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TITLE OF THESIS..QUANTITATIVE...GENETIC..ANALYSIS..OF CHROMOSOMES..1B..AND..1A..OF..COMMON... WHEAT.....

UNIVERSITY.....UNIVERSITY..OF..ALBERTA.....

DEGREE.....Ph.D.....YEAR GRANTED...1970.....

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THE UNIVERSITY OF ALBERTA

QUANTITATIVE GENETIC ANALYSIS OF CHROMOSOMES 1B AND 4A OF COMMON WHEAT

by

Sadeque Uddin Ahmed

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF GENETICS

EDMONTON, ALBERTA

SPRING, 1970

UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled 'Quantitative Genetic Analysis of Chromosomes 1B and 4A of common wheat' submitted by Sadeque Uddin Ahmed in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

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ABSTRACT

The chromosome-pairs 1B of Timstein and 4A of Thatcher were analysed in relation to their homologues in recipient Chinese Spring. Six quantitative characters, viz., days-to-heading, plant height, number of tillers, number of kernels, weight of kernel and yield per plant, were studied. 'Triparental-groups' technique was used for analysing and interpreting the experimental results obtained. Each of the triparental groups consists of three parents, of which one or two are disomic substitution lines, together with their F_1, F_2 and backcross generations.

The results obtained in this study show the effect of each substituted chromosome in the genetic background of its own variety and in that of the recipient variety, by itself, and/or in combination with the remaining chromosomes.

Highly significant allelic and nonallelic interactions within and between chromosomal levels were observed for all characters considered. Both the chromosome-pairs 1B and 4A were found to contain effective gene(s) for tallness. The chromosome-pair 1B was also found to contain effective genes for number of kernels per spike and yield per plant.

Of the six characters considered, earliness and number of kernels were found to be controlled by one gene with major effect and one or more minor genes with small effects, whereas plant height, number of tillers, weight of kernel and yield per plant were found to be controlled by polygenes.

ACKNOWLEDGEMENTS

It is a great pleasure to record my deep gratitude and sincere thanks to Dr. Rustem Aksel for his guidance and encouragement throughout the course of this study. His valuable suggestions and helpful criticisms enabled me to complete this manuscript. I am grateful to the Canadian International Development Agency (formerly External Aid of Canada) and the Canadian Commonwealth Scholarship and Fellowship Administration for awarding me a Commonwealth Scholarship for the duration of this study. I am also grateful to the Department of Genetics for providing me with the research facilities for this study. Thanks are also due to the staff of the Parkland Farm for their assistance with sowing and harvesting. I would also like to extend my thanks to Dr. L. P. V. Johnson for editing the manuscript.

Finally, I owe a deep debt of gratitude to my wife who assisted me with the computational works and for constantly encouraging me in a number of intangible ways.

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QUANTITATIVE GENETIC ANALYSIS OF CHROMOSOMES 1B AND 4A OF COMMON WHEAT

I INTRODUCTION

Allelic and nonallelic interactions generally complicate genetic studies of metric characters. In case of common wheat (Triticum aestivum L.) further complications are introduced by its polyploid nature.

Crosses of chromosome substitution lines with the recipient variety permit, to a certain degree, the analysis of the genetic constitution of the substituted chromosomes in relation to their homologues in the recipient variety. However, the complexity of within- and between-chromosome interactions, in most cases, tend to obscure the effects of different gene(s) controlling a specific character.

A method involving the use of triparental groups developed by Aksel (1967) permits a fairly detailed analysis of gene actions and interactions. The triparental groups consist of three parents, of which one or two are disomic substitution lines, and of their corresponding F_1, F_2, and some of the backcrosses. By means of this method it is possible to measure the allelic and nonallelic interactions within homologous and between nonhomologous chromosome-pairs. Incomplete triparental groups (donor varieties and backcrosses were not included) have been used by Aksel and Kuspira (1968) and Aksel (1970).

This study was designed to make use of complete triparental-groups. The object of this study was to determine the genetic constitution, as it relates to various metric characters, of chromosomes

1B of Timstein and 4A of Thatcher.

II REVIEW OF LITERATURE

There is an extensive literature on the origin and genetic constitution of cultivated wheats.

