THE THEORETICAL DISTRIBUTION OF LENGTHS OF PARENTAL GENE BLOCKS IN THE GAMETES OF AN F_1 INDIVIDUAL¹

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GENETIC factors located on a chromosome form a gene block (linkage block) which tends to be transmitted as a unit in inheritance. The extent to which these gene blocks are broken and to which genetic recombination occurs between these factors within a gene block is of critical interest to the plant breeder since the success of his breeding program depends upon obtaining desirable genetic recombinations. Information on the extent to which gene blocks are broken in a breeding system is extremely limited. FISHER (1949) and BARTLETT *et al.* (1935) have presented formulas for estimating the lengths of segments which are still heterozygous following selected breeding procedures. The objective of this paper is to develop the probability distributions for the lengths of undisturbed gene blocks or chromosome segments in the gametes of an F_1 individual. The genetic blocks are considered intact with reference to either of the two original parental chromosomes.

Genetic map scale

Existing evidence indicates that crossing over (genetic recombination) in diploid organisms occurs in the chromatid (four strand) stage and that crossing over involves only nonsister chromatids. The six assumptions listed by LINDEGREN *et al.* (1957) are essential for the correlation of the linkage metric with cytogenetic information but are not essential for linkage measurement. To define a linkage measure, one needs only to assume that chromatids resulting from a genetic exchange between two chromatids are produced by a meiotic division since the recombination value, and hence the metrics for linkage, is measured in terms of the frequency of chromatid types produced by the system. The recombination value p between two loci can be defined as the probability of obtaining a chromatid carrying a genetic recombination between two loci. The definition of the genetic map scale taken with reference to the recombination metric involves the distribution of chromatid types. This distribution is a function of the average chromosome interference for a chromosome. A segment analysis requires an additional assumption for a distribution of breaks within a chromatid. The assumptions made for the development of the distributions of gene block lengths together with the ramifications of these assumptions will be discussed in detail.

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While linkage measurements are made in terms of p , the genetic map length must be measured on a true genetic map scale (γ), which can be explicitly defined. Consider a true genetic map length s , and divide this length into n segments. Then

$$s \geq \sum_{i=1}^n p_i,$$

where p_i is the recombination measure for the i th increment. The value of p_i can be expressed in terms of the probability (p'_i) of identifying crossovers only in the i th increment, of the probability (p'_{ij}) of identifying crossovers only in the i th and j th increments, etc. Making this substitution and collecting terms one obtains:

$$\begin{aligned} s &\geq \sum_{i=1}^n p'_i + 2 \sum_{i < j}^n p'_{ij} + 3 \sum_{i < j < k}^n p'_{ijk} + \dots, \\ s &\geq \sum_{x=1}^n x P'_x, \end{aligned}$$

where P'_x is the probability of observing x crossovers within a segment of length s for a selected set of n increments. Thus, one obtains in the limit the equality,

$$s = \sum_{x=0}^{\infty} x P_x = E[x],$$

where P_x represents the true probability of obtaining x crossovers within a segment of length s . The distribution of x is unknown for a selected segment and depends upon an assumption for an average chromosome interference for the segment. Chromosome interference is the tendency of breaks occurring in adjacent regions to occur less frequently than that expected if the occurrence of breaks is independent in a statistical sense. Measurements taken with reference to the true genetic map scale represent the expected number of breaks per segment length (FISHER 1948). Thus, for any selected chromosome length, the assumption made for interference affects the distribution of x with the restrictions, $s = E[x]$.

The genetic map distance measured on the recombination scale (p) denotes a probability concept, while the measurements taken with respect to the γ scale do not. Distance along the γ scale is defined in terms of the average number of breaks occurring within a segment of length s . A distance of .20, for example, on the γ scale would infer that in 100 gametes one would expect to find 20 breaks to have occurred within the segment. This does not infer that the probability of obtaining a break in any one gamete is .20 since this probability statement requires a probability distribution for x which would be defined by some discrete function.

The true genetic map scale (γ) represents the ideal metric scale since the measurements taken within a chromosome are additive and units of measurement between chromosomes are comparable. Distances on the γ scale are measured on a scale of equal density with respect to genetic recombination. Ramifications for the correlation of the linkage measurements and cytogenetic information will not be considered in this paper. Measurements on the physical length of the chromosome cannot be used in a segment analysis since discrepan-

cies exist between physical length and genetic map distance between chromosomes of different species and between non-homologous chromosomes of the same species.

