and $\underline{v_4}$. The translocations in chromosome 9 were placed with reference to the genes $\underline{C}$, $\underline{sh_1}$, and $\underline{wx}$. In all cases plants heterozygous for the translocation and for the marker genes employed were backcrossed to the appropriate tester stocks

and the progeny classified. Detailed accounts of the specific techniques employed in each case are presented in later sections.

Chromosome rearrangements were also used to give information on the mechanism of crossing over. The specific question which was investigated is whether the amount of crossing over within a certain chromosome region is an inherent property of that region or whether it is dependent upon the position of the region with respect to the rest of the chromosome complement. As a result of a reciprocal translocation or an inversion, a portion of a chromosome arm may be reattached in such a way that a region included within it comes to occupy a position cytologically considerably nearer to or farther from a centromere, or at approximately the same distance from a different centromere. From the large stockpile of reciprocal translocations and inversions available at the California Institute of Technology, rearrangements were selected whose cytological placements indicated a shifting of the $\underline{lg_1}$-$\underline{gl_2}$ region of the short arm of chromosome 2 or the $\underline{C}$-$\underline{wx}$ region of the short arm of chromosome 9. Plants were then produced which were homozygous for each rearrangement and heterozygous for the genes being followed. These plants were test-crossed reciprocally to standard $\underline{lg_1}$-$\underline{gl_2}$ or $\underline{C}$-$\underline{wx}$ testers, and the progeny classified. In each case the percent of recombination has been compared with that obtained when the regions are in their standard positions in the chromosome complement. Since the plants tested were made homozygous for the rearrangements used, pairing

relations should have been normal. Such plants differed from normal, however, in that the regions studied did not occupy their usual positions in the chromosomes. If crossover values for a certain region are dependent only upon the nature of the region itself, no change in recombination percentages would be expected from shifting its position in the chromosome complement. If the amount of crossing over within a region is dependent upon the position of the region with respect to a centromere, however, this relation should be reflected in altered recombination percentages under the conditions described. Since the genetic markers employed in each case were classified as endosperm or seedling characters, it was possible to obtain data on a large number of backcross progenies.

In order to explain terminology and procedures used in the course of studies reported here, it is most convenient to present first the linkage data on reciprocal translocations in chromosomes 9 and 2, in that sequence, followed by results of linkage studies involving homozygous chromosome rearrangements.

PART IV. LINKAGE RELATIONS OF SOME TRANSLOCATIONS IN CHROMOSOME 9

Cytological Positions of Interchange Points

In Table 1 are listed the chromosome 9 translocations on which linkage data are reported in this study, together with the cytological determinations for each and the authority for the indicated placements. Following the procedure of Anderson (1938), the cytological position of an interchange point in a chromosome is recorded as a decimal fraction of the distance from the centromere to the end of the arm. The capital letters S and L denote the short and long arms, respectively. Thus, a designation 9 S.2 indicates that a point of interchange is in the short arm of chromosome 9 at a position two-tenths of the distance from the centromere to the end of that arm. Cytological positions reported by Longley have usually been indicated to the second decimal place, without, however, the implication that the cytological determinations involve any such degree of exactness. In general, the cytological placements by Longley are based upon calculations from three or more camera lucida drawings of what appeared to be the most characteristic pachytene configurations among those that were analyzed. Where cytological positions have been determined independently by different investigators, these positions are also indicated, along with the source.

It should be cautioned that one should not accept the cytological positions of translocations listed in Table 1 and subsequent tables as

Table 1. Cytological positions of chromosome 9 translocations used in linkage placements.

Translocation	Cytological Determination		Authority*
1-9 4398-4	1L.51	9S.19	
1-9 4995-5	1L.21	9S.14	
2-9 6656-4	2L.36	9S.32	
3-9 c	3L.15	9S.20	
	3L.1	9L.2	Anderson and Brink (1940)
4-9 5657-2	4L.30	9S.14	
4-9 6222-1	4L.03	9S.69	
5-9 a	5L.80	9S.21	
	5L.7	9S.0+	Burnham (1934a)
5-9 4817-7	5L.07	9S.08	
5-9 5614-3	5S.25	9S.25	
6-9 4505-4	6L.12	9S.16	
7-9 a	7L.72	9S.08	
7-9 b	7S.92	9S.24	
7-9 4363-1	7L.09	9S.11	
7-9 7074-6	7L.03	9S.84	
8-9 5300-3	8L.86	9S.41	
8-9 6673-6	8L.30	9S.15	

* Except where otherwise indicated all cytological determinations listed here were made by Dr. A. E. Longley (1950, and Unpubl.).

indicating too literally the actual sequence of the interchange points in the chromosomes themselves. For short chromosomes, especially, a distance of one-tenth of a chromosome arm may represent a very short cytological distance in terms of the prophase chromosomes. McClintock (1942b), for example, has reported that the short arm of chromosome 9 is composed of about twenty chromomeres. A distance of one-tenth of this arm, then, represents about two chromomeres of the observed pachytene chromosome.

Many of the translocations in chromosome 9, especially those with interchange points near the centromere, have been difficult to place cytologically because of pairing irregularities of the translocation complex. Regions near the center of the "cross" have often been unpaired or have paired non-homologously. For these reasons, several of the translocations listed in Table 1 as having interchange points in the short arm, were considered only tentative placements. As genetic evidence presented later will indicate, some of them are probably located in the proximal portions of the long arm.

Nomenclature of Translocations

The capital letter T has been used as a general designation of translocations in maize. A specific interchange is indicated by numbers denoting the chromosomes involved. To differentiate translocations involving the same chromosomes, the small letters a, b, c, etc. are appended to serve as permanent symbols of particular

translocations. A complete list of translocations bearing such permanent designations has recently been compiled by Anderson (1952b) and includes all available translocations accumulated prior to the Bikini and Eniwetok series. Translocations herein listed by temporary numerical designations (e.g., 1-9 4398-4) represent largely interchanges induced in mature kernels exposed to radiations of the first Bikini atomic bomb, the "Able" bomb of July 1, 1946. It is anticipated that they, too, will eventually be given permanent letter designations.

Description and Classification of Genetic Markers Used

The linkage data reported here involve various chromosome 9 translocations and some or all of the genes C, sh_1, and wx. Classification for the presence or absence of a translocation was made by examining pollen of each plant for the occurrence of partial sterility. An additional check on the accuracy of these classifications was possible in the instances where ears of the same plants could be later classified for ovule abortion. The three marker genes are all concerned with endosperm characters, with the gene wx also being classifiable in pollen.

In the presence of other necessary complementary genes, C and c (East and Hayes, 1911) produce respectively, colored and colorless aleurone (For interactions of genes known to concern aleurone pigments in maize, see Emerson, Beadle, and Fraser, 1935). Classification of C requires that dominant alleles of the complementary genes A_1, A_2, A_3,

and R be present. A stock having all the proper alleles necessary for the development of aleurone color except for C is termed a "c-tester" stock. Aleurone color is developed relatively late in the maturing of the endosperm. In the stocks used in this study, classification for C was clear-cut.

The gene sh_1 (Hutchison, 1921) in homozygous state brings about a shrunken, collapsed condition of the endosperm. Classification of kernels for this character is usually good if they are mature. Germination and viability of shrunken kernels is somewhat lowered, especially under adverse growing conditions. The classification of wx is often more difficult in shrunken seeds. Since only sh_1 was dealt with in these studies, the subscript is omitted in the tables in the interests of convenience.

The wx allele used in these linkage studies is the one reported by Collins (1909). In heterozygous or homozygous condition, the wx allele modifies the nature of the reserve starch deposited in the endosperm, embryo sac, and pollen grain. Weatherwax (1922) first reported that waxy and non-waxy kernels could be distinguished by the iodine-staining reaction of their endosperm starch. Later, Demerec (1924a) and Brink and MacGillivray (1924) found that Wx wx plants produced red-staining and blue-staining pollen grains in equal numbers.

According to the two-component theory of starch structure (Meyer, 1942; Hassid, 1943; Schoch, 1945) naturally-occurring starches that stain blue with dilute iodine are mixtures of two types of

molecules, amylose and amylopectin. Structurally, these are thought to differ in the degree of branching of the starch chain, the latter being more highly branched. Endosperm starch of normal, non-waxy maize has been found to contain about 28 percent amylose, the rest being amylopectin. Starch of this constitution stains dark blue with dilute iodine solution. On the other hand, endosperm starch of waxy maize, which stains red with iodine, has been found to consist of 100 percent amylopectin (Sprague, Brimhall, and Hixon, 1943; Brimhall, Sprague and Sass, 1945). Though these same investigators have demonstrated a dosage effect of Wx alleles on the percent of anylose in endosperm starch, the widespread use of dilute iodine solution by geneticists to aid in differentiation of non-waxy and waxy phenotypes is restricted in practice to classifying for the presence or absence of a Wx allele.

In the work reported here, routine classification of pollen for the waxy character was accomplished by using a 1 percent stock solution of I_2 and KI in 70 percent ethanol, which was then diluted perhaps twenty-fold in water immediately before use. The dilution employed can be varied considerably to satisfy particular circumstances and for most purposes is satisfactory over a rather wide range of concentrations. When, as in this work, several hundred pollen samples are checked daily, it is important that the staining differentiation be clear and rapid. The speed of staining may be increased by using more concentrated iodine solution, but usually it was found

more satisfactory to stain several slides of pollen at once with a solution of lesser strength and then examine them serially. This procedure also has the advantage of grouping similar manipulations and materially increases the speed of pollen classification. Whenever it was desirable to subject pollen samples to more extended examination as in making pollen counts, a piece of the tassel, usually from the main spike, was placed in 70 percent alcohol for preservation until some later time. Such samples are conveniently labeled with small jewelers' tags carrying pertinent identification. It is helpful in later examination if the identification tag is attached to the tassel sample at a point marking a region of optimum anther exsertion.

For simultaneous observations on waxy segregation and degree of starch deposition in the pollen a special mounting medium suggested by Dr. Thad Pittenger was employed. It was prepared by mixing equal volumes of glycerol, phenol, lactic acid, and dilute aqueous iodine solution. This staining medium also has the advantage of maintaining the pollen grains in a normal, undried appearance for a considerable length of time and is particularly useful whenever a pollen sample is to be put to an extended analysis, as in making pollen counts.

The visual identification of stained wx and Wx pollen grains under the microscope is greatly facilitated if, instead of viewing them in transmitted light from below, one observes them in light reflected from a light source above the level of the stage. This is conveniently done by placing a piece of heavy white paper or thin cardboard (index cards are suitable) on the microscope stage beneath

the slide. This technique is routinely used by some maize investigators but is apparently not known to many others.

Since the genetic markers employed in mapping the chromosome 9 translocations were all endosperm genes, separation for the various phenotypic classes was made previous to planting. In kernels not having colored aleurones, separations for the wx gene are usually accurate without the necessity for staining. In doubtful cases, particularly in the presence of the shrunken phenotype, the endosperms were chipped and stained with dilute iodine solution as an aid in classification. Kernels with colored aleurone could usually be classified accurately simply by chipping with a scalpel or knife and observing the texture of the endosperm. Doubtful cases were again confirmed by staining. In addition, as a check upon the accuracy of separation, the genotype of each of the resulting plants with regard to the wx gene was determined by classification of the stained, mature pollen at the time of observations on pollen sterility.

Description of Crosses

In all cases the linkage data reported were derived from backcrosses. All backcross progenies tabulated in Tables 2 to 10 represent cultures which were grown as fall generations in 1950 or 1951. In many cases there is a wide discrepancy in contrary crossover classes among the mature plants. Except where specifically indicated, however, under the discussion of the individual translocations, no large discrepancy existed between the contrary endosperm

classes planted. The unequal classes among the mature progeny were due largely to the reduced germination and lower viability of individuals of shrunken phenotype, the selection being accentuated since the plants were grown as fall generations under less favorable growing conditions. In order to reduce such discrepancies to a minimum an effort was made at planting time to select for testing, when possible, from those crosses which yielded large, mature kernels. In most cases, the cultures grown were those in which the less vigorous tester stock represented the pollen parent, and which thus gave information on recombination values when the various translocations were female-transmitted. Wherever feasible, cultures of each of the translocations were planted in which F_1's were transmitted both as female and as male parents in order to permit comparison of recombination values in mega- and microsporogenesis.

Uses of Duplicate-deficient Gametes and Pollen Grains in Linkage Studies.

Adjacent segregations of chromosomes from heterozygous translocation complexes result in the production of spores of varying degrees of duplication and deficiency. Functioning of duplicate-deficient sperm in maize is at most very rare, but in the case of some translocations, such aneuploid eggs may function with high frequency. When it occurs, ordinarily an aneuploid type representing only one of the possible types of adjacent segregation is transmitted, and leads

to a distortion of genetic ratios in the progeny. In the absence of reliable methods for recognizing the aneuploid individuals in the progeny in most cases, maize workers in the past have usually preferred to transmit such translocations through the pollen in linkage studies.

In translocations involving chromosome 9, however, such aneuploid gametes can be used in many instances to yield linkage information. In the majority of chromosome 9 translocations which have been characterized by female transmission of duplicate-deficient gametes, pollen containing these unbalanced complements have formed an appreciable amount of starch. In the best cases such pollen grains appear partly filled with starch, the unfilled portion being a clearly-defined empty sector. Usually the amount of starch present is adequate to permit classification for the waxy character. It is thus possible to correlate the occurrence of sectored pollen grains with the waxy staining reaction.

A more complete description of the method and its uses may be made by reference to Figure 1. In Figure 1(A) is represented diagrammatically the chromosome pairing relations observed in meiotic prophase in microsporocytes of a plant heterozygous for a reciprocal translocation involving chromosomes 6 and 9. The interchange points are represented as being far out in 6L and in 9S very near the centromere. In (B) the break point in 6L is represented as being at the same location while the point of interchange in 9 is now represented as being in the long arm adjacent to the centromere. In each case

adjacent-1 disjunction -- separation of homologous centromeres at the first meiotic division (McClintock, 1945) -- would produce pollen grains containing a 6^9 chromosome and a normal 9 chromosome. Those resulting from (A) would be duplicated for nearly all of 9S while those receiving the same two chromosomes from the configuration represented in (B) would be duplicated for nearly all of 9L. In both cases such aneuploid pollen grains would lack the tip of 6L. Presuming the lack of the tip of 6L were not too detrimental, some starch might develop in pollen grains in each case. The presence of certain chromosome regions in duplicate in the pollen probably does not decrease starch deposition, since it is known that pollen grains hyperploid for entire chromosomes appear normally-filled. Adjacent-2 disjunction — homologous centromeres going to the same pole at the first meiotic division (McClintock, 1945) -- gives rise to pollen lacking at least an entire chromosome arm. It is probable that in most, if not all, such cases no more than a trace of starch is deposited. This was found to be true for both arms of chromosome 9, in particular. Occasionally aneuploid pollen grains were produced which appeared to be normally filled. In no case, however, was such an aneuploid type found which functioned with equal frequency in competition with normal pollen grains.