1. The Origin of Cultivated Wheats

Jenkins (1966) gave a full account of the long standing problem regarding the origin of the cultivated wheats. Kihara (1924) and Gaines and Aase (1926 and Aase, 1930) independently proposed that cultivated wheat had the following genome formulas: diploid species AA, tetraploid species AABB, and hexaploid species AABBDD. The source of the A genome was recognized to be the wild Triticum monococcum (Melburn and Thompson, 1927; Zohary and Feldman, 1962), that of the B genome T. speltoides (Aegilops speltoides) (Sarkar and Stebbins, 1956; Riley, Unrau, and Chapman, 1958; Sears and Okamoto, 1958), and that of the D genome Ae. squarrosa (Percival, 1921; Sax and Sax, 1924; Kihara,1944; Kihara and Lilienfeld, 1949; McFadden and Sears, 1944, 1946).

For references cited above see Jenkins (1966).

Although T. speltoides (Ae. speltoides) is generally accepted as the possible source of B genome, results obtained from various contemporary studies gave contradictory evidence (Sears, 1956; Kimbler, 1966; Riley and Kimbler, 1966; Morris and Sears, 1967). Okamoto (1957), Riley (1958), and Sears and Okamoto (1958) discovered that chromosome 5B of wheat inhibits pairing of homoeologous (related) chromosome. Riley, Unrau and Chapman (1958) and Riley and Chapman (1966) suggested that if the activity of 5B is suppressed (by mutation), the amphidiploid of T. speltoides x T. monococcum would become fertile and stable with diploid-like pairing. Furthermore, Chennaveeraiah (1960) and Riley, Unrau and Chapman (1958) found that, of all the conceivable donors of B genome, only T. speltoides and T. tripsacoides (Ae. mutica)

have two satellited chromosomes similar to those of 1B(I) and 6B(X) of common wheat.

The electrophoretic studies by Johnson and Hall (1965, 1966) found no support for T. speltoides as the source of B genome. Other possibilities are the close relatives of speltoides: T. longissimum (Ae. longissima and Ae. sharonensis), T. bicorna (Ae. bicornis), T. tripsacoides (Ae. mutica) and other diploides not yet tested (Sears, 1969).

2. The Cytogenetics and Genetics of Common Wheat

Kuspira and Unrau (1957) have most elegantly reviewed the literature on cytology and cytogenetics of common wheat available up to that time. Sears (1953, 1954) isolated the complete series of 21 monosomics and 21 nullisomics in the variety Chinese Spring. Sears (1953) also described the cytological procedures for producing inter-varietal chromosome substitution lines which were later elaborated by Unrau, Person and Kuspira (1956).

Sears and Rodenhiser (1948), Unrau (1950), Heyne and Livers (1953). Wiggins (1955), Sikka et al. (1956), Nyquist (1957), Sikka, Jha and Swaminathan (1959), Campbell and McGinnis (1958) Larson (1952, 1959), Larson and MacDonald (1959a, 1959b, 1962), Knott (1959), Singh and Swaminathan (1959, 1960), Kuspira and Unrau (1960), Okamoto (1960), Tsunewaki (1960, 1961, 1962), Tsunewaki and Jenkins (1961), Tsunewaki and Kihara (1961), Allan and Vogel (1960, 1963), Kritzinger (1962), Macer (1963), Driscoll and Jensen (1963, 1964), Snyder, Miller and Pi (1963), Curtis, Schlehuber and Moore (1965), McIntosh and Baker (1965, 1966), McGinnis and Boyd (1965), Watson and Welsh (1966), and Tahir and Tsunewaki (1969) used monosomics for the location of genes most of which refer to qualitative characters.

The substitution of each of the 21 chromosomes from a donor variety for its homologues in a recipient variety, although demanding a rather lengthy backcrossing programme and intensive cytological testing, is a step towards an efficient and more exact way of studying genetic characters, both qualitative and quantitative, in wheat. Kuspira and Unrau (1957) and Law (1966a), using this method, identified a number of chromosomes with the control of some quantitative characters. Unrau (1958) proposed the use of F_1s from the cross of the substitution lines with the recipient variety for pollinating the recipient variety deficient (nullisomics or monosomics) for the chromosomes under study. This method was later modified by Law (1966b). The usefulness of this method is that it permits the location of factor(s) on specific chromosomes.