Considerable reference has been made in the literature, FISHER *et al.* (1947), KOSAMBI (1944), OWEN (1950) and others, to a mapping function of p on y such that a recombination measurement (p) can be converted to the true genetic map scale. This mapping function can be defined if one assumes that crossovers are independent in a statistical sense. However, crossovers do not occur independently. Unfortunately, the lack of independence cannot be defined in a strict mathematical sense. The degree of chromosome interference differs from chromosome arm to chromosome arm and from chromosome to chromosome. Any relationship which one might derive to include interference can at best be approximate.

Distribution of lengths of gene blocks

Let us consider next the derivation of the distribution for gene block lengths (c) generated in any meiotic division within a chromosome of length s . The segment lengths represent the genetic block lengths between two consecutive loci at which recombination had occurred. A chromosome resulting from a meiotic division can be characterized by having exactly x breaks or points of genetic recombination. Consider the partition of the array of chromosomes into sets, A_x , based on the number of points of genetic recombination, $0, 1, \dots, x, \dots$, which had occurred within a chromosome. A denumerable number of sets have been defined which are disjoint since the intersection of any two sets is empty. A_x represents an infinite set of chromosomes containing exactly x breaks, and any chromosome resulting from a meiotic division is an element of the union of sets, $\bigcup_{x=0}^{\infty} A_x$. Each chromosome of the set will contain $(x+1)$ segments identified by the sequence 0 to γ_1 , γ_1 to γ_2 , $\dots$, and γ_x to s , where γ_i represents the locus of a break. Identify these segments with the subsets, $A_{x1}, A_{x2}, \dots, A_{xr}, \dots$, respectively, where $1 \leq r \leq (x+1)$. For example, A_{x2} is an infinite subset containing all possible segments generated between the first and second breaks of the chromosomes containing x breaks. Thus, $(x+1)$ disjoint subsets have been generated for each A_x . The defined partition has utility since the probability that any randomly selected chromosome will occur in set A_x is P_x while the probability that any segment of a chromosome in set A_x will occur in subset A_{xr} is $\frac{1}{x+1}$.

The subsets as defined are disjoint, and a segment can occur in only one subset. However, it should be equally apparent that the existence of subset A_{xr} implies the existence of the remaining x subsets of A_x since a pattern of x breaks within a chromosome generates $(x+1)$ segments of total length s . This peculiarity of set structure will not complicate the solution since we are interested in describing the distribution which characterizes the length of any one segment per chromosome.

The probability that a segment (ω) is an element of A_{xr} , $\omega \in A_{xr}$, is $P_x \left[\frac{1}{x+1} \right]$.

Consider next a segment Z with a length $Z(\omega)$ randomly selected from subset A_{xr} . The probability that $Z(\omega)$ will be less than or equal to c is $Pr[Z(\omega) \leq c : \omega \in A_{xr}]$. The cumulative distribution for c becomes:

$$F(c) = \sum_{x=0}^{\infty} P_x \left[\frac{1}{x+1} \right] \sum_{r=1}^{x+1} [Pr(Z(\omega) \leq c : \omega \in A_{xr})]. \quad (i)$$

Let us first assume that the occurrence of a crossover is independent in a statistical sense. Since only a limited number of breaks from an infinite number of possible breaks will occur for any chromosome, the distribution of x will follow the Poisson distribution, and

$$P_x = \frac{e^{-s} s^x}{x!}, \quad (ii)$$

since $E[x] = s$ for a chromosome of length s .

The solution for the cumulative distribution, $F(c)$, requires the probability that the length of a randomly selected segment is less than or equal to c , given a subset A_{xr} , or in terms of the loci of the x breaks per chromosome, $Pr[\gamma_r - \gamma_{r-1} \leq c]$, where $0 < \gamma_1 < \dots < \gamma_{r-1} < \gamma_r < \dots < \gamma_x < s$. Since the density distribution of a γ_i is uniform and the assumption of independence is made, the solution can be obtained by the proper identification of the region for integration in the integral:

$$Pr[Z(\omega) \leq c : \omega \in A_{xr}] = \frac{1}{s^x} \int \dots \int_R dy_x \dots dy_1.$$