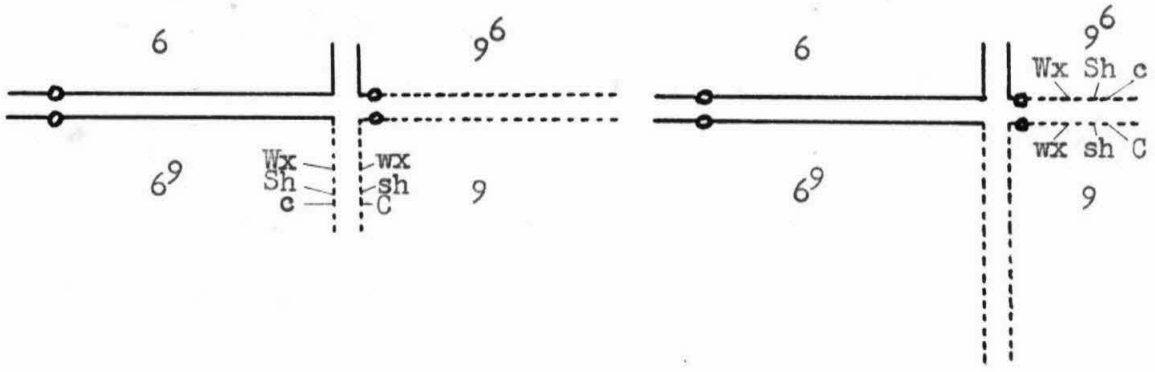
If from the configurations indicated in Figure 1, it is presumed in each case that pollen grains receiving chromosomes 6^9 and 9 produce clearly-discernible amounts of starch, it may be seen that in (A)

such pollen grains will have both Wx and wx loci while in (B) only the wx locus is present. The former type of pollen grain, having both Wx and wx loci, is found to stain blue with iodine solution. The latter type, having only the wx locus, stains red. These two situations -- one in which one translocation break is just to the left of the centromere and the other in which it is just to the right -- can here be clearly distinguished on the basis of the staining reaction of the partly-filled pollen. The method is especially useful in assigning certain translocations in the centromere region of chromosome 9 to one arm or the other. It should be noted that in this technique the wx allele has been carried on the normal chromosome 9.

As a result of crossing over between the wx locus and the point of translocation in chromosome 9, partly-filled pollen of opposite staining reaction may result, the percentage of which may, in fact, be used to estimate the wx-T distance. For translocations located between wx and the centromere, the wx-T distance is twice the percentage of partly-filled grains which are phenotypically waxy. This relation results from the fact that only wx wx pollen grains are identifiable as crossovers and that in partly-filled grains the frequency of homozygosis for the wx allele is one-fourth the chiasma frequency. In the case of breaks in the long arm of chromosome 9, only one allele at the wx locus is present in any pollen grain and the percentage of partly-filled grains which display the alternative

staining reaction (Wx in the genic arrangement in Figure 1 (B)) represents the map distance directly, presuming the distance is short enough to preclude multiple crossovers.

The actual measurement of wx-T distances by this means necessitates that the partly-filled grains be clearly classifiable since wx-T crossovers are rare for translocations close to the centromere. In pollen samples which were preserved for the purpose of making such counts, slight alteration of the appearance of the contents of the pollen grains lessened the classifiability of partly-filled grains to what was considered too great a degree. Fresh pollen of several of the translocations which have been studied, however, appears to satisfy the necessary requirements. Among these is T_{5-9a}, which is known to be in the short arm of chromosome 9 close to the centromere (Burnham, 1934a). The latter's data on this interchange have been used by Anderson and Randolph (1945) in estimating the minimum map distance from wx to the centromere.



(A) Interchange point in 9S (B) Interchange point in 9L

Figure 1

As mentioned previously, spores arising from adjacent-1 disjunction are deficient for one chromosome region and are duplicated for another. In Figure 1, spores which receive chromosomes 6^9 and 9 will in each case be deficient for a distal piece of 6L. In the instance diagrammed in 1 (A), they will also be duplicated for most of 9S, while in 1 (B) they will have most of 9L in duplicate. If eggs of such duplicate-deficient constitutions are functional, plants which arise following fertilization by sperms of normal chromosome constitution will have one chromosome segment in triplicate and another represented only once. Upon being appropriately testcrossed, these plants give modified trisomic ratios for genes carried in the triplicated segment and a hemizygous test for genes in the non-duplicated segment.

The functioning of duplicate-deficient gametes is often evidenced by the occurrence of one or more phenotypic classes in high proportion in the progeny. For example, the functioning of chromosomes 6^9 and 9 in Figure 1 (A) results in a marked excess of kernels of phenotype CShWx. From alternate disjunction this class would ordinarily be produced only rarely as a result of crossing over in the short C-sh region. In studies of chromosome 9 translocations, then, plants of suspected aneuploid nature could be observed somewhat more critically and tested for confirmation of their genetic constitution.

Aneuploid plants of the type just described usually produce partly-filled and normal pollen in approximately equal proportion,

this serving as the routine means of identifying them. In most cases duplicate-deficient pollen grains are differentiable from the slightly abnormal pollen grains sometimes produced by plants of normal stocks. A given duplicate-deficient type commonly displays a fairly constant pattern of starch deposition in the pollen grain that is distinct from the more variable, slightly abnormal pollen grains that occur occasionally in normal stocks and probably have their basis in causes other than chromosome unbalance. The mounting medium mentioned earlier has been found helpful in critical discrimination of various degrees of pollen abortion.

In several instances duplicate-deficient pollen types have not been microscopically distinguishable from normal pollen grains. Where it was suspected, however, that aneuploid types were involved on the basis of aberrant phenotypic ratios in the kernels planted, an effort was made to use each of the suspected aneuploid plants as a pollen parent in crosses with gene tester stocks that would check the chromosome transmission of the paternal parent. Because of strong selection against the functioning of aneuploid pollen grains in fertilization in maize, the greatly reduced frequency of certain phenotypic classes in the progeny is considered strong evidence of the aneuploid nature of the pollen parent. These crosses were made in a fall generation and, unfortunately, many did not mature sufficiently to be classifiable. The instances in which this evidence and evidence of the types described in the foregoing discussion were available are presented in the

discussion of individual translocations later in the paper.

The identification of aneuploid plants by cytological observation of microsporocytes has been done in some cases, particularly with T_{7-9b}. In each instance, results were in accord with expectations based on the other means of detection outlined.

Previous information on chromosome 9.

The following linkage map of chromosome 9 was prepared by Rhoades (1950):

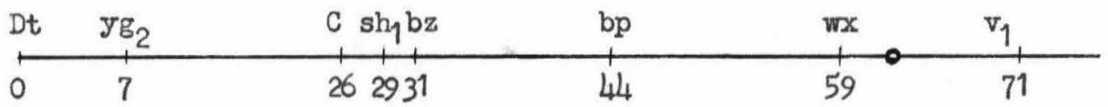


Figure 2. Linkage map of chromosome 9 in maize.

The most distal known gene in the short arm of chromosome 9 is Dt, which Rhoades has found to be located 7 crossover units beyond yg_2, which in turn is reported to be about 19 units beyond C (from data summarized by Emerson, Beadle, and Fraser, 1935). From investigations of McClintock involving small terminal deficiencies of the short arm, yg_2 is known to be in the terminal chromomere (McClintock, 1942b), while C is within the fifth or sixth chromomere from the end (McClintock, 1943). The locus of sh_1 is just to the right of C, and wx is at approximately the middle of the short arm (McClintock, 1941). The locus of bz has been indicated as two units to the right of sh_1 (Rhoades, 1950). On the basis of limited data cited in Emerson, Beadle, and Fraser (1935), bp is placed midway between sh_1 and wx.

The gene $\underline{v}_1$ is believed to be in the proximal part of the long arm (Beadle, 1932; Burnham, 1934b). Its map position is listed as 12 units from wx.

Data of Burnham (1934a) placed T 5-9a in the short arm between wx and the centromere and indicated about two percent recombination with wx. Data of Anderson (1938) on several translocations in the long arm of chromosome 9 indicate that the centromere is probably not much more than two units from wx.

The long arm of the chromosome is notable for its scarcity of known genes. It has been suggested by Anderson (1938) and by Rhoades (1945) that this region may include redundant chromatin represented elsewhere in the chromosome complement. Recent data of Rhoades (1951) on duplicate loci lends support to this hypothesis.

The linkage information thus far accumulated on chromosome 9 indicates quite unequal frequencies of crossing over in different regions, with a very large amount of crossing over in the terminal portions of the short arm as compared with the proximal half. The wx gene, which McClintock has placed at approximately the half-way point in the chromosome, appears to be only a few map units from the centromere, while data of McClintock (1943) indicate that as much as ten percent crossing over may occur in half of a chromomere at the tip of the arm. Thus, if $\underline{yg}_2$ is located in the proximal portion of the terminal chromomere, the location of Dt seven map units beyond it is not necessarily inconsistent.

The proximal one-third of the short arm consists of heavy chromomeres (McClintock, 1942b). When interchanges occur in this region and the distal fragment becomes attached to a lightly-staining region elsewhere in the complement, the point of breakage may sometimes be placed quite accurately by observing pachytene preparations of the homozygous interchange.

Linkage Data

Backcross linkage data of the chromosome 9 translocations studied are presented in Tables 2 to 10. In each table, the parental F_1 genotype is indicated in the heading. Since in genetic studies a translocation may be treated as a dominant gene for partial pollen and ovule abortion, the presence of a translocation is indicated in the linkage tables by a large T. The absence of the translocation (presence of the chromosomes in their standard arrangement) is indicated by the symbol +. The distribution of the progeny is tabulated according to the system used by Emerson, Beadle, and Fraser (1935). The following example will serve as an illustration:

$$F_1 \text{ genotype } \frac{c\ Wx\ T}{C\ wx\ +}$$

Parental Combinations		Recombinations					
		Region 1		Region 2		Regions 1 and 2	
c Wx T	C wx +	c wx +	C Wx T	c Wx +	C wx T	c wx T	C Wx +

In the column headed Culture Numbers are grouped the family designations under which progeny of individual pollinations were grown, together with a notation of whether the F_1 was used as the female (♀) or male (♂) parent in the final backcross. From some F_1 backcrosses, kernels mainly of parental endosperm phenotypes were grown in the fall of 1950 in order to secure specific crossover types to be used in other studies. In those cases where the remainder of the progeny from such crosses were grown in the fall of 1951, the data have been combined and the totals entered in the tables. In the instances where only a portion of the progeny from a given pollination were grown, the data are treated separately. Since the partial progenies grown represented mainly parental combinations for the C-wx region and may thus represent a selected population with a low interference value for this region, the probability of crossing over in adjoining regions may be somewhat greater than the average value for the total progeny.

In some instances, the position of a translocation is not evident from information presented in a single table. Where its sequence is indicated, however, that information was derived from the combined data or from some other source. The nature of the information available in each case is indicated under the discussion of the individual translocations.

Where numbers of individuals in reciprocal classes are markedly unequal, the disparity is usually due mainly to reduced viability of

plants of shrunken phenotype. Whenever aneuploid individuals occurred and could be identified they are included in the tables in their appropriate phenotypic classes. They are designated by circled numbers and are not included in the linkage calculations. In some progenies there occurred plants with slightly abnormal pollen that were probably not aneuploid types. These individuals are enclosed in parentheses but included in the linkage calculations.

Table 2. Backcross progenies from $\frac{c\ Sh\ Wx\ T}{C\ sh\ wx\ +}$

Translocation	Culture Numbers	Parental Combinations		Recombinations: Reg. 1	Reg. 2	Reg. 3	Regs. 1,2	Regs. 1,3	Regs. 2,3	Regs. 1,2,3	Total	% recombination: C-sh	sh-wx	wx-T
1-9 4398-4	5803 4307 4308 ♀ +	19	21	1 0	7 4	1 0					53	1.9	18.9	1.9
	5804 4309 4310 ♀ +	32	44	5 5	10 5	1 0	0 1				103	10.7	15.5	1.0
	5805 ♀ +	61	41	3 4	11 6	3 2					131	5.3	13.0	3.8
		112	106	9 9	28 15	5 2	0 1							
		218		18	43	7	1				287	6.6	15.3	2.4
1-9 4995-5	5806 4301 4302 ♀ +	31	24	1 0	5 2	1 1			1 0		66	1.5	12.1	4.5
	5807 4303 4304 ♂	51	47	2 2	12 15	3 2				1 0	135	3.7	20.7	4.4
	5808 ♀ +	56	31	3 7	6 8	1 0		0 3	0 1		116	11.2	12.9	4.3
		138	102	6 9	23 25	5 3		0 3	1 1	1 0				
		240		15	48	8		3	2	1	317	6.0	16.1	4.4

Table 2 (cont.)