Schmidt, Morris, Johnson and Mattern (1966) clearly demonstrated the superiority of the chromosome substitution method over monosomic method for the analysis of polygenetically controlled characters.

Kuspira and Unrau (1957, 1958), Sears, Loegering and Rodenhiser (1957), Wehrhahn (1961), Hermsen, (1963), Schmidt et al. (1966), Law (1966a, 1966b, 1967), Law and Wolfe (1966), Loegering and Sears (1966), Morris et al. (1966), Halloran and Boydell (1967), Welsh, Watson and Green (1968), and others identified a number of genes controlling some of the quantitative as well as qualitative characters of certain varieties of common wheat, viz., Chinese Spring, Thatcher, Timstein, Hope, Cheyenne and Red Egyptian, by making use of substitution lines.

Thoday (1961) emphasized that the genes responsible for the control of quantitative characters must be isolated so that their properties, relationships with one another, and mode of interaction and inheritance may be investigated. This method essentially requires the use of genetic

markers followed by progeny testing of the marker classes. By using this technique Thoday and his co-workers have isolated a number of genes in Drosophila and located their position on a genetic map. The chromosome substitution method is analogous to the genome assays which are a first step in the location of factors.

Sears (1962, 1963) suggested that if proper telocentric chromosomes are available, then the substitution chromosome can be combined with a telocentric chromosome and recombination in only one arm can be studied. The centromere, in this case, will act as marker and the distance from the centromere can readily be determined. Using this technique, genetic maps for chromosome 7B of Hope (Law, 1966b, 1967), chromosome 6B of Chinese Spring (Sears, 1963), and chromosome 2D of Federation (McIntosh and Baker, 1968) and of Kenya W1483 and Festiguay (Luig and McIntosh, 1968) have been constructed. Endrizzi (1962) and Endrizzi and Kohel (1966) successfully used this technique to construct genetic maps for three chromosomes of cotton.

Aksel (1967) proposed the use of 'triparental-groups' consisting of three parents, of which one or two are disomic substitution lines, and of the corresponding crosses and some of the backcrosses. This method, especially if supplemented by that of Wehrhahn and Allard (1965), would permit a detailed chromosome-by-chromosome analysis of the genetic make up of common wheat. Considered alone the method provides information on allelic and nonallelic interactions at both the homologous- and nonhomologous-chromosomal levels. Aksel and Kuspira (1968) and Aksel (1970) have demonstrated the efficacy of this method. However, their results were obtained from analyses of incomplete triparental groups. The donor parents and the backcrosses were not used.

III MATERIALS AND METHODS

1. Materials

The recipient variety Chinese Spring (R), two disomic substitution lines $L(Tm)_{1B}$ and $L(Th)_{4A}$, and the respective donor varieties Timstein (Tm) and Thatcher (Th) were used as initial materials for this study. The following crosses were made:

(1) R x $L(Tm)_{1B}$

(2) R x $L(Th)_{4A}$

(3) R x Tm

(4) R x Th

(5) $L(Tm)_{1B}$ x $L(Th)_{4A}$

(6) Tm x $L(Tm)_{1B}$

(7) Th x $L(Th)_{4A}$

L stands for the substitution line, and 1B and 4A refer to the chromosomes substituted.

All the F_1s, the F_2s and the backcrosses were made reciprocally. The parents, the F_1s, the F_2s, the backcrosses and their reciprocals were space seeded (60 cms. between rows, 15 cms. between plants within rows) at Parkland Farm in the summer of 1968. Twenty-five kernels were seeded in each row and the rows were randomized within each block. There were seven blocks, one for each combination of crosses. These blocks were again randomized within each of the four replications. The plants were harvested individually by hand.

The following characters were studied:

(1) Days-to-heading (earliness),

(2) Plant height,

(3) Number of tillers per plant,

(4) Number of kernels per spike,

(5) Weight per kernel, and

(6) Yield of seed per plant.