For any chromosome class, A_x , the probability that the random variable is less than or equal to c in length is identical for each of the $(x+1)$ subsets (A_{xr}) and is equal to:

$$1 - (s-c)^x / s^x. \quad (iii)$$

From (i) and (iii) one obtains:

$$\begin{aligned} F(c) &= \sum_{x=1}^{\infty} P_x [1 - (s-c)^x / s^x] \\ &= 1 - \sum_{x=0}^{\infty} P_x (s-c)^x / s^x, \quad 0 \leq c < s, \\ Pr[Z(\omega) = s] &= P_0. \end{aligned} \quad (iv)$$

With the assumption of independence, P_x can be obtained from (ii), and $F(c)$ reduces to:

$$\begin{aligned} F(c) &= 1 - e^{-c}, \quad 0 \leq c < s, \\ Pr[Z(\omega) = s] &= e^{-s}. \end{aligned} \quad (v)$$

If one considers the segment lengths expressed as a proportion of the chromosome, $t = c/s$, then:

$$\begin{aligned} F(t) &= 1 - \sum_{x=0}^{\infty} P_x (1-t)^x = 1 - e^{-st}, \quad 0 \leq c < s, \\ Pr[Z(\omega) = 1.0] &= e^{-s}. \end{aligned} \quad (vi)$$

$F(c)$ represents the probability that a segment per chromosome is less than or equal to c in length. Hence, the average segment length per chromosome is:

$$E[c] = \int_0^s c dF(c) + s[P_o], \quad (\text{vii})$$

$$= [1 - e^{-s}],$$

noting that $F(c)$ is discontinuous at $c=s$. Formula (iii) represents $F(c)$ for a given set A_x , and $E[c]=s/(x+1)$ for the class of chromosomes, A_x . This result would also follow from the fact that a pattern of x recombinations divides the chromosome into $(x+1)$ segments. Thus, with the assumption of independence, $E[c]$ can be calculated from formula (vii). In general,

$$E[c] = \sum_{x=0}^{\infty} P_x \left[\frac{s}{x+1} \right], \quad (\text{viii})$$

where the assumption made for interference will involve P_x only.

The average segment length per chromosome for selected chromosome map lengths and for the assumption of independence can be summarized:

Length of chromosome (s)					
	.5	.7	1.0	2.0	3.0
$E[c]$	.393	.503	.632	.865	.950
$E[\frac{c}{s}]$	.786	.719	.632	.432	.317
$Pr[Z(\omega)=s]$	.606	.497	.368	.135	.050

The striking aspect of these expected lengths is that for relatively short chromosomes the chromosome is essentially inherited as a unit. Even with the longer chromosomes the undisturbed gene blocks following a meiotic division are of considerable size. In fact, they are discouragingly large when considering a plant breeding program in which crosses are made between two desirable genetic types with the objective of recombining the desirable genes from each source.

The cumulative distribution for c has been plotted in Figure 1 for selected values of the chromosome length (s). The length of the segment has been plotted on the scale $t=c/s$. A point of discontinuity exists for the probability distribution at the point, $c=s$.

Effects of interference

LINDEGREN *et al.* (1939, 1942) have presented data from *Neurospora* which indicate the presence of chromatid interference and both positive and negative chromosome interference, depending upon the relative positions of the segments considered. The limitations, however, imposed by the assumption of independence are not as critical as might be expected. This is due in part to the restrictions imposed in relating a segment length to the true genetic map scale and to the small frequencies of chromatids carrying the higher number of exchanges as compared to the 0 and 1 classes. Unfortunately, the degree of interference be-

FIGURE 1.—Cumulative distributions for the proportionate segment length per chromosome transmitted intact through a meiotic division for selected chromosome lengths (s) and for the assumption of independence.

tween two breaks occurring at some distance (c) apart on the chromosome is not a consistent feature if the measurement is taken at different regions of the chromosome but depends upon the heterochromatic regions in the chromosome arm and upon the position of the breaks relative to the centromere. This means that if a chromosome of length s were divided into i segments, $\sum c_i$ may or may not equal s . However, if all possible partitions were considered, the average sum would be s . For a segment analysis one must assume some average degree of interference for a chromosome.