Backcross progenies from $\frac{c\ Sh\ Wx\ T}{C\ sh\ wx\ +}$

Trans-location	Culture Numbers	Parental Combi-nations	Recombinations: Reg. 1	Reg. 2	Reg. 3	Regs. 1,2	Regs. 1,3	Regs. 2,3	Regs. 1,2,3	Total	% recombination: C-sh	sh-wx	wx-T
2-9 6656-4	5833, 4349, 4350 ♀ +	41 39	1 0	3 7			0 1						
		80	1	10			1			92	2.2	10.9	1.1
5-9	5818 ♀ +	26 17 (+1)	1 4	14 6	7 5			4 3		87	5.7	31.0	21.8
	5819 ♀ +	29 (+4) 12 (+15)	1 7	2 8	4 14		0 1	1 (+6) 3		82	11.0	17.1	28.0
	5838 ♂	91 10	0 10	27 2	19 6	0 1	0 1	2 1		170	7.1	19.4	17.1
		146 39	2 21	43 16	30 25	0 1	0 2	7 7					
		185	23	59	55	1	2	14		339	7.7	21.8	20.9
5-9 4817-7	5820 ♂	93 53	5 1	25 15	2 4					198			
		146	6	40	6						3.0	20.2	3.0
5-9 5614-3	5840 ♀ +	40 19	0 1	9 4									
		59	1	13						73	1.4	17.8	(0.0)
8-9 5300-3	5827, 4357, 4358 ♀ +	52 59	0 1	5 9						126	0.8	11.1	(0.0)
	5828 ♀	20 51	4 2 (+2)	6 1						84	7.1	8.3	(0.0)
		72 110	4 3	11 10									
		182	7	21						210	3.3	10.0	(0.0)

Table 3. Backcross progenies from $\frac{C\ Sh\ Wx\ T}{c\ sh\ wx\ +}$

Translocation	Culture Numbers	Parental Combinations	Recombinations: Region 1	Region 2	Region 3	Regions 1,2	Total	% recombination: C-sh	sh-wx	wx-T
3-9c	5835 ♀	39 37	1 2	4 11	0 1	0 1				
		76	3	15	1	1	96	4.2	16.7	1.0

Table 4. Backcross progenies from $\frac{c\ sh\ wx\ T}{C\ Sh\ Wx\ +}$

Translocation	Culture Numbers	Parental Combinations	Recombinations: Region 1	Region 2	Region 3	Regions 1,2	Regions 2,3	Total	% recombination: C-sh	sh-wx	wx-T
5-9a	5836, 4325, 4326a ♀	93 99	1 0	4 9			0 1	207	0.5	6.8	0.5
	5837, 4326 ♀	87 106	2 2	11 14	0 1	0 1		224	2.2	11.6	0.4
		180 205	3 2	15 23	0 1	0 1	0 1				
		385	5	38	1	1	1	431	1.4	9.3	0.5

Table 5. Backcross progenies from $\frac{c\ T\ Sh\ Wx}{C\ +\ sh\ wx}$

Translocation	Culture Numbers	Parental Combinations		Recombinations: Region 1		Region 2		Region 3		Regions 1,2		Regions 1,2,3		Total	% recombination: C-T	T-sh	sh-wx
4-9 6222-1	5815 ♀	37	29	0	3			2	3	(26)				74	4.1	(0.0)	6.8
	5816 ♀	74	60	1	5			4	5	(50)		(2)	0	149	4.0	(0.0)	6.0
	5817 ♀	65	67	1	2	0	1	7	2	(34)		(1)	0	145	2.1	0.7	6.2
		176	156	2	10	0	1	13	10			0	0				
		332		12		1		23				0		368	3.3	0.3	6.3

Table 6. Backcross progenies from $\frac{T\ c\ Sh\ Wx}{+\ C\ sh\ wx}$

Translocation	Culture Numbers	Parental Combinations		Recombinations: Region 1		Region 2		Region 3		Regions 1,3		Total	% recombination: T-C	C-sh	sh-wx
7-9 7074-6	5831 ♀	24	3	0	(37)			6	1	0	(6)	34	(0.0)	(0.0)	20.6
	5842, 4353, 4354 ♀	46	78	1	(27)	0	2	4	14	0	(2)	145	0.7	1.4	12.4
		70	81	1	0	0	2	10	15	0	0				
		151		1		2		25		0		179	0.6	1.1	14.0

Table 7. Backcross progenies from $\frac{c\ Wx\ T\ Y}{C\ wx\ +\ y}$

Trans-location	Culture Numbers	Parental Combi-nations	Recombinations						Total	% recombination		
			Region 1	Region 2	Regions 1,2	Regions 1,3	Regions 2,3	Regions 1,2,3		C-wx	wx-T	T-Y
6-9 4505-4	5822 ♀	65 56 121	32 25 57	8 6 14	0 1 1	0 1 1	0 1 1	1 0 1	196	30.6	8.7	1.5

Table 8. Backcross progenies from $\frac{c\ Wx\ T}{C\ wx\ +}$

Translocation	Culture Numbers	Parental Combinations	Recombinations Region 1	Recombinations Region 2	Total	% recombination C-wx	% recombination wx-T
4-9 5657-2	5813 ♀	69 52	10 4		135	10.4	(0.0)
	5814 ♀	56 35	3 13		107	15.0	(0.0)
		125 87 (212)	13 17 (30)		242	12.4	(0.0)
5-9 4817-7	5839 ♀	33 31 (64)	11 9 (20)	2 1 (3)	87	23.0	3.4
5-9 5614-3	5821 ♂	45 76 (121)	22 34 (56)	2 3 (5)	182	30.8	2.7
6-9 4505-4	5841 ♂	78 73 (151)	41 19 (60)	4 2 (6)	217	27.6	2.8
8-9 6673-6	5830 ♂	71 68 (139)	11 15 (26)	1 4 (5)	170	15.3	2.9

Table 9. Backcross progenies from $\frac{C\ Wx\ T}{c\ wx\ +}$

Translocation	Culture Numbers	Parental Combinations	Recombinations Reg. 1	Recombinations Reg. 2	Recombinations Regs. 1,2	Total	% recombination C-wx	% recombination wx-T
3-9c	5834 ♀	42 21 (63)	3 0 (3)	1 0 (1)		67	4.5	1.5

Table 10. Backcross progenies from $\frac{c\ T\ Wx}{C\ +\ wx}$

Translocation	Culture Numbers	Parental Combinations	Recombinations Reg. 1	Recombinations Reg. 2	Recombinations Regs. 1,2	Total	% recombination C-T	% recombination T-wx
7-9 4363-1	5823 ♀	68 10	10 1	0 2	0 1	92	13.0	3.3
	5824 ♀	28 11	0 3			42	7.1	(0.0)
		96 21 (117)	10 4 (14)	0 2 (2)	0 1 (1)	134	11.2	2.2

Summary of Information on Individual Translocations

T 1-9 4398-4

In addition to the data of Table 2, a backcross partial progeny of chiefly parental endosperm phenotypes gave 1 crossover in 90 plants in the wx-T interval. The data may be summarized as follows:

Table 2	287 plants	C 6.6 sh 15.3 wx 2.4 T
Additional	90 plants	wx 1.1 T

The genes C and wx are linked in the homozygous translocation, confirming that the interchange point is to the right of wx. There are no clear partly-filled pollen grains and probably no functioning duplicate-deficient gametes.

T 1-9 4995-5

The data of Table 2, together with wx-T data from partial progenies are as follows:

Table 2	317 plants	C 6.0 sh 16.1 wx 4.4 T
Additional	139 plants	wx 5.0 T

The data of Table 2 show a higher frequency of multiple crossovers than expected and suggest that some individuals may have been misclassified. However, all wx-T values are fairly uniform.

The position of the translocation to the right of wx is confirmed by the linkage of C and wx in the homozygous translocation. There are no clear partly-filled pollen grains and no evidence of functioning of duplicate-deficient gametes.

T 2-9 6656-4

Information is available from Table 2 and from wx-T linkage in partial progenies:

Table 2	92 plants	C 2.2 sh 10.9 wx 1.1 T
Additional	118 plants	wx 2.5 T

The translocation is to the right of wx, as is confirmed by C-wx linkage in the homozygous translocation.

T 3-9 c

This translocation, which appeared in material X-rayed by Anderson in 1935, has previously been studied by Anderson (1938) and Anderson and Brink (1940). Data from Tables 3 and 9, together with linkage data of Anderson (1938), are as follows:

Anderson (1938)	328 plants	wx 7.6 T
Table 3	96 plants	C 4.2 sh 16.7 wx 1.0 T
Table 9	67 plants	C 4.5 wx 1.5 T
Combined data, Tables 3 and 9	163 plants	wx 1.2 T

The reasons are not known for the erratic linkage results obtained with this translocation. Data from Tables 3 and 9 indicate markedly different recombination values for the C-wx region, while all wx-T values were uniformly lower than those obtained by Anderson (1938). The results do not seem explainable on the basis of misclassifications. The linkage data from both Tables 3 and 9 were

derived from female transmission. In view of Burnham's (1950, 1951) findings that plants heterozygous for T 5-9a give much higher recombination values when used as male than when used as female parents, it would be of interest to make a similar comparison with this translocation.

Linkage of C and wx in the homozygous translocation confirms the placement of the translocation breakpoint to the right of wx.

T 4-9$_{5657-2}$

Linkage information is available from Table 8 and from partial progenies:

Table 8	242 plants	C 12.4 wx 0.0 T
Additional	201 plants	wx 4.0 T

From partial progenies involving 201 plants, 8 crossovers were obtained. The indicated order was wx-T. It should be re-emphasized that data from the partial progenies are not strictly comparable with those in the tables. Linkage of C and wx in the homozygous translocation places the interchange point to the right of wx, in agreement with the evidence from the partial progenies. The translocation gives no clearcut partly-filled grains and probably no duplicate-deficient gametes function.

T 4-9$_{6222-1}$

Data from Table 5 are as follows:

Table 5	368 plants	C 3.3 T 0.3 sh 6.3 wx

Pollen of plants heterozygous for this translocation appears about twenty-five percent sterile. About two-thirds of the grains are non-waxy in phenotype in a cross of the type indicated in Table 5. Otherwise, it has not proven possible to distinguish any differences in the appearance of the normal grains. As is evident from Table 5, progeny of the phenotype c + Sh Wx appear in high frequency. Since these individuals would otherwise have to arise by double crossing over within the very short C-sh region, it is clear that they are aneuploid types, lacing the tip of 9S (including the C locus). McClintock (1941) has reported that terminal deficiencies up to and including one-third of the short arm of chromosome 9 may be transmitted through the female gamete. She also reported the locus of C to be approximately one-fourth of the distance in from the end of the arm. Though pollen lacking more than the terminal chromomere of the short arm of chromosome 9 is non-functional, pollen grains lacking up to one-third of the arm are not visibly abnormal (McClintock, 1942). The behavior of the duplicate-deficient gametes and the appearance of the pollen grains produced from this translocation are in complete agreement with her findings.

The presumed aneuploid individuals are indicated as circled numbers in Table 5. Those that were test-crossed as pollen parents and yielded classifiable progeny gave very unbalanced phenotypic classes of the types expected from their presumed aneuploid nature. On the basis of the several kinds of evidence mentioned, all the plants

which appeared to represent crossovers in regions 1,2 or in regions 1,2,3 are considered to have resulted from the functioning of duplicate-deficient eggs. The three plants which appeared to represent triple crossovers probably arose in each case from the functioning of a duplicate-deficient egg with a crossover in the sh-wx region.

The interchange point is probably somewhat closer to the sh locus than to C. Of the eleven individuals phenotypically C Sh Wx, ten were crossovers between C and T, the remaining one being in the T-sh interval. The two plants in the reciprocal c sh wx class both had normal pollen. Tests for male transmission from these plants did not yield classifiable kernels. They may, thus, have represented either crossovers between C and T or aneuploid types which crossed over between T and sh. Considering the former to be true for purposes of calculations, the linkage relations on the basis of these data become

C 3.3 T 0.3 sh

This translocation has been placed cytologically at L.01 in chromosome 4. Though the test has not yet been made, close linkage of C and su in the homozygous translocation would provide clear confirmation that the interchange point is actually in the long arm of chromosome 4.

T 5-9a

Results of Burnham (1934a) indicate this translocation is in the proximal part of the short arm of chromosome 9. His data indicated the linkage order sh-wx-T with less than one percent crossing over

between wx and T. He also reported much non-homologous pairing and reduction of crossing over in the heterozygous translocation. The data of Table 4 are in close agreement with his placement:

Table 4	431 plants	C 1.4 sh 9.3 wx 0.5 T

The position of this interchange to the right of wx is confirmed by the linkage of C and wx in the homozygous translocation.

Unpublished results of Burnham (1950, 1951) indicate that plants heterozygous for this translocation show a much higher recombination value for the sh-wx region when used as the male parent than when used as the female parent. Data in Table 4 are all from female-transmission so information bearing upon this relation is not available here.

$T\ 5\text{-}9_{4817\text{-}7}$

Data from male-transmission are found in Table 2 and from female-transmission in Table 8:

Table 2	198 plants	C 3.0 sh 20.2 wx 3.0 T
Table 8	87 plants	C 23.0 wx 3.4 T
Combined data	285 plants	C 23.2 wx 3.2 T

Linkage values from the two sources agree closely in indicating the interchange point in chromosome 9 to be to the right of wx.

$T\ 5\text{-}9_{5614\text{-}3}$

Linkage values from reciprocal crosses of this translocation suggest that crossover values may be somewhat higher when the interchange is male-transmitted. The numbers involved are, however, not

large. Data from Tables 2 and 8 (female and male transmission, respectively) are as follows:

Table 2	73 plants	C 1.4 sh 17.8 wx (0) T
Table 8	182 plants	C 30.8 wx 2.7 T
Combined data	255 plants	C 27.5 wx 2.0 T

Pollen observations have indicated that most of the partially filled grains produced are of waxy staining reaction. Of 682 partly-filled grains counted from one semi-sterile plant only 6 stained non-waxy. The interchange point thus appears to be in 9L close to the centromere.

T 6-9$_{4505-4}$

From the data in Tables 7 and 8, the indicated linkage order is C-wx-T:

Table 7	196 plants	C 30.6 wx 8.7 T
Table 8	217 plants	C 27.6 wx 2.8 T

Clearly-classifiable partially filled pollen grains are produced which give the waxy staining reaction in nearly all cases. Counts of several hundred such pollen grains yielded fewer than one percent staining non-waxy. The interchange point thus appears to be in the proximal part of 9L. These relations are in agreement with the linkages shown in Table 8, which represent data from male transmission of the translocation.

The data of Table 7, which also involve the additional gene, Y,

are from female-transmission. The considerably higher wx-T crossover value calculated from this cross is due partly to the occurrence of more single crossovers in this region and partly to the classification of a few plants as representing certain rather unexpected multiple crossovers. Certain of these latter categories suggest strongly that misclassifications were made. The possibility of differential rates of crossing over in megasporogenesis and microsporogenesis is not ruled out, however.

Pollen observations of plants heterozygous for this translocation indicate that the functioning of duplicate-deficient gametes in crosses of the type tabulated in Table 7 would probably give rise chiefly to kernels of colored, waxy phenotype. There is no evidence of an excess of this phenotypic class in the progeny. Neither were any aneuploid plants giving clearly partly-filled pollen recognized. It appears, then, that in this particular cross duplicate-deficient gametes were not functional. This does not preclude the possibility, however, that with this translocation and others reported, such unbalanced gametes may function under proper environmental conditions.

On the basis of information in Table 7, the translocation appears to be somewhat more closely linked to Y, in chromosome 6, than to wx. Similar results were obtained in another test when plants representing reciprocal crossover classes between wx and Y were grown and classified for pollen sterility. Of thirty-four plants tested, thirty were of the types expected from crossing over between wx and T. They have not

been tested individually for confirmation, however.

This translocation may be of particular value in giving information on the cytological position of the Y locus in chromosome 6. If the above conclusions are correct, linkage of wx and Y in the homozygous translocation will indicate that the Y locus in 6L is distal to the point of interchange. Absence of linkage will indicate that Y is proximal to the interchange point.

T 7-9 a

A total of 575 plants were grown in backcross tests measuring wx-T linkage. Two crossovers were obtained giving a wx-T value of 0.3 percent. The linkage order is not known.

T 7-9 b

This translocation is very closely linked to wx. Several hundred plants have been grown by Dr. Anderson, K. L. Retherford, and by the writer in the course of linkage studies. The single crossover obtained was recovered by Retherford from a plant population of unknown size. The wx-T distance is thus probably less than one percent. Table 1 indicates cytological positions of 7S.92 and 9S.24 for this interchange. The partly-filled pollen produced stains non-waxy, with very few exceptions, indicating the translocation break is between wx and the centromere in chromosome 9 (in all cases where reference is made to the staining reaction of the partly-filled pollen, it is presumed that the wx allele is carried on the normal chromosome 9).

Duplicate-deficient eggs function with frequencies ranging up to complete transmission, based on excess kernels in certain phenotypic classes. Several resulting aneuploid plants have been examined cytologically by Dr. Longley and found to have resulted from the functioning of eggs containing chromosomes 7^{9} and 9. Such gametes are duplicated for most of the short arm of 9 and deficient for the tip of the short arm of chromosome 7.