2. Methods of Collecting Data

The 'days-to-head' observations, used as an indication of earliness, were recorded separately for each plant and expressed as number of days from seeding to heading. A plant was considered headed when the first spike had just emerged from the boot. The data was recorded every day until all the plants headed.

Plant height (in cms.) was measured on each plant shortly after harvest. The measurements were taken from the base of the stem to the base of the main spike.

Number of tillers per plant was determined by a count of all the tillers on each plant shortly after harvest.

Number of kernels per spike was determined by taking the average of the number of kernels from three main spikes of each plant.

Weight per kernel (the mean weight of one kernel in mgs.) was obtained by weighing all kernels of the three main spikes of each plant.

Yield of seed per plant (in gms.) was determined by weighing the kernels after threshing from all the spikes of each plant including also the three main spikes used for determining the number and weight of kernels.

3. Method of Analysis

The method of analysis of the experimental results used in this study basically follows the 'triparental-groups' analysis developed by Aksel (1967). The definitions and concepts underlying the triparental groups, and part of their analysis have been given by Aksel (1967, 1970),

and Aksel and Kuspira (1968).

The five parental lines and their crosses are arranged into three triparental groups:

Triparental group 1	R
	$L(Tm)_{1B}$
	$L(Th)_{4A}$
Triparental group 2.1	R
	$L(Tm)_{1B}$
	Tm
Triparental group 2.2	R
	$L(Th)_{4A}$
	Th

of which group 1 is of Type 1, and groups 2.1 and 2.2 are of Type 2 (Aksel, 1967). Each of the three groups contain their corresponding selfs, crosses and reciprocal crosses involving the parents, the F_1s, the F_2s, and the backcrosses.

For the sake of simplicity of notation, the allelic sets involved in this study, viz., $U_{m\epsilon M_{1B}}\{a_{Tm}\}_m$ and $U_{m\epsilon M_{4A}}\{a_{Th}\}_m$, and their respective homologues $U_{m\epsilon M_{1B}}\{a_R\}_m$ and $U_{m\epsilon M_{4A}}\{a_R\}_m$ (Aksel, 1967; Aksel and Kuspira, 1968) are denoted as Tm_{1B}, Th_{4A}, R_{1B}, and R_{4A}, respectively (Aksel, 1970). Thus, the notation refers to both the chromosomes considered and to the sets of alleles located in them.

The genotypes of the parents and of the F_1 hybrids of the three triparental groups in terms of the two sets of substituted chromosomes are given in Table 1.

Table 1. The genotypes of the parents and of the F_1 hybrids in the triparental groups 1, 2.1, and 2.2.

Numerical order	Generations	Genotypes
	Triparental Group 1	
	Parents	
1	R	$R_{1B}R_{1B}R_{4A}R_{4A}$
2	$L(Tm)_{1B}$	$Tm_{1B}Tm_{1B}R_{4A}R_{4A}$
3	$L(Th)_{4A}$	$R_{1B}R_{1B}Th_{4A}Th_{4A}$
	F_1 crosses	
1	R x $L(Tm)_{1B}$	$R_{1B}Tm_{1B}R_{4A}R_{4A}$
2	R x $L(Th)_{4A}$	$R_{1B}R_{1B}R_{4A}Th_{4A}$
3	$L(Tm)_{1B}$ x $L(Th)_{4A}$	$R_{1B}Tm_{1B}R_{4A}Th_{4A}$
	Triparental Group 2.1	
	Parents	
1	R	$R_{1B}R_{1B}R_{4A}R_{4A}$
2	$L(Tm)_{1B}$	$Tm_{1B}Tm_{1B}R_{4A}R_{4A}$
3	Tm	$Tm_{1B}Tm_{1B}Tm_{4A}Tm_{4A}$
	F_1 crosses	
1	R x $L(Tm)_{1B}$	$R_{1B}Tm_{1B}R_{4A}R_{4A}$
2	Tm x $L(Tm)_{1B}$	$Tm_{1B}Tm_{1B}R_{4A}Tm_{4A}$
3	R x Tm	$R_{1B}Tm_{1B}R_{4A}Tm_{4A}$

The formulas used for estimating the parameters pertinent to this study (Aksel,1967) are:

Table 2. The parameters