Chromosome interference will not affect appreciably the expected value of c . The expected value for c for a selected x is $s/(x+1)$ regardless of the distribution of breaks within the chromosome (formula viii). The value of P_x is affected by the assumption made for interference. With independence P_x is defined by the Poisson distribution. Interference would tend to restrict the occurrence for the larger values of x (P'_x) such that $P_x > P'_x$ for some values of x larger than $E[x]$.

However, $P_x > P'_x$ for some values of x less than $E[x]$. This follows from the restrictions, $s = \sum_{x=0}^{\infty} xP_x$ and $\sum_{x=0}^{\infty} P_x = 1$. Thus, the expected value of c will not be affected appreciably by the assumption made for interference.

Compensating features are found if one examines the distribution functions for c . Levels of nonindependence would exist for selected values of x and the probability distributions for c within the A_{xr} sets for the selected x would be different. Although the probability that $Z(\omega) \leq c$ should be decreased for sets generated from internal segments, the decrease in probability must be associated with an increase in probability that $Z(\omega) \leq c$ in the sets arising from the terminal segments since the lengths of segments generated by the occurrence of x breaks within a chromosome must add to s . The distribution for c can be appreciably affected by the failure to properly identify the frequency distribution for x (P_x).

Thus, the critical feature in the segment analysis appears to be the proper identification of the frequency distribution for x . With the assumption of independence the frequencies with which entire chromatids are transmitted through a meiotic process and with which chromatids carrying the larger number of breaks result from a meiotic division are overestimated. An approximate adjustment for interference could be made by estimating a modification for the distribution of x based on experimental data.

Application of segment analysis to genetic data

Sources of linkage data involving multiple point backcross and being of sufficient detail to be used in a segment analysis are limited in the literature. Two sources of data from *Drosophila* were analyzed, one source involving seven point linkage data for the X chromosome (ANDERSON *et al.* 1930) and the other source involving eight point linkage data for chromosome II (GRAUBARD, Table 9, 1932). Five point linkage data for the sex chromosome in *Neurospora crassa* (LINDEGREN *et al.* 1942) were considered. The third locus in LINDEGREN's data was identified by the centromere. Since linkage between the locus of a factor pair and the centromere is calculated from frequency of asci types, it is impossible to identify the frequency of all chromatid types produced in the linkage study. Therefore, the data were reduced to a four point linkage study involving the four factor pairs. The linkage measurements identified by segments are summarized in Table 1.

TABLE 1

Summary of multiple point backcross data in Drosophila (Anderson et al. 1930 and Graubard 1932) and Neurospora (Lindgren 1942)

Source data	Segment identity							Appr. s	n
	1	2	3	4	5	6	7		
ANDERSON	.038	.097	.084	.147	.112	.113	...	.621	26,908
GRAUBARD	.109	.270	.058	.022	.113	.048	.304	.924	5,284
GRAUBARD (ad.)	.109	.281	.058	.022	.113	.048	.318	.950	5,284
LINDEGREN	.047	.055	.081	...	...	...	...	.183	6,300

Segments 2 and 7 in GRAUBARD's data were of sufficient length that adjustments were made for double crossovers which probably occurred in these two regions, the occurrence of triple exchanges being ignored. Based on the coefficients of interference observed in Graubard's data, an average coefficient of interference ($\frac{\text{observed frequency of doubled crossovers}}{\text{expected frequency of doubled crossovers}}$) of 0.4 was assumed for exchanges within the two regions with independence between exchanges occurring in segments 2 and 7. The adjustments were then made based on the assumed coefficient of interference and on the assumption that each segment could be divided into three sub-segments of equal length.

The data are summarized in terms of the proportions of chromosomes having 0, 1, 2, . . . identified crossovers and are given in Table 2. The expected or average

TABLE 2

Observed frequencies and expected frequencies, based on the assumption of independence, of gametes having x breaks per chromosome

x	ANDERSON		GRAUBARD			LINDEGREN	
	Observed	Expected*	Observed	Adj. observed†	Expected*	Observed	Expected*
0	.4595	.5375	.3072	.2998	.3849	.8265	.8324
1	.4625	.3337	.4784	.4707	.3675	.1635	.1527
2	.0764	.1036	.1974	.2030	.1754	.0100	.0140
3	.0017	.0214	.0161	.0196	.0558	.0000	.0009
4	.0001	.0033	.0010	.0028	.0133	.0000	.0000
5	.0000	.0004	.0000	.0016	.0025	.0000	.0000
6	.0000	.0000	.0000	.0000	.0004	.0000	.0000
7	.0000	.0000	.0000	.0000	.0001	.0000	.0000
$E(x) = \sum xP_x$	.6208	.6203	.9255	.9547	.9545	.1835	.1834
$\bar{c} = \sum \frac{sP_x}{x+1}$	.4449	.4621		.5810	.6149	.1673	.1676

* Based on the assumption that crossovers are independent in a statistical sense.