T $7\text{-}9_{4363\text{-}1}$

The data of Table 10 indicate a linkage order of C-T-wx:

Table 10 134 plants C 11.2 T 2.2 wx

Staining reactions of the partially filled pollen are consistent with this order.

T $7\text{-}9_{7074\text{-}6}$

Linkage data are available from Table 6:

Table 6 179 plants T 0.6 C 1.1 sh 14.0 wx

The linkage of C and wx in the homozygous interchange confirms the placement of the interchange point distal to C. Only one cross-over between T and C was obtained, its genotypic constitution being verified in a subsequent progeny test.

Duplicate-deficient eggs functioned with high frequency and gave rise to plants of the expected phenotype. Pollen from such plants is all of normal appearance. Most of the aneuploid plants are thus tabulated in the column headed Region 1 Recombinations. Those entered

as being phenotypically recombinants for regions 1 and 3 presumably represent duplicate-deficient types with associated crossing over in region 3.

McClintock (1943) states that C is located within the fifth or sixth chromomere from the end of the short arm of chromosome 9. The position of this translocation, then, is at some point within the terminal few chromomeres. This agrees closely with the cytological determination. Observation of pachytene figures of the homozygous translocation confirms the position of the other interchange point in the proximal part of the long arm of chromosome 7.

$$T\ 8\text{-}9_{5300\text{-}3}$$

No wx-T crossovers have yet been obtained. The linkage data from Table 2 and from partial progenies are as follows:

Table 2	210 plants	C 3.3 sh 10.0 wx (0) T
Additional	74 plants	wx (0) T

Partly-filled pollen grains produced by plants heterozygous for this interchange are nearly all of non-waxy staining reaction. Of 336 partially-filled grains counted in one sample, none was waxy. Several other slides of pollen which were scanned showed considerably less than one percent waxy.

The interchange point in chromosome 9 is therefore apparently between wx and the centromere.

Two plants of Family 5828 were classified as aneuploid. Both were of the phenotypic class expected if eggs deficient for the outer

portion of 8L and duplicated for most of 9S had functioned.

T 8-9$_{6673-6}$

Information bearing on the position of this translocation is available from Table 7 and from partial progenies:

Table 8	170 plants	C 15.3 wx 2.9 T
Additional	187 plants	wx 2.7 T

That the translocation is to the right of wx is confirmed by linkage of C and wx in the homozygous translocation.

The linkage relations of the various translocations just discussed are summarized in Table 11. The translocations are listed roughly in the order of their position from left to right in the chromosome on the basis of their genetical placement. In most instances recombination values are also indicated for neighboring chromosome regions to indicate the degree of influence exerted by a translocation on linkage relations of adjoining genes. Recombination values in parentheses are based on totals which include the data from partial progenies. In no case did the inclusion of these data appear to distort the linkage values appreciably. In the next to last column is indicated the probable position of some of the translocations with respect to the short arm or long arm of the chromosome. In some cases, the arm is obvious from the position of the interchange point to the left of wx; in the other instances notes, the evidence is derived from the staining reaction of the partly-filled pollen produced by the heterozygous interchange. In

Table 11. Summary table of linkage information on chromosome 9 translocations.

Translocation	Linkage Relations*	Number of Plants*	Prob. Chromosome Arm	Cytolog. Position in chromosome 9
7-9 7074-6	T 0.6 c 1.1 sh 14.0 wx	179	S	S.84
4-9 6222-1	c 3.3 T 0.3 sh 6.3 wx	368	S	S.82
7-9 4363-1	c 11.2 T 2.2 wx	134	S	S.11
8-9 5300-3	c 3.3 sh 10.0 wx 0.0(0.0)T	210(284)	S	S.41
7-9 b	wx < 1.0 T >	200	S	S.24
7-9 a	wx 0.3 T or T 0.3 wx	575		S.08
4-9 5657-2	c 12.4 wx 0.0(1.8) T	242(443)		S.14
5-9 a	c 1.4 sh 9.3 wx 0.5 T	431		S.21
2-9 6656-4	c 2.2 sh 10.0 wx 1.1(1.9)T	92(210)		S.32
3-9 c	c 12.9 wx 1.2 T	163		S.20
5-9 5614-3	c 27.5 wx 2.0 T	255	L	S.25
1-9 4398-4	c 6.6 sh 15.3 wx 2.4(2.1)T	287(377)		S.19
6-9 4505-4	c 27.6 wx 2.8 T	217	L	S.16
8-9 6673-6	c 15.3 wx 2.9(2.8)T	170(357)		S.15
5-9 4817-7	c 23.2 wx 3.2 T	285		S.08
1-9 4995-5	c 6.0 sh 16.1 wx 4.4(4.6)T	317(456)		S.14

* Linkage values in parentheses are based on the number of plants indicated in parentheses.

addition to those noted, T 5-9a is also in the short arm on the basis of Burnham's (1934a) evidence. In the cultures reported here, the Wx allele was carried on the normal 9 chromosome. To differentiate between a position in the short arm or in the long arm, it would be necessary under these circumstances to be able to distinguish partly-filled pollen grains of Wx wx and Wx constitutions by their staining reactions. This was not attempted.

Discussion

The results of the linkage studies just presented have been in close agreement with previous information on linkage relations in chromosome 9. One translocation (T $7\text{-}9_{7074\text{-}6}$) was shown to have its interchange point in chromosome 9 distal to the locus of C. Cytological placement of this translocation at 9S.84 is in good agreement with McClintock's (1941) statement that C is in the fifth or sixth chromomere from the end of the short arm. A second translocation (T $4\text{-}9_{6222\text{-}1}$) was shown to be between C and sh_1. In each case, female gametes deficient for the region beyond the interchange point in the short arm of chromosome 9 were functional. Pollen grains of like duplicate-deficient constitution were of normal appearance in each case. These results conform with previous observations of McClintock, cited earlier. Except for T $7\text{-}9_{4363\text{-}1}$, which was found to be between C and wx, the remainder of the translocations were placed to the right of wx. Those which gave clearly-classifiable partly-filled pollen could be assigned

to either the short or long arm. Translocations with interchange points near the centromere of chromosome 9 have given somewhat variable amounts of crossing over. Several of them have been reported to show much asynapsis and nonhomologous pairing. Of the translocations listed in Table 11, two are designated as being located in the long arm. Each gave about two percent crossing over with wx, conforming with the statement of Anderson and Randolph (1945) that the centromere is probably not far beyond a minimum of two crossover units from wx. Since McClintock (1941) found wx to be located at about the middle of the short arm, it is obvious that chiasma frequencies are greatly reduced in the proximal half of the arm.

Evidence presented by Rhoades (1951) suggests strongly that the long arm of chromosome 9 contains regions duplicated elsewhere in the chromosome complement. The entire arm cannot be considered redundant chromatin, however, since the presence of at least some portions of the long arm are known to be essential for normal gametophyte development. Adjacent segregations from some translocations involving chromosome 9 have resulted in spores lacking various amounts of the terminal portions of the long arm of 9. Gametophytes lacking these segments have usually been abortive.

Several translocations with interchange points near the centromere of chromosome 9 have shown much asynapsis and non-homologous pairing. This behavior may be related to duplications or rearrangements of chromatin in this region of the chromosome.

The waxy-staining reaction has been found valuable in assigning certain chromosome 9 translocations to one arm or the other. It is probable that with improvements in techniques and experience in classification of various abortive pollen types, many more of the chromosome 9 translocations could be assigned in this manner with a fair degree of assurance.

The appearance of the aborted pollen grains produced by plants heterozygous for translocations varies considerably in different instances both in degree of starch deposition and in size of the pollen grains. If this appearance is largely an effect of the region missing and is relatively less affected by the region duplicated, a characterization of pollen types might prove useful as a check on cytological placements. Translocation 5-9a, for example, gives partly-filled grains which are uniformly about one-third filled and which are considerably smaller than the normal grains. This is apparently an expression of the lack of the distal one-fifth of the long arm of chromosome 5. Other translocations in the long arm of chromosome 5 give pollen grains filled to a greater or lesser degree than does T 5-9a. In several translocations examined, the degree of starch deposition appeared to be roughly correlated with the extent of the deficiency indicated by the cytological placement. A similar effect of deficiencies is noted for the short arm of chromosome 9. Pollen grains lacking up to about one-third of the distal part of the arm appear normal. Lacking more than that, they appear progressively less

filled. Those that lack most of the arm have only a trace of starch. The appearance of the pollen grains thus may give information on the position on an interchange point in the short arm of chromosome 9. A correlation of pollen types and interchange points would undoubtedly prove helpful in other chromosome regions, as well.

PART V. LINKAGE RELATIONS OF SOME TRANSLOCATIONS IN CHROMOSOME 2

Previous information on chromosome 2

The following map of chromosome 2 (Figure 3) is based on a linkage map prepared by Rhoades (1950):

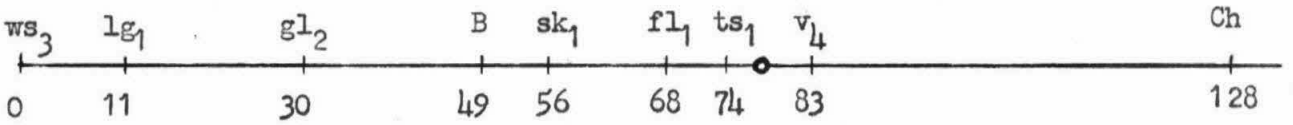


Figure 3. Linkage map of chromosome 2 in maize.

The most distal known locus in the short arm is ws$_3$. Its map position is 11 units beyond lg$_1$, which has been reported by McClintock (1931) to be within the very short region consisting of the terminal four chromomeres of the short arm. The very high chiasma frequency in the distal few chromomeres is thus seen to resemble the behavior of the tip of the short arm of chromosome 9, mentioned earlier. Pericentric inversion 2b is proximal to and gives 17 percent crossing over with B (Morgan, 1950). Since the inversion break in the short arm is at approximately the half-way point, B is placed in the distal half of the short arm. The centromere is somewhere in the region between ts$_1$ and v$_4$, probably somewhat closer to ts$_1$ (Anderson and Randolph, 1945). Translocation 2-9b, which has been placed cytologically at 2S.1, is approximately 5 units to the right of ts$_1$. Linkage relations in the homozygous translocation confirmed the position of the break in the short arm. Translocation 2-5a, studied by Rhoades (1933) and placed

in the long arm near the centromere, is to the left of $\underline{v}_4$ and gave 7.3 percent crossing over with that gene. Inversion 2b, placed cytologically at 2L.15, was found to be 5.5 units proximal to $\underline{v}_4$ (Morgan, 1950). Thus, the centromere is at least 5 units to the right of $\underline{ts}_1$ and 7 or more units to the left of $\underline{v}_4$. The only other moderately satisfactory gene known to be in the long arm is Ch, which is located 45 units from $\underline{v}_4$.

Studies by Morgan (1950) clearly illustrate the disproportionately large amount of crossing over in the distal half of the short arm. The genetic length of the entire arm is about 79 units, yet a minimum of 66 units in the distal half is indicated by his data. The fact that $\underline{gl}_2$-$\underline{v}_4$ recombination was not significantly reduced in plants heterozygous for inversion 2b was also taken to indicate that recombination is low in regions adjacent to the centromere in chromosome 2.

Descriptions and classification of marker genes used

Linkage relations were determined in crosses involving various combinations of the genes $\underline{lg}_1$, $\underline{gl}_2$, B, $\underline{sk}_1$, and $\underline{v}_4$. Leaves of plants homozygous for the $\underline{lg}_1$ allele (Emerson, 1912a, 1912b) usually lack the ligule and auricles and stand upright at the base. Classification was made at the seedling stage and checked in mature plants. Leaves of plants homozygous for $\underline{gl}_2$ (Hayes and Brewbaker, 1928) have characteristic glossy surfaces. Classification of young seedling leaves is excellent, with classification becoming more difficult as the plants develop. Separation of mature plants for this character is

not reliable. Classification of seedlings is easily made by spraying the leaves with a fine water mist. Water adheres in large droplets to the leaf surfaces of glossy seedlings, whereas on normal leaves it forms small beads, which easily roll off. The gene B (Emerson, 1921) influences plant coloration. As used in these studies it differentiated purple and sunred plants from those which were of dilute coloration or were green. It was classified as a mature plant character (See Emerson, Beadle, and Fraser, 1935, for plant color interactions). Plants homozygous for the sk_1 allele (Jones, 1925) have abortive pistils. Since silks do not develop, the plants are female-sterile. Classification must be made in the mature plant stage. Seedlings homozygous for the v_4 allele (Demerec, 1924b) are a pale yellowish-green. As they mature they turn green slowly and at later stages cannot be distinguished from normal green plants. Classification of the virescent seedlings is good in the greenhouse but may be uncertain when they are field-grown.

In linkage tests involving these genes, separations for lg_1, gl_2, and v_4 were made in the greenhouse in the seedling stage, and the seedlings then transplanted to the field. Plants were classified at maturity for sk_1 and B, and for pollen sterility due to the translocation.

Cytological positions of chromosome 2 translocations used

The translocations selected for genetic placement in chromosome 2 were restricted to those which were reported on the basis of

cytological determinations to have one interchange point in either the short arm or near the centromere. The translocations studied, together with their cytological determinations, are listed in Table 12.

Linkage data

The linkage data in the tables are all from backcrosses, with the exception of some progenies which were F_2's for the $\underline{v}_4$ gene. In the latter progenies, recombination with $\underline{v}_4$ was calculated with the phenotypically virescent plants, and the resulting linkage values were enclosed in parentheses. In some instances backcross and F_2 data with $\underline{v}_4$ were combined. In each case this combined value was also enclosed in parentheses in the tables and in the summaries.

Since the $\underline{sk}_1$ gene was followed in most of these backcrosses, it was necessary that the F_1 be used as the female parent. For this reason, comparable data on linkage relations from male and female transmission of the translocations are not available.

The linkage relations of $\underline{lg}_1$, $\underline{gl}_2$, $\underline{B}$, $\underline{sk}_1$, and $\underline{v}_4$ in the normal chromosome 2 were measured in the crosses tabulated in Table 13. The resulting recombination values (based on 413 plants) were as follows:

$\underline{lg}_1$ 15.7 $\underline{gl}_2$ 18.2 $\underline{B}$ 10.6 $\underline{sk}_1$ 28.3 $\underline{v}_4$

The map distances for the corresponding intervals on the linkage map shown earlier are as follows:

$\underline{lg}_1$ 19 $\underline{gl}_2$ 19 $\underline{B}$ 7 $\underline{sk}_1$ 27 $\underline{v}_4$

The linkage data from crosses involving various chromosome 2 translocations are presented in Tables 14-22. The recombination values

Table 12. Cytological positions of chromosome 2 translocations used in linkage placements.

Translocation	Cytological Determination		Authority *
1-2 4937-8	1L.07	2S.11	
1-2 5255-8	1S.21	2S.25	
2-3 c	2S.51	3S.66	
	2S.6	3S.8	Anderson and Brink (1940)
2-3 e	2S.90+	3L.34	
(2-3a)	2S.9	3L.6	Burnham & Cartledge (1939)
2-3 5304-3	2S.67	3L.39	
2-3 6862-6	2S.34	3L.16	
2-5 e	2S.12	5S.23	
2-5 g	2S.79	5S.28	
2-5 4741-4	2S.30	5L.26	
2-7 6372-2	2S.13	7L.19	
2-8 c	2S.17	8S.13	
2-8 5483-4	2S.35	8S.60	
2-9 a	2S.48	9L.85	
	2S.7	9L.6+	Anderson (1938)
2-10 5561-3	2S.22	10S.12	

* Except where otherwise indicated all cytological determinations listed here were made by Dr. A. E. Longley (1950, and Unpubl.).

obtained for the various regions are indicated in the discussion of the individual translocations. Where reciprocal crossover classes in the tables are unequal, reduced viability of certain of the recessive phenotypes was often responsible. In some cultures virescents, in particular, did not survive as well as green seedlings. Extreme inequalities of certain contrary classes were usually due to the functioning of duplicate-deficient eggs. In still other cases, results were obtained which suggested trisomic plants may have arisen by 3:1 disjunction from the translocation complex. These alternative possibilities are discussed later in the descriptions of the individual translocations. In order that the gametic types might be written more easily in the linkage tables, the subscripts of the genes have been omitted.

Summary of Information on Individual Translocations

T 1-2_{4937-8}

The data from Tables 17 and 18 may be summarized as follows:

Table 17	95 plants	$\underline{gl}_2$ 26.3 $\underline{B}$ 11.6 $\underline{sk}_1$ 14.7 T 7.4 $\underline{v}_4$
Table 18	95 plants	$\underline{gl}_2$ 26.3 $\underline{B}$ 6.3 $\underline{sk}_1$ 14.7 T (3.4) $\underline{v}_4$
Combined data	190 plants	$\underline{gl}_2$ 26.3 $\underline{B}$ 8.9 $\underline{sk}_1$ 14.7 T (6.5) $\underline{v}_4$

The combined T-$\underline{v}_4$ value is based on 124 plants (95 in Table 17 and 29 in Table 18). Two plants in Table 17 that were classified as quadruple crossovers may represent misclassifications, though it seems unlikely. Another possibility is that they were trisomics that arose

from an egg produced by 3:1 disjunction and had all gene loci heterozygous. This would account for the dominant phenotype for all the genes, though such plants should have shown a considerable amount of sterility.

T 1-2$_{5255-8}$

The following data are from Tables 18 and 22:

Table 18	92 plants	$\underline{gl}_2$ 20.7 $\underline{B}$ 7.6 $\underline{sk}_1$ 7.6 T (3.7) $\underline{v}_4$
Table 22	91 plants	$\underline{gl}_2$ 19.8 $\underline{B}$ 18.7 $\underline{sk}_1$ 11.0 T
Combined Data	183 plants	$\underline{gl}_2$ 20.2 $\underline{B}$ 13.1 $\underline{sk}_1$ 9.3 T

There was one T-$\underline{v}_4$ crossover in 27 virescent plants of Table 18. Since this one plant was not silkless, the placement of T to the left of $\underline{v}_4$ is more likely. This position is also supported by the low $\underline{sk}_1$-T value.

T 2-3 c

Data are available from Table 21:

Table 21	199 plants	$\underline{gl}_2$ 12.1 $\underline{B}$ 2.0 T 4.0 $\underline{sk}_1$

Three plants were classified as double crossovers between $\underline{B}$ and $\underline{sk}_1$. It seems likely that they were misclassifications for sterility since double crossovers in this region are very improbable, particularly with the translocation present. Transferring these three plants to the non-crossover class gives the linkage values $\underline{B}$ 0.5 T 2.5 $\underline{sk}_1$.

This translocation was identified by Anderson (1935) and later studied by Anderson and Brink (1940). Data of Anderson (1947)

indicated the following order and linkage values: B 0.5 T 4.9 sk_1.

T 2-3e

This translocation, which has been carried in the writer's stocks under the designation 2-3e, is probably the same translocation used by Burnham under the designation 2-3a. Burnham and Cartledge (1939) reported the latter translocation to be less than one map unit from lg_1 and cytologically at 2S.9. The information on 2-3e below agrees closely with their data:

Table 15 280 plants T 0.4 lg_1 3.6 gl_2 7.1 B 12.5 sk_1

The interchange point in chromosome 2 of the translocation reported here was within the terminal few chromomeres of the short arm. McClintock (1931), through the use of terminal deficiencies, placed the locus of lg_1 somewhere within the terminal four chromomeres.

Three plants in Family 4367 were classified as being duplicate-deficient on the basis of the segregation of the pollen for normal and partly-filled grains. All were in the phenotypic class expected from the functioning of an egg lacking the tip of 2S beyond the locus of lg_1 and duplicated for the outer portion of 3L.

T $2\text{-}3_{5304\text{-}3}$

Table 16 gives the following linkage information:

Table 16 109 plants lg_1 7.3 gl_2 2.8 T 4.6 B 40.4 v_4

T $2\text{-}3_{6862\text{-}6}$

Data are available from Table 14:

Table 14 69 plants $\underline{lg}_1$ 21.7 $\underline{gl}_2$ 20.3 $\underline{B}$ 2.9 $\underline{sk}_1$ 8.7 T

T 2-5e

This translocation is near $\underline{v}_4$. The data from Table 18 are as follows:

Table 18 199 plants $\underline{gl}_2$ 24.6 $\underline{B}$ 13.1 $\underline{sk}_1$ 15.1 T (0) $\underline{v}_4$

Unpublished data of Dr. E. G. Anderson indicate that the translocation is to the left of $\underline{v}_4$. In the data of Table 18, there were no crossovers with the translocation among the 45 virescent plants.

T 2-5g

Information in Table 20 indicates the translocation is between $\underline{gl}_2$ and $\underline{B}$:

Table 20 146 plants $\underline{lg}_1$ 6.8 $\underline{gl}_2$ 2.1 T 4.1 $\underline{B}$

T $2\text{-}5_{4741\text{-}4}$

The backcross data from Table 22 are as follows:

Table 22 117 plants $\underline{gl}_2$ 12.6 $\underline{B}$ 4.2 $\underline{sk}_1$ 3.7 T

T $2\text{-}7_{6372\text{-}2}$

Data from Tables 17 and 19 are as follows:

Table 17 200 plants $\underline{gl}_2$ 20.0 $\underline{B}$ 7.5 $\underline{sk}_1$ 8.0 T 14.0 $\underline{v}_4$

Table 19 76 plants $\underline{lg}_1$ 15.8 $\underline{gl}_2$ 26.3 $\underline{B}$ 22.4 T

T 2-8c

The following linkage information is from Table 18:

Table 18 202 plants $\underline{gl}_2$ 16.8 $\underline{B}$ 6.9 $\underline{sk}_1$ 13.9 T (2.0 $\underline{v}_4$

The position of the translocation with respect to $\underline{v}_4$ is uncertain. There was one crossover with the translocation among the fifty virescent plants. This plant was non-silkless (Sk), making the order $\underline{sk}_1$-T-$\underline{v}_4$ more likely.

T 2-8$_{5483-4}$

Information on this translocation is available from Tables 17 and 18:

Table 17	94 plants	$\underline{gl}_2$ 19.1 $\underline{B}$ 13.8 $\underline{sk}_1$ 28.7 T 11.7 $\underline{v}_4$
Table 18	107 plants	$\underline{gl}_2$ 19.6 $\underline{B}$ 10.3 $\underline{sk}_1$ 26.2 T (0) $\underline{v}_4$
Combined data	201 plants	$\underline{gl}_2$ 19.4 $\underline{B}$ 11.9 $\underline{sk}_1$ 27.4 T (9.4) $\underline{v}_4$

There were no T-$\underline{v}_4$ recombinants among the 23 virescent plants of Table 18. The combined T-$\underline{v}_4$ value is based on 117 plants (94 from Table 17 plus 23 from Table 18).

T 2-9a

This translocation was previously placed cytologically at 2S.7 by Anderson (1938) and was shown to be near $\underline{sk}_1$ (Anderson, 1947). The following data are available:

Anderson (1947)	784 plants	$\underline{sk}_1 \pm 0.5$
Table 14 (Family 4430)	81 plants	$\underline{lg}_1$ 27.2 $\underline{gl}_2$ 11.1 $\underline{B}$ 1.2 $\underline{sk}_1$ 1.2 T

Apparently, duplicate-deficient eggs functioned with high frequency in Family 4431, Table 14. As a result, more than half of

the progeny were classified as phenotypically lg gl b sk T. The aneuploid plants were probably actually Bbb, but other experience has indicated that plants of this constitution often develop little color except in the tassel glumes. Since non-silkless (Sk) individuals are in excess, the translocation is apparently proximal to $\underline{sk_1}$. If the interchange point were distal to $\underline{sk_1}$, the duplicate-deficient plants would probably be phenotypically silkless ($\underline{sk_1}$,$\underline{sk_1}$). Thus, the duplicate-deficient eggs which functioned in 4431 were apparently duplicated for the distal part of 2S (including the loci of $\underline{lg_1}$, $\underline{gl_2}$, $\underline{B}$, and $\underline{sk_1}$) and deficient for a distal part of 9L.

Family 4430 gave no indication of a large duplicate-deficient class. Here, as with certain duplicate-deficients described in connection with the chromosome 9 translocations, functioning of duplicate-deficient eggs may be quite variable.

T $2\text{-}10_{5561\text{-}3}$

Data in Table 17 place this translocation to the right of $\underline{v_4}$:

Table 17 211 plants $\underline{gl_2}$ 16.6 $\underline{B}$ 10.0 $\underline{sk_1}$ 24.6 $\underline{v_4}$ 3.8 T

The linkage relations of the chromosome 2 translocations are summarized in Table 23. The translocations are listed in their approximate order from left to right in the chromosome, on the basis of genetic information. Of the translocations studied, only $2\text{-}10_{5561\text{-}3}$ gives evidence of being to the right of $\underline{v_4}$. Certain of the others may be in the proximal part of the long arm between the centromere and $\underline{v_4}$, however. This possibility may be checked in some instances

Table 13.

Data from $\frac{+\ +\ +\ +\ +}{lg_1\ gl_2\ B\ sk_1\ v_4}$ x $lg_1\ gl_2 + sk_1\ v_4$

Regions	Gametic types	Numbers observed			
		Family 4432	Family 4433	Family 4434	Total
0	+ + + + +	27	31	37	95
0	lg gl B sk v	23	23	29	75
1	+ gl B sk v	4	5	7	16
1	lg + + + +	2	9	11	22
2	+ + B sk v	3	9	9	21
2	lg gl + + +	11	8	12	31
3	+ + + sk v	3	1	7	11
3	lg gl B + +	3	4	5	12
4	+ + + + v	6	20	11	37
4	lg gl B sk +	11	15	14	40
1,2	+ gl + + +	1	0	0	1
1,2	lg + B sk v	0	0	0	0
1,3	+ gl B + +	0	0	2	2
1,3	lg + + sk v	0	1	4	5
1,4	+ gl B sk +	1	2	5	8
1,4	lg + + + v	1	2	3	6
2,3	+ + B + +	0	3	0	3
2,3	lg gl + sk v	0	0	1	1
2,4	+ + B sk +	2	4	4	10
2,4	lg gl + + v	1	2	2	5
3,4	+ + + sk +	1	1	2	4
3,4	lg gl B + v	1	0	2	3
1,2,3	+ gl + sk v	0	0	0	0
1,2,3	lg + B + +	0	0	1	1
1,2,4	+ gl + + v	0	0	1	1
1,2,4	lg + B sk +	0	1	0	1
1,3,4	+ gl B + v	0	0	1	1
1,3,4	lg + + sk +	1	0	0	1
	Totals	102	141	170	413

Table 14.

Data from $\frac{+\ +\ +\ +\ T}{lg_1\ gl_2\ B\ sk_1\ +}$ x $lg_1\ gl_2 + sk_1 +$

Regions	Gametic types	Numbers observed		
		T2-3 6862-6 Family 4389	T2 - 9a Family 4430	T2 - 9a Family 4431
0	+ + + + T	15	27	47
0	lg gl B sk +	22	23	14
1	+ gl B sk +	8	9	10
1	lg + + + T	5	12	6
2	+ + B sk +	7	3	5
2	lg gl + + T	4	5	4
3	+ + + sk +	1		1
3	lg gl B + T	0		0
4	+ + + + +	1		2
4	lg gl B sk T	1		0
1,2	+ gl + + T			1
1,2	lg + B sk +			0
1,4	+ gl B sk T	1	1	
1,4	lg + + + +	1	0	
2,3	+ + B + T	1	1	
2,3	lg gl + sk +	0	0	
2,4	+ + B sk T	2		
2,4	lg gl + + +	0		
	Totals	69	81	90

Table 15.

Data from $\frac{T \; + \; + \; + \; +}{+ \; lg_1 \; gl_2 \; B \; sk_1} \times + \; lg_1 \; gl_2 + sk_1$

Regions	Gametic types	Numbers observed T 2-3e		
		Family 4366	Family 4367	Total
0	T + + + +	57	53 ③	110
0	+ lg gl B sk	58	56	114
1	T lg gl B sk	0	0	0
1	+ + + + +	0	1	1
2	T + gl B sk	1	1	2
2	+ lg + + +	1	0	1
3	T + + B sk	2	2	4
3	+ lg gl + +	4	3	7
4	T + + + sk	7	9	16
4	+ lg gl B +	7	9	16
2,3	T + gl + +	3	0	3
2,3	+ lg + B sk	0	3	3
3,4	T + + B +	1	1	2
3,4	+ lg gl + sk	0	0	0
2,3,4	T + gl + sk	0	0	0
2,3,4	+ lg + B +	1	0	1
	Totals	142	138	280

Table 16.

Data from $\frac{+\ +\ T\ +\ +}{lg_1\ gl_2\ +\ B\ v_4}$ x $lg_1\ gl_2\ +\ +\ v_4$

Regions	Gametic types	Numbers observed T 2-3 5304-3 Family 4395
0	+ + T + +	26
0	lg gl + B v	29
1	+ gl + B v	5
1	lg + T + +	1
2	+ + + B v	1
2	lg gl T + +	0
3	+ + T B v	0
3	lg gl + + +	2
4	+ + T + v	20
4	lg gl + B +	20
1,3	+ gl + + +	1
1,3	lg + T B v	0
1,4	+ gl + B +	1
1,4	lg + T + v	0
2,4	+ + + B +	0
2,4	lg gl T + v	1
3,4	+ + T B +	1
3,4	lg gl + + v	0
2,3,4	+ + + + v	0
2,3,4	lg gl T B +	1
	Total	109

Table 17.