† Adjusted as outlined in text.

length of gene blocks is calculated with reference to the genetic map length identified between the two terminal loci, being .621, .955 and .183 for the three sets of data. Discrepancies in s found in Tables 1 and 2 are attributable to rounding errors. Discrepancies between the observed and the expected frequencies can be attributed to the lack of independence between crossovers and to the failure to observe the even number of exchanges within a segment. The failure to identify the even number of exchanges within a segment leads to an underestimation of s .

One can demonstrate that the observed and expected distributions are different based on statistical tests. However, when considering the biological ramifications in the use of this information, the agreement between expected and observed distributions is extremely encouraging. Also, the expected or average length of gene block estimated from the observed and from the expected frequencies are

quite similar. In fact, as a reference for the evaluation of the breakup of gene blocks resulting from some breeding procedure, the assumption of no interference appears to yield an adequate criterion for a segment analysis. One can improve his model by considering a modified distribution for x .

Empirical distribution for x

A theoretical distribution for x based on an assumed level of interference would be difficult to derive. A modified Poisson distribution ($V(x) < E[x]$) can be considered based entirely upon empirical ramifications. Such a distribution could be defined:

$$P'_x = (P_x)e^{-f(x)},$$

where P_x indicates the probability of observing x crossovers based on the assumption of independence. The factor ($e^{-f(x)}$) permits a restriction in occurrence of the larger number of breaks in a chromosome and should be a constant feature for the three sets of data.

A number of functions were considered and fitted by empirical procedures to the three sets of data. The function:

$$P'_x = \frac{Ke^{-(\lambda + .4x^2)}\lambda^x}{x!},$$

where $\Sigma P'_x = 1$ and $\Sigma xP'_x = s$, appeared to yield an approximate fit. The agreement of observed and expected for the three sets of data (Table 3) is surprising

when one considers the diversity of the data analyzed. The probability distributions for the proportions of the total chromosome length ($t = c/s$) transmitted in a meiotic process is (formula vi):

$$1 - \sum_{x=0}^{\infty} P_x(1-t)^x.$$

The probability distributions for chromosome lengths of $s = 0.7$ and $s = 1.0$ for the assumption of independence and for an approximate adjustment for interference

TABLE 3

Observed frequencies of x breaks in three sets of linkage data and the expected frequencies based on an empirical adjustment for interference

x	ANDERSON'S data		GRAUBARD'S data		LINDEGREN'S data	
	Observed	Expected	Observed	Expected	Observed	Expected
0	.4595	.4761	.2998	.2871	.8265	.8242
1	.4624	.4308	.4707	.4966	.1635	.1680
2	.0764	.0876	.2030	.1929	.0100	.0077
3	.0017	.0053	.0195	.0225	.0000	.0001
4	.0001	.0001	.0028	.0009	.0000	.0000
5	.0000	.0000	.0016	.0000	.0000	.0000
$E(x)$	.621	.622	.955	.954	.184	.184
P'_x	$(.4761)(e^{-.4x^2})(1.35)^x$		$(.2871)(e^{-.4x^2})(2.58)^x$		$(.8242)(e^{-.4x^2})(.304)^x$	
	$x!$		$x!$		$x!$	

are given in Figure 2. The principal effect of the assumption of independence upon the distribution of lengths of chromosome segments transmitted intact through a meiotic process is to yield an overestimation of the frequency of transmission of entire chromatids and an underestimation of the frequencies of transmission of the larger segment lengths ($c < s$). For the short chromosomes the correction for interference is negligible.

DISCUSSION

The concept of genetic map distances has arisen from the study of genes controlling qualitative characters. The units for the linkage metric are defined in

FIGURE 2.—Cumulative distributions for the proportionate segment length per chromosome transmitted intact through a meiotic division for assumption of independence and for an approximate adjustment for interference.

distances of equal frequency of recombination. The unit of measure on the true genetic map scale is the distance on the map scale with which one would expect to find an average of one break per chromatid. Centimorgans have been defined as 100 γ . The units of measure for the lengths of gene blocks transmitted intact through a meiotic cycle are taken with reference to this scale. One assumes that genes controlling quantitative characters are distributed within the linkage groups.