Data from $\frac{+\ +\ +\ T\ +}{gl_2\ B\ sk_1\ +\ v_4}$ x $gl_2 + sk_1 + v_4$

Regions	Gametic types	Numbers Observed					
		T1-2 4937-8	T2-7 6372-2		T2-8 5483-4	T2-10 5561-3	
		Family 4382	Family 4412	Family 4413	Family 4414	Family 4423	Family 4424
0	+ + + T +	32	32	34	25	32	32
0	gl B sk + v	17	24	36	17	17	26
1	+ B sk + v	13	7	5	7	8	5
1	gl + + T +	6	9	5	3	8	7
2	+ + sk + v	4	2	1	3	2	3
2	gl B + T +	3	2	3	1	6	7
3	+ + + + v	5	0	2	6	11	7
3	gl B sk T +	5	3	0	11	14	10
4	+ + + T v	0	0	0	0	1	0
4	gl B sk + +	3	7	5	5	0	1
1,2	+ B + T +	2		1	2		
1,2	gl + sk + v	0		0	1		
1,3	+ B sk T +	0	1	1	2	3	
1,3	gl + + + v	1	1	0	1	2	
1,4	+ B sk + +	1	6	1	1		
1,4	gl + + T v	0	1	1	0		
2,3	+ + sk T +		0		2	1	
2,3	gl B + + v		2		1	1	
2,4	+ + sk + +		2		1		
2,4	gl B + T v		0		1		
3,4	+ + + + +	0	1	3	1	3	1
3,4	gl B sk T v	1	0	0	2	0	1
1,2,3	+ B + + v			1	0		1
1,2,3	gl + sk T +			0	1		0
1,2,4	+ B + T v						
1,2,4	gl + sk + +						
1,3,4	+ B sk T v						1
1,3,4	gl + + + +						0
2,3,4	+ + sk T v			0			
2,3,4	gl B + + +			1			
1,2,3,4	+ B + + +	(2)*					
1,2,3,4	gl + sk T v	0					
	Totals	95	100	100	94	109	102

* May be misclassifications or trisomics.

Table 18.

Data from $\frac{+\ +\ +\ T\ +}{gl_1\ B\ sk_1\ +\ v_4}$ x $gl_2 + sk_1 + \frac{v_4}{+}$

Regions	Gametic types	Numbers observed						
		T1-2 4937-8 Family 4381	T1-2 5255-8 Family 4383	T2 - 5e Family 4371	T2 - 5e Family 4372	T2 - 8c Family 4373	T2 - 8c Family 4374	T2-8 5483-4 Family 4415
0	+ + + T +	33	22	27	21	36	37	22
0	gl B sk + v	13	22	12	18	10	12	12
1	+ B sk + v	8	2	4	2	8	3	4
1	gl + + T +	8	8	12	11	4	8	9
2	+ + sk + v	0	1	2	2	2	3	2
2	gl B + T +	2	2	5	5	1	2	3
3	+ + + + v	5	1	1	1	5	4	3
3	gl B sk T +	4	3	5	6	3	2	12
4	+ + + T v	1	1	0	0	0	1	
4	gl B sk + +	8	18	15	15	17	19	19
1,2	+ B + T +	2	4	3				
1,2	gl + sk + v	1	0	0				
1,3	+ B sk T +	1		1	0		2	
1,3	gl + + + v	1		0	1		1	2
1,4	+ B sk + +	4	5	5	6	3	3	4
1,4	gl + + T v	0	0	0	0	0	0	
2,3	+ + sk T +			1	1			1
2,3	gl B + + v			0	0			
2,4	+ + sk + +	1		4		1	3	4
2,4	gl B + T v	0		0		0	0	
3,4	+ + + + +	3	3	5	4	3	7	7
3,4	gl B sk T v	0	0	0	0	0	0	
1,2,3	+ B + + v			2			1	
1,2,3	gl + sk T +			0			0	
1,2,4	+ B + T v					0		
1,2,4	gl + sk + +					1		
1,3,4	+ B sk T v				0			
1,3,4	gl + + + +				1			2
2,3,4	+ + sk T v							
2,3,4	gl B + + +							1
1,2,3,4	+ B + + +			1				
1,2,3,4	gl + sk T v			0				
	Totals	95	92	105	94	94	108	107

Table 19.

Data from $\frac{+\ \ +\ \ +\ T}{lg_1\ gl_2\ B\ +}$ x $lg_1\ gl_2\ +\ +$

Regions	Gametic types	Numbers observed T2-7 6372-2 Family 4411
0	+ + + T	19
0	lg gl B +	14
1	+ gl B +	3
1	lg + + T	5
2	+ + B +	7
2	lg gl + T	11
3	+ + + +	5
3	lg gl B T	6
1,2	+ gl + T	
1,2	lg + B +	
1,3	+ gl B T	3
1,3	lg + + +	1
2,3	+ + B T	2
2,3	lg gl + +	0
1,2,3	+ gl + +	
1,2,3	lg + B T	
	Totals	76

Table 20.

Data from $\frac{+\ +\ T\ +}{lg_1\ gl_2\ +\ B}$ x $lg_1\ gl_2\ +\ +$

Regions	Gametic types	Numbers observed T2-5g Family 4364	Family 4365	Total
0	+ + T +	33	29	62
0	lg gl + B	32	34	66
1	+ gl + B	3	3	6
1	lg + T +	2	2	4
2	+ + + B	2	0	2
2	lg gl T +	0	0	0
3	+ + T B	0	3	3
3	lg gl + +	2	0	2
2,3	+ + + +	0	1	1
2,3	lg gl T B	0	0	0
	Totals	74	72	146

Table 21.

Data from $\frac{gl_2\ +\ +\ +}{+\ B\ T\ sk_1}$ x $gl_2\ +\ +\ sk_1$

Regions	Gametic types	numbers observed T2-3c Family 4427	Family 4428	Family 4429	Total
0	gl + + +	34	24	22	80
0	+ B T sk	25	32	29	86
1	gl B T sk	3	4	2	9
1	+ + + +	2	6	7	15
2	gl + T sk	0			0
2	+ B + +	1			1
3	gl + + sk		0	0	0
3	+ B T +		3	2	5
2,3	gl + T +		0	0	0
2,3	+ B + sk		1	2	3
	Total	65	70	64	199

Table 22.

Data from $\frac{+\ +\ +\ T}{gl_2\ B\ sk_1\ +}$ x $gl_2 + sk_1 +$

Regions	Gametic types	Numbers observed		
		T1-2 5255-8 Family 4384	T2-5 4741-4 Family 4405	Family 4406
0	+ + + T	18	43	53
0	gl B sk +	34	40	42
1	+ B sk +	4	3	4
1	gl + + T	10	6	10
2	+ + sk +	6	0	1
2	gl B + T	7	2	0
3	+ + + +	4	0	1
3	gl B sk T	2	1	2
1,2	+ B + T	2	1	2
1,2	gl + sk +	0	0	0
1,3	+ B sk T	1	1	0
1,3	gl + + +	1	0	0
2,3	+ + sk T	0	0	0
2,3	gl B + +	2	1	2
1,2,3	+ B + +			
1,2,3	gl + sk T			
	Totals	91	98	117

Table 23. Summary table of linkage information on chromosome 2 translocations.

Translocation	Linkage Relations*								No of Plants*	Cytolog. Position in chromosome 2
2-3 e	T	0.4	lg	3.6	gl	7.1	B		280	S.90+
2-5 g	lg	6.8	gl	2.1	T	4.1	B		146	S.79
2-3 5304-3	lg	7.3	gl	2.8	T	4.6	B		109	S.67
2-3 c	gl	12.1	B	2.0	T	4.0	sk		199	S.51
2-9 a	B	1.2	sk	1.2	T				81	S.48
2-5 4741-4	B	4.2	sk	3.7	T				117	S.30
2-7 6372-2	B	7.5	sk	8.0	T	14.0	v_{l_4}		200	S.13
2-3 6862-6	B	2.9	sk	8.7	T				69	S.34
1-2 5255-8	B	13.1	sk	9.3	T	(3.7)	v_{l_4}		183 (27)	S.25
2-8 c	B	6.9	sk	13.9	T	(2.0)	v_{l_4}		202 (50)	S.17
1-2 4937-8	B	8.9	sk	14.7	T	(6.5)	v_{l_4}		190 (124)	S.11
2-5 e	B	13.1	sk	15.1	T	(0)	v_{l_4}		199 (45)	S.12
2-8 5483-4	B	11.9	sk	27.4	T	(9.4)	v_{l_4}		210 (117)	S.35
2-10 5561-3	B	10.0	sk	24.6	v_{l_4}	3.8	T		211	S.22

* Linkage values in parenthese are based on the number of plants indicated in parentheses.

by observing linkages in the homozygous translocations.

Discussion

The linkage data summarized in Table 23 are in agreement with the placement of the gene B at about the half-way point in the short arm of chromosome 2. Three translocations were placed distal to B, two between B and gl_2, and one distal to lg_1. None was found between lg_1 and gl_2. All three translocations placed in the outer half of the short arm are seen from Table 23 to have had a marked effect in decreasing lg_1-gl_2 recombinations (standard map distance 19 units).

In many instances duplicate-deficient eggs functioned and gave rise to plants having portions of the short arm of chromosome 2 in triplicate. The marker genes in the triplicated portions in each case were represented by one dominant and two recessive alleles. Plants of Lg_1 lg_1 lg_1 constitution were found to be intermediate in phenotype between normal and liguleless. The leaf angle and faintness of the leaf collar resembled the liguleless phenotype, but usually a faint ligule could be detected. Plants of Gl_2 gl_2 gl_2 constitution gave a non-glossy phenotype when tested with water spray. It was not noted that they were especially difficult to classify. As stated under the discussion of T 2-9a, plants of B b b constitution often develop little color. The most reliable criterion appeared to be the development of color in the glumes. Plants of Sk_1 sk_1 sk_1 constitution appeared non-silkless. The triplicate nature of these chromosome regions was not suspected at the time the plants were classified, so no critical notes of the phenotypic effects were made, however.

PART VI. LINKAGE STUDIES OF SOME HOMOZYGOUS REARRANGEMENTS

Evidence was cited earlier that in certain maize chromosomes chiasma frequencies appear to be very unequally distributed in different regions. The short arm of chromosome 2 comprises about 79 units of the linkage map for that chromosome, yet Morgan (1950) found that a minimum of 66 units is in the distal half of the arm. Cytogenetic evidence indicates that both $\underline{ws}_3$ and $\underline{lg}_1$ are within the distal four chromomeres. Since they are 11 map units apart, a minimum chiasma frequency of 22 percent is indicated for this very short terminal region. Similarly, studies of McClintock (1941) have placed the wx gene at about the middle of the short arm of chromosome 9. A recent map by Rhoades (1950) indicates a map distance of 59 units distal to wx, while the centromere is probably not much more than 2 units to the right of wx. As in the case of chromosome 2, a large amount of crossing over may occur within a few chromomeres at the tip of the short arm of chromosome 9 (McClintock, 1943). The question arises whether the amount of crossing over characteristic of a region is due to the nature of its chromatin or whether it is also related to its position in the chromosome.

The relative positions of parts of the chromosome complement may be shifted by chromosome rearrangement. If the interchange points are at different distances from the centromeres, one region may be shifted closer to a centromere while another region is shifted farther away. The region shifted also becomes situated adjacent to a different chromosome region. If the recombination value of a region is affected by

its position within the chromosome, a change of position might be expected to produce a measurable change in crossing over.

Materials and Methods

The $\underline{lg_1}$-$\underline{gl_2}$ region of the short arm of chromosome 2 and the $\underline{C}$-$\underline{wx}$ region of the short arm of chromosome 9 were selected for testing the possible effect of chromosome position upon recombination values of a region. Both regions are normally in distal portions of their respective chromosomes. There have been numerous rearrangements in which an interchange has occurred in the interval between one of these regions and its centromere.

It was anticipated that the recombination values of a region might be dependent upon its position with respect to a centromere. Consequently, in selecting chromosome rearrangements for testing, attention was focused mainly on those whose cytological determinations indicated that the interchange points were at different distances from centromeres, and which thus shifted the regions under study either nearer to or farther from a centromere.

In Tables 24 and 25 are listed the chromosome rearrangements which were used in this study, together with their reported cytological positions. In each case the distance (in microns) of the interchange points from the centromeres has been calculated from the cytological placements. These calculations are based on a chart of the lengths of the pachytene chromosome arms relative to chromosome 10, the shortest

Table 24. Chromosome 2 rearrangements studied in homozygous condition.

Rearrangement		Cytological Determinations*		Calculated distance (μ) of interchange points from centromeres		Shift of $\frac{lg_1}{gl_2}$ region (μ)
				2S	other chrom	
Inv 2	a	2S.7	2L.8	22.7	36.8	out 14.1
2 - 3	c	2S.51	3S.66	16.5	15.8	in 0.8
2 - 7	6372-2	2S.13	7L.19	4.2	7.7	out 3.5
2 - 8	6612-2	2S.40	8L.55	12.9	23.1	out 10.2
2 - 9	a	2S.48	9L.85	15.5	27.6	out 12.1

* The positions for Inv 2a are from Morgan (1950). The remaining determinations were made by Longley (1950, and Unpubl.).

Table 25. Chromosome 9 translocations studied in homozygous condition.

Translocation		Cytological Determinations*		Calculated Distance (μ) of interchange points from centromeres		Shift of $\frac{C\text{-}wx}{}$ region (μ)
				9S	other chrom.	
1 - 9	4398-4	1L.51	9S.19	3.1	25.8	out 22.7
1 - 9	4995-5	1L.21	9S.14	2.3	10.6	out 8.3
2 - 9	6656-4	2L.36	9S.32	5.2	16.6	out 11.4
3 - 9	c	3L.15	9S.20	3.3	7.2	out 3.9
4 - 9	5657-2	4L.30	9S.14	2.3	13.0	out 10.7
5 - 9	a	5L.80	9S.21	3.4	28.9	out 25.5
6 - 9	b	6L.13	9S.42	6.8	5.6	in 1.2
7 - 9	7074-6	7L.03	9S.84	13.7	1.2	(39.3 added)
8 - 9	6673-6	8L.30	9S.15	2.4	12.6	out 10.2

* All cytological determinations by Longley (1950, and Unpubl.)

Table 26. Calculated lengths (in microns) of the pachytene chromosome arms of Zea mays.*

Chromosome	Short Arm	Long Arm
1	41.08	50.52
2	32.36	46.04
3	23.88	47.72
4	26.60	43.40
5	33.84	36.16
6	6.04	42.76
7	15.52	40.48
8	14.00	42.00
9	16.28	32.52
10	11.12	28.88

* based on unpublished data of Dr. A. E. Longley.

chromosome (Longley, unpubl.). The calculated length of each of the arms, indicated in Table 26, is based on a length of 40 microns for chromosome 10. In general, one chromomere of a pachytene chromosome has a diameter (or length) of about one micron. In the last column of Tables 24 and 25 is indicated the distance which the $\underline{lg_1}$-$\underline{gl_2}$ and $\underline{C}$-$\underline{wx}$ regions have been shifted in each rearrangement, and whether these regions have been moved outward from or inward toward a centromere. In the case of $7\text{-}9_{7074\text{-}6}$ evidence presented earlier indicates that a portion of 7L has been added on beyond the $\underline{C}$-$\underline{wx}$ region. In those instances where cytological determinations have been reported by more than one investigator, an attempt was made to select the placements which are in best agreement with genetic information. Several of the chromosome 9 placements must still be regarded as doubtful. Data summarized earlier in this paper indicate that some

of them may actually be in the long arm. In this case, of course, the C-wx regions will not have been shifted by the rearrangement. The reliability of the cytological evidence in specific instances is discussed in a later section.

Linkage Data

The backcross progeny classifications are entered in Tables 27 to 41. The individual plants which were tested are indicated in the first column. The direction in which the cross was made is indicated in the last column. Where no symbol is entered, the F_1 was used as the female parent; where a capital M is entered, it was used as the male parent. Reciprocal crosses of individual plants are listed adjacently in the tables to permit ready comparison of the data. The totals from female and male transmission are entered at the bottom of each table. With the exception of Table 39, all data are from backcrossing the homozygous rearrangements. Table 39 gives linkage values of normal sister plants of the homozygous translocation plants listed in Table 38.

Discussion.

Because of the number of rearrangements followed in this study, the amount of information on any one is necessarily limited. It was hoped, however, that sufficient information might be obtained to indicate whether or not chromosome position appeared to be altering normal linkage values in any of the rearrangements tested. With this

preliminary information, it would then be possible to select a few of the most promising ones for more critical testing on a larger scale.

A reference to the list of translocations used indicates that in most cases the regions studied were not shifted appreciably. In the absence of critical corroborative information on break points, differences of less than about ten microns are probably not to be considered significant. In most of the rearrangements available in stock, the two interchange points are at approximately the same distance from the centromeres. This is particularly true among the Bikini-induced translocations (Longley, 1950). In several instances, translocations in which the interstitial regions were first reported to be unequal have been indicated to be more nearly equal in later cytological observations. The cytological positions indicated in Tables 24 and 25 represent the best present information on the interchange points. The positions of inversion 2a and of T 5-9a may be considered fairly accurate. The former has been studied by Anderson (Unpubl.) and by Morgan (1950). Their cytological observations, together with those of Longley (1950), indicate that the $\underline{lg}_1$-$\underline{gl}_2$ region has been shifted outward slightly from the centromere. T 5-9a has been studied extensively by Burnham (1934a, 1950, 1951). Both his observations and those of Longley indicate the $\underline{C}$-$\underline{wx}$ region has been moved out a considerable distance. In the case of T $7\text{-}9_{7074\text{-}6}$, it is clear from evidence presented earlier that a long chromosome segment has been attached beyond the $\underline{C}$-$\underline{wx}$

region of chromosome 9.

The significance of small differences obtained is made uncertain in view of the number of variables in the tests. The stocks used were not inbred and are not strictly comparable. The Bikini-induced translocations arose in kernels of a commercial single cross hybrid and undoubtedly there is still much heterogeneity present. An effort was made to make exact reciprocal pollinations, where possible. There are, however, many cases in which plants have been crossed in only one direction. In some cases, data from more than one growing season are combined. Thus, it is not surprising to find some variability in recombination values.

In the case of T 6-9b, data are available (Tables 38 and 39) for linkage values in the normal sister plants for comparison with those obtained from the homozygous translocations. There appears to be no significant difference between the normals and their sister homozygous translocation plants. The recombination value for the normals is, however, unexpectedly low, and differs from the average C-wx distance of 26 shown in the Linkage Summary (Emerson, Beadle, and Fraser, 1935). Since the latter value is based on more than three hundred thousand individuals, the crossing over based on the normal plants segregating in the cultures with homozygous T 6-9b is almost certainly different from that average value.

Recombination values for the lg_1-gl_2 region appear to be somewhat higher for homozygous T $2\text{-}8_{6612\text{-}2}$ than for the other homozygous chromosome 2 translocations. The data are, however, not strictly comparable,

and should be considered only as a suggestion for further investigation.

Among the chromosome 9 translocations tested in the homozygous condition, several gave recombination values somewhat above the average value of 26 reported in the Linkage Summary. Only in the case of T 6-9b, however, were there sister plants of normal chromosome constitution for comparison. As mentioned above, there is in this instance some question as to whether the value from the normal plants may be taken as a standard for comparison. If linkage values of homozygous translocations be compared, it may be seen that T $8\text{-}9_{6673\text{-}6}$ gave somewhat higher values than did either T 6-9b or T 5-9a. Both of the latter translocations have shown much non-homologous pairing in the heterozygous condition, however, and it cannot be assumed that such difficulties would necessarily be absent in the homozygous translocation.

The single plant of T $2\text{-}9_{6656\text{-}4}$ that was used as a female parent gave a considerably lower recombination value when female-transmitted than when male-transmitted. Values from male-transmission of other plants also gave considerably higher values. The significance of these results is subject to question, but certainly a more extensive test seems warranted.

On the basis of data in Table 40, plants homozygous for T $7\text{-}9_{7074\text{-}6}$ gave a significantly higher C-wx recombination value when female-transmitted than when male-transmitted. Here, as before, the data are limited.

For results of convincing statistical nature it is obvious that several conditions need be fulfilled. It is desirable that all trans-

location stocks be backcrossed to the same stock to increase their homogeneity. If male and female transmission are to be compared, exact reciprocal crosses should be made, when possible. It is also important that the crosses be made at very nearly the same time during the same growing season. By restricting the number of tests to a few selected translocations, considerably larger populations can be tested in each case and the significance of the results increased.

For comparing recombination values in normals and homozygous translocations, T 2-8 $_{6612-2}$, T 6-9b, and T 8-9$_{6673-6}$ appear promising. For comparing differences in male and female transmission of the translocation homozygotes, T 2-9$_{6656-4}$ and T 7-9$_{7074-6}$ warrant more investigation.

Summarized results are indicated in Table 42. In each case the shift of either the $\underline{lg_1}$-$\underline{gl_2}$ region or the $\underline{C}$-$\underline{wx}$ region is listed along with the resultant mean percent crossing over in the region. The latter figure represents a mean of the actual percentages obtained in individual instances. Individual progenies of less than one hundred are not included in the calculations of the mean percents. In Tables 27-41 is indicated in each instance the percent recombination as calculated from the total number of individuals and the total recombinants. Comparison of these calculated percentages with the mean percentages listed in Table 42 indicates that the values are not appreciably different.

Table 27. Inversion 2a F_1 genotype: $\frac{+ \text{ gl } T}{\text{lg } + \quad T}$

Plant Numbers*	Number of Individuals					Recombinations		Transmitted as
	+ +	+ gl	lg +	lg gl	Total	Number	%	
820-7	5	67	54	3	129	8	6.20	
-7	3	1	3	1	8	4		M
-8	9	35	44	10	98	19		M
821-9	37	155	175	38	405	75	18.52	
-9	43	146	165	48	402	91	22.64	M
822-12	9	44	46	11	110	20	18.18	
-12	35	108	119	32	294	67	22.79	M
-15	6	25	23	7	61	13		M
-15T	5	11	14	2	32	7		M
823-6T	31	141	148	36	356	67	18.82	M
824-1T	6	30	27	6	69	12		M
-6T	25	125	127	32	309	57	18.45	M
-7	31	171	171	41	414	72	17.39	
-7	35	120	122	34	311	69	22.19	M
-10	29	141	134	24	328	53	16.16	
-10T	3	11	16	4	34	7		M
-13	15	117	123	28	283	43	15.19	
825-3	51	154	202	47	454	98	21.59	
-3T	17	54	67	14	152	31	20.39	M
-14	31	145	141	16	333	47	14.11	
826-10	23	101	111	29	264	52	19.70	
Totals(F)	231	1095	1157	237	2720	468	17.21	
Totals(M)	218	807	875	226	2126	444	20.88	
Combined Totals					4846	912	18.82	

* all plants listed were confirmed as homozygous inversions by progeny tests.

Table 28. T 2-3c F_1 genotype: $\frac{+\ +\ T}{lg\ gl\ T}$

Plant Numbers	Number of Individuals + +	+ gl	lg +	lg gl	Total	Recombinations Number	%	Transmitted as
802-3	114	32	24	116	286	56	19.58	
-6	126	38	31	138	333	69	20.72	
-7	165	38	33	170	406	71	17.49	
-7	77	21	27	71	196	48	24.49	M
-9	172	46	38	161	417	84	20.14	
-9T	117	30	19	122	288	49	17.01	M
803-2	106	26	17	120	269	43	15.99	M
806-1T	108	27	30	98	263	57	21.67	M
-4	96	36	46	98	276	82	29.71	
808-4	63	14	11	55	143	25	17.48	
-7	87	23	31	71	212	54	25.47	
2084-8	97	28	15	81	221	43	19.46	
-11	255	45	53	247	600	98	16.33	
2085-6	125	32	30	107	294	62	21.09	
-13	156	37	37	173	403	74	18.36	
2087-1	127	34	41	144	346	75	21.68	
Totals(F)	1583	403	390	1561	3937	793	20.14	
Totals(M)	408	104	93	411	1016	197	19.39	
Combined Totals					4953	990	19.99	

Table 29. T 2-7$_{6372-2}$ F_1 genotype: $\frac{+\ +\ T}{lg\ gl\ T}$

Plant Numbers	Number of Individuals ++	+ gl	lg +	lg gl	Total	Recombinations Number	%	Transmitted as
2074-7	37	13	8	36	94	21		M
-21	116	21	27	129	293	48	16.38	M
2076-2	257	41	47	194	539	88	16.33	
-2	109	21	24	116	270	45	16.67	M
-11	58	12	10	61	141	22	15.60	M
-14	45	13	16	57	131	29	22.14	M
2077-8	27	5	2	38	72	7		
-14	114	31	31	107	283	62	21.91	
-21	119	15	31	126	291	46	15.81	
2078-1	137	47	30	163	377	77	20.42	
-8	257	53	63	247	620	116	18.71	
Totals(F)	911	192	204	875	2182	396	18.15	
Totals(M)	365	80	85	399	929	165	17.76	
Combined Totals					3111	561	18.03	

Table 30. T 2-8$_{6612-2}$ F_1 genotype $\frac{+\ +\ T}{lg\ gl\ T}$

Plant Numbers	Number of Individuals					Recombinations		Transmitted as
	+ +	+ gl	lg +	lg gl	Total	Numbers	%	
2079-14	147	55	60	128	390	115	29.49	
-14	33	13	13	39	98	26		M
-18	117	27	38	114	296	65	21.96	
2080-14	152	42	60	153	407	102	25.06	
-14	96	33	46	105	280	79	28.21	M
-20	138	32	42	113	325	74	22.77	
-20	96	40	31	77	244	71	29.10	M
2081-8	111	28	29	99	267	57	21.35	
2082-17	64	22	19	62	167	41	24.55	
-17	106	35	28	108	277	63	22.74	M
2083-16	27	15	11	27	80	26		
-16	62	19	31	61	173	50	28.90	M
Totals(F)	756	221	259	696	1932	480	24.84	
Totals(M)	393	140	149	390	1072	289	26.96	
Combined Totals					3004	769	25.60	

Table 31. T 2-9a F_1 genotypes $\frac{+\ +\ T}{lg\ gl\ T}$ or $\frac{+\ gl\ T}{lg\ +\ T}$

Plant Numbers	Number of Individuals + +	+ gl	lg +	lg gl	Total	Recombinations Numbers	%	Transmitted as
354-11	123	31	41	127	322	72	22.36	
-14	81	20	28	78	207	48	23.19	
-15	98	35	33	106	272	68	25.00	
356-7	3	2	1	3	9	3		
-9	87	20	19	85	211	39	18.48	
357-1	29	77	59	28	193	57	29.53	
-7	47	11	13	49	120	24	20.00	
811-1	7	31	40	7	85	14		
-1	26	136	119	23	304	49	16.12	M
-2	27	162	144	42	375	69	18.40	M
815-3	108	25	32	112	277	57	20.58	
-7T	68	21	30	72	191	51	26.70	M
2090-2	45	89	120	26	280	81	28.93	M
2091-9	13	77	86	14	190	27	14.21	
-12	18	93	110	22	243	40	16.46	
-12T	30	180	147	38	395	68	17.22	M
-13	21	113	106	32	272	53	19.49	
-13	22	137	138	36	333	58	17.42	M
-23	11	45	36	10	102	21	20.59	
-27	26	90	100	27	243	53	21.81	M
2092-1	118	36	47	130	331	83	25.08	
2093-2	77	21	26	87	211	47	22.27	
-2	69	32	15	66	182	47	25.82	
-2	128	51	51	167	397	102	25.69	M
Coupling totals (F)	840	310	314	871	2335	545	23.34	
Repulsion totals(F)	70	359	378	85	892	155	17.38	
Grand totals (F)					3227	700	21.69	
Coupling totals(M)	196	72	81	239	588	153	26.02	
Repulsion totals(M)	176	794	768	192	1930	378	19.59	
Grand totals (M)					2518	531	21.09	
Combined totals					5745	1231	21.43	

Table 32. T 1-9$_{4398-4}$ F_1 genotype $\frac{C\ wx\ T}{c\ Wx\ T}$

Plant Numbers	Number of Individuals					Recombinations		Transmitted as
	C Wx	C wx	c Wx	c wx	Total	Number	%	
2010-1	70	119	112	45	346	115	33.24	
-1	46	79	108	34	267	80	29.96	M
-1	40	115	94	47	296	87	29.39	M
-1	54	58	78	35	225	89	39.56	M
-1	48	84	88	34	254	82	32.28	M
-1	65	90	124	65	344	130	37.79	M
Totals (F)	70	119	112	45	346	115	33.24	
Totals (M)	253	426	492	215	1386	468	33.77	
Combined Totals					1732	583	33.66	