The application of this information to the genetic recombination in a breeding program presupposes information on the lengths of the genetic maps for the respective linkage groups of the species. This information is limited in most species of economic importance. Although the information on genetic maps may be incomplete for a species, the probability distribution and expected lengths of gene blocks transmitted intact through a meiotic cycle will serve as a point of reference. These distributions can serve as the basis for evaluating the extent to which gene blocks are broken in a breeding system.

In corn the measured map lengths range from 0.28 for linkage group 7 to 1.61 for linkage group 1 with an average length of 0.91 (RHOADES 1955, p. 148). These measurements would be considered minimum lengths due to limitations in the number of loci identified within a linkage group and to the failure of identifying lengths terminal to the available loci for any linkage group. A realistic estimate for the length of chromosomes in corn would be between 0.4 and 2.0 with an average near 1.0. This would mean that the average length of gene block transmitted through a meiotic cycle would be about four fifths of a chromosome for the shortest chromosome to two fifths of a chromosome for the longest chromosome with an average length of about one third of a chromosome. These lengths represent considerable blocks of genetic material which would remain intact in the gametes from an F_1 individual. These results certainly suggest the merit of examining breeding methods currently used for the purpose of determining the extent to which linkage blocks have been broken.

The effects of interference on the probability distribution of c are difficult to assess. A clear-cut mathematical expression defining interference is not available. Arguments were presented for an approximate adjustment for interference. This adjustment can be made by modifying the distribution for x , the number of points of genetic recombinations per chromosome. Under the assumption of independence the distribution for x can be defined by the Poisson distribution; however, one tends to overestimate the occurrence of chromatids in which a large number of breaks had occurred but at the same time overestimate the occurrence of transmission of entire chromatids through a meiotic division, since interference tends to restrict the occurrence of the large values for x . A modified Poisson-like distribution ($V(x) < E[x]$) is needed. A modified distribution for x was determined empirically based on detailed linkage data available in *Drosophila* and *Neurospora*. For short chromosome lengths, this adjustment would be negligible. The assumption of independence yields an estimation of the average segment

length transmitted intact through a meiotic division which appears satisfactory for practical purposes.

It is entirely possible that the density distribution for a break γ is not uniform with respect to the scale based on the physical length of a chromosome since the crossover density is undoubtedly greater in certain portions of the chromosome than others. The density of γ , however, is uniform with respect to the true genetic scale. The assumption for the distribution within a linkage group for genes controlling a quantitative character is made with reference to the true genetic scale.

The relationship between chromosome length as measured on the true genetic map scale and crossover frequency should be of interest to the cytologists. The average frequency of crossovers for a pair of homologous chromosomes is $2s$. If a chiasma represents a crossover, then the average chiasmata frequency is $2s$ and the distribution for z , the number of chiasmata per chromosome pair, must follow the distribution for x discussed in this paper.

SUMMARY

The derivation of the probability distribution for the length of gene block (c) remaining intact through a meiotic cycle has been presented. The derivation required first an adequate definition for the measurement scale. True genetic map length is defined in terms of the expected number of breaks for a length (s) and is a probability concept only in the limited case where the segment length is such that the probability of two (or more) exchanges occurring within the segment is negligible.

The probability distributions for a segment length per chromosome (c) remaining intact together with the average or expected segment length per chromosome were presented based on the assumption of independence. The effects of interference on these distributions were discussed. The assumptions made for interference will condition the probability distribution for c and, hence, the expected value for c . Ramifications for the effects of interference were given. An approximate adjustment for interference can be made by considering a modified distribution for x , the number of breaks per chromosome. An empirical approximation for the distribution of x was determined from two sets of data from *Drosophila* and a set of data from *Neurospora*. The assumption of independence did not appear to be critical for a segment analysis for a chromosome length of 0.7 which had been selected for analysis.

The distributions presented should be of interest to plant breeders since the information presented clearly demonstrates the limited extent to which linkage groups are broken during a meiotic division. Also, the distributions will serve as the basis for the evaluation of the extent to which the original linkage groups from a parent are broken under selected breeding procedures.

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