Table 33. T 1-9$_{4995-5}$ F_1 genotype $\frac{C\ wx\ T}{c\ Wx\ T}$

Plant Numbers	Number of Individuals					Recombinations		Trans-mitted as
	C Wx	C wx	c Wx	c wx	Total	Number	%	
2001-1	35	106	86	40	267	75	28.09	
-1	44	78	86	31	239	75	31.38	M
-2	31	63	66	25	185	56	30.27	
-3	38	83	80	32	233	70	30.04	
-5	54	77	78	59	268	113	42.16	M
2002-4	51	73	96	44	264	95	35.98	
-5	39	102	104	45	290	84	28.97	
2003-2	24	94	97	19	234	43	18.38	
-3	40	115	105	46	306	86	28.10	
-3	27	101	83	38	249	65	26.10	M
-4	45	111	85	52	293	97	33.11	
-4	60	103	104	62	329	122	37.08	
-4	61	96	113	69	339	130	38.35	M
2004-1	48	81	99	37	265	85	32.08	
-2	40	42	58	24	164	64	39.02	
-3	16	34	28	14	92	30		
-3	70	116	157	76	419	146	34.84	M
-5	79	148	135	67	429	146	34.03	
-5	12	30	32	19	93	31		M
-6	45	91	94	46	276	91	32.97	
-7	67	146	144	76	433	143	33.03	
-7	57	90	93	66	306	123	40.20	M
2005-1	65	123	111	60	359	125	34.82	
-1	50	77	74	50	251	100	39.84	M
-2	48	89	83	48	268	96	35.82	
-2	17	18	25	11	71	28		
-3	67	93	97	58	315	125	39.68	
-4	42	88	128	52	310	94	30.32	
2006-1	31	84	61	39	215	70	32.56	
-2	51	111	94	36	292	87	29.79	
-2	50	79	85	56	270	106	39.26	M
-3	71	151	145	86	453	157	34.66	
-3	65	112	116	55	348	120	34.48	M
-4	52	80	107	52	291	104	35.74	
-6	58	102	106	60	326	118	36.20	
2008-1	41	70	72	42	225	83	36.89	
-2	30	74	68	45	217	75	34.56	
2009-5	29	64	78	27	198	56	28.28	
-5	37	81	84	23	225	60	26.67	M
-6	17	73	88	20	198	37	18.69	
Totals (F)	1277	2612	2644	1265	7798	2542	32.60	
Totals (M)	527	937	1001	542	3007	1069	35.55	
Combined Totals					10805	3611	33.42	

Table 34. T 2-9$_{6656-4}$ F_1 genotype $\frac{C\ wx\ T}{c\ Wx\ T}$

Plant Numbers	Number of Individuals C Wx	C wx	c Wx	c wx	Total	Recombinations Number	%	Transmitted as
2046-4	55	81	106	40	282	95	33.69	M
2047-2	83	114	156	53	406	136	33.50	M
-5	49	105	88	41	283	90	31.80	M
2048-2	17	65	59	16	157	33	21.02	
-2	44	88	83	54	269	98	36.43	M
-2	58	136	123	64	381	122	32.02	M
-4	66	125	120	59	370	125	33.78	M
-4	61	93	113	46	313	107	34.19	M
-4	23	37	46	27	133	50	37.59	M
-4	44	69	69	35	217	79	36.41	M
Totals (F)	17	65	59	16	157	33	21.02	
Totals (M)	483	848	904	419	2654	902	33.99	
Combined Tables					2811	935	33.26	

Table 35. T 3-9c F_1 genotype $\frac{C\ Wx\ T}{c\ wx\ T}$

Plant Numbers	Number of Individuals					Recombinations		Trans-mitted as
	C Wx	C wx	c Wx	c wx	Total	Number	%	
4313-4*	86	38	24	92	240	62	25.83	
-9*	38	11	12	22	83	23		M
-10*	90	38	40	86	254	78	30.71	
-10T*	25	10	9	27	71	19		M
4314-3*	88	30	51	76	245	81	33.06	M
4316-2*	57	38	42	71	208	80	38.46	M
2014-1	79	9	18	104	210	27	12.86	M
-3	144	56	55	159	414	111	26.81	
-3	97	38	48	85	268	86	32.09	M
-5	133	70	57	135	395	127	32.15	
-6	93	28	19	77	217	47	21.06	M
-8	117	51	49	115	332	100	30.12	
-8	53	24	22	47	146	46	31.51	M
-11	106	42	38	111	297	80	26.94	
-11	149	47	58	102	356	105	29.49	M
-12	178	68	74	157	477	142	29.77	
-15	21	10	12	29	72	22		M
-15	34	15	13	34	96	28		M
-18	112	37	36	108	293	73	24.91	
-19	117	38	54	105	314	92	29.30	
-20	108	54	63	104	329	117	35.56	M
-24	131	71	69	123	394	140	35.53	
-24	53	28	24	64	169	52	30.77	M
2015-2	113	74	84	115	386	158	40.93	M
-4	141	61	70	129	401	131	32.67	
-6	101	37	42	97	277	79	28.52	
-9	113	50	53	121	337	103	30.56	
2016-2	98	49	50	89	286	99	34.62	M
-3	97	44	63	102	306	107	34.97	
-10	168	96	69	154	487	165	33.88	
-12	99	45	25	81	250	70	28.00	
-17	192	69	78	167	506	147	29.05	
-19	139	68	60	143	410	128	31.22	
Totals (F)	2264	979	956	2185	6384	1935	30.31	
Totals (M)	1106	465	525	1046	3142	990	31.51	
Combined Totals					9526	2925	30.71	

* confirmed as homozygous translocation by progeny tests.

Table 36. T 4-9$_{5657-2}$ F_1 genotype $\frac{C\ wx\ T}{c\ Wx\ T}$

Plant Numbers	Number of Individuals					Recombinations		Transmitted as
	C Wx	C wx	c Wx	c wx	Total	Number	%	
2017-2	28	100	134	41	303	69	22.77	M
-3	70	152	133	69	424	139	32.78	
-3	44	133	184	48	409	92	22.49	M
-5	6	2	8	3	19	9		
-5	47	71	102	40	260	87	33.46	M
2018-2	47	91	126	43	307	90	29.32	
-3	68	95	94	54	311	122	39.23	M
-5	52	55	89	38	234	90	38.46	
-5	59	104	112	54	329	113	34.35	M
2019-3	21	28	32	24	105	45	42.86	
-5	65	111	133	66	375	131	34.93	M
-6	43	74	94	58	269	101	37.55	
-8	96	137	146	69	448	165	36.83	M
2020-1	28	45	51	22	146	50	34.25	
-1	22	56	61	24	163	46	28.22	M
-2	47	117	110	47	321	94	29.28	
-2	47	90	86	43	266	90	33.83	M
-3	12	26	24	19	81	31		
-5	32	72	77	33	214	65	30.37	
-5	37	58	72	35	202	72	35.64	M
2021-1	63	83	91	43	280	106	37.86	
-1	83	155	141	71	450	154	34.22	M
-5	1	4	8	2	15	3		
2022-1	38	64	56	41	199	79	39.70	
-1	68	75	74	52	269	120	44.61	M
-4	18	42	57	29	146	47	32.19	
-4	83	128	175	66	452	149	32.96	
-5	55	109	85	56	305	111	36.39	M
2023-1	27	26	31	13	97	40		M
-4	61	105	108	54	328	115	35.06	
2024-2	47	105	117	45	314	92	29.30	
-3	54	102	123	50	329	104	31.61	M
-5	93	141	152	73	459	166	36.17	
-6	54	107	116	56	333	110	33.03	M
-7	87	157	137	71	452	158	34.96	
Totals (F)	856	1540	1668	796	4860	1652	33.99	
Totals (M)	847	1480	1671	756	4754	1603	33.72	
Combined Totals					9614	3255	33.86	

Table 37. T 5-9a F_1 genotype $\frac{C\ Wx\ T}{c\ wx\ T}$

Plant Numbers	Number of Individuals				Recombinations			Trans-mitted as
	C Wx	C wx	c Wx	c wx	Total	Number	%	
2025-1	112	33	51	84	280	84	30.00	M
-4	121	29	37	128	315	66	20.95	
-4	103	32	35	83	253	67	26.48	M
-8	182	60	58	164	464	118	25.43	
-9	63	23	23	50	159	46	28.93	
-10	103	26	35	83	247	61	24.70	
2026-1	31	13	12	22	78	25		M
-8	143	49	42	130	364	91	25.00	
2027-1	135	52	45	112	344	97	28.20	M
-1T	67	19	16	39	141	35	24.82	M
-4	173	35	43	157	408	78	19.12	
-9	43	7	6	35	91	13		
2028-1	137	56	65	156	414	121	29.23	
-6	118	52	37	111	318	89	27.99	
-6	135	51	45	99	330	96	29.09	M
2029-2	161	46	40	124	371	86	23.18	M
-3	160	47	48	156	411	95	23.11	
-3	63	19	19	75	176	38	21.59	M
-4	155	43	53	155	406	96	23.65	
-5	70	4	12	57	143	16	11.19	
-6	140	36	38	149	363	74	20.39	
-6	66	43	48	138	295	91	30.85	M
-7	88	30	47	102	267	77	28.84	M
-7	65	18	13	47	143	31	21.68	M
2030-5	76	13	17	105	211	30	14.22	
2031-3	105	41	50	79	275	91	33.09	M
-4	70	31	22	80	203	53	26.11	M
2032-3	144	25	52	110	331	77	23.26	M
-4	103	26	25	101	255	51	20.00	M
Totals (F)	1684	480	514	1636	4314	994	23.04	
Totals (M)	1448	479	520	1295	3742	999	26.70	
Combined Totals					8056	1993	24.74	

Table 38. T6-9b F_1 genotype $\frac{C\ wx\ T}{c\ Wx\ T}$

Plant Numbers	Number of Individuals					Recombinations		Transmitted as
	C Wx	C wx	c Wx	c wx	Total	Number	%	
2036-2	35	82	94	28	239	63	26.36	M
-8	23	90	105	23	241	46	19.09	
-18	31	94	69	25	219	56	25.57	
-20	42	132	113	43	330	85	25.76	
-35	38	127	131	49	345	87	25.22	
2037-8	28	94	92	28	242	56	23.14	
-8	26	76	94	13	209	39	18.66	M
-22	39	86	106	42	273	81	29.67	M
-34	34	114	118	32	298	66	22.15	
-42	35	125	133	32	325	67	20.62	
Totals (F)	231	776	761	232	2000	463	23.15	
Totals (M)	100	244	294	83	721	183	25.38	
Combined Totals					2721	646	23.74	

Table 39. Normals - sister plants of homozygous T 6-9b

F_1 genotype $\frac{C\ Wx\ +}{c\ wx\ +}$

Plant Numbers	Number of Individuals					Recombinations		Transmitted as
	C Wx	C wx	c Wx	c wx	Total	Number	%	
2036-6	149	49	39	155	392	88	22.45	
-7	107	40	35	138	320	75	23.44	
-21	115	29	33	121	298	62	20.81	
-22	186	66	66	188	506	132	26.09	
-23	181	41	38	162	422	79	18.72	
-26	110	33	33	128	304	66	21.71	
-27	100	9	21	90	220	30	13.64	M
-31	150	38	41	136	365	79	21.64	
-31	63	13	16	65	157	29	18.47	
-31	132	39	41	129	341	80	23.46	M
-33	83	30	26	85	224	56	25.00	
-36	69	29	27	73	198	56	28.28	
2037-4	118	26	24	118	286	50	17.48	
-7	43	17	19	38	117	36	30.77	
-10	138	49	31	147	365	80	21.92	
-12	57	29	27	77	190	56	29.47	
-17	137	27	26	129	319	53	16.61	
-19	107	33	27	129	296	60	20.27	
-24	120	36	23	102	281	59	21.00	M
-25	141	44	38	131	354	82	23.16	
-26	72	17	19	74	182	36	19.78	M
-32	197	35	59	218	509	94	18.47	
-36	142	38	31	122	333	69	20.72	
Totals (F)	2293	666	636	2360	5955	1302	21.86	
Totals (M)	424	101	104	395	1024	205	20.02	
Combined totals					6979	1507	21.59	

Table 40. T 7-9$_{7074-6}$ F_1 genotype $\frac{C\ wx\ T}{c\ Wx\ T}$

Plant Numbers	Number of Individuals C Wx	C wx	c Wx	c wx	Total	Recombinations Number	%	Transmitted as
2050-2	54	136	125	44	359	98	27.30	M
2051-3	84	161	158	81	484	165	34.09	
2052-1	52	110	106	44	312	96	30.77	
-1	40	84	87	38	249	78	31.33	
-3	33	98	126	44	301	77	25.58	M
-6	30	56	60	30	176	60	34.09	
2053-2	49	100	98	39	286	88	30.77	
-3	33	153	148	35	369	68	18.43	M
-3T	35	152	177	49	413	84	20.34	M
Totals (F)	255	511	509	232	1507	487	32.32	
Totals (M)	155	539	576	172	1442	327	22.68	
Combined totals					2949	814	27.60	

Table 41. T 8-9$_{6673-6}$ F_1 genotype $\frac{C\ wx\ T}{c\ Wx\ T}$

Plant Numbers	Number of Individuals C Wx	C wx	c Wx	c wx	Total	Recombinations Number	%	Transmitted as
2039-1	34	94	79	39	246	73	29.67	
-2	6	15	11	6	38	12		
-2	29	52	55	30	166	59	35.54	M
-6	44	110	82	53	289	97	33.56	
-10	23	43	30	13	109	36	33.03	
2041-1	53	105	107	51	316	104	32.91	
-4	68	132	125	82	407	150	36.86	
2042-2	51	80	84	53	268	104	38.81	
-3	36	58	58	28	180	64	35.56	
-3	43	70	69	53	235	96	40.85	M
-4	39	64	70	43	216	82	37.96	M
2043-2	30	71	59	35	195	65	33.33	M
-3	56	115	107	56	334	112	33.53	M
2045-3	16	29	29	12	86	28		
Totals (F)	331	666	605	337	1939	668	34.45	
Totals (M)	197	372	360	217	1146	414	36.13	
Combined totals					3085	1082	35.07	

Table 42. Influence of chromosome position on recombination values in the $\underline{lg_1}$-$\underline{gl_2}$ and $\underline{C}$ $\underline{wx}$ regions.

Rearrangement		Shift of Region (μ) ($\underline{lg_1}$-$\underline{gl_2}$)	Mean percent Recombination*	Number of Progeny**
Inv 2	a	out 14.1	18.15 ± 2.34	4544
2 - 3	c	in 0.8	20.42 ± 1.97	4953
2 - 7	6372-2	out 3.5	18.22 ± 2.04	2945
2 - 8	6612-2	out 10.2	25.41 ± 2.57	2826
2 - 9	a	out 12.1	21.61 ± 1.89	5651
		($\underline{C}$ - $\underline{wx}$)		
1 - 9	4398-4	out 22.7	33.70 ± 4.34	1732
1 - 9	4995-5	out 8.3	33.04 ± 1.79	10549
2 - 9	6656-4	out 11.4	(M)34.38 ± 1.55	2654
			Total33.04 ± 3.84	2811
3 - 9	c	out 3.9	30.39 ± 2.00	9204
4 - 9	5657-2	out 10.7	34.02 ± 1.78	9402
5 - 9	a	out 25.5	24.48 ± 1.97	7887
6 - 9	b	in 1.2	23.62 ± 2.52	2721
Normal(sisters of 6-9b)		--	21.89 ± 1.77	6979
7 - 9	7074-6	(39.3 added)	(F)32.21 ± 2.15	1507
			(M)22.91 ± 6.70	1442
			(Total)28.08 ± 4.36	2949
8 - 9	6673-6	out 10.2	35.13 ± 1.98	2961

* based on progenies larger than 100. Includes both male and female transmission where not specified.

** total number of individuals in progenies larger than 100.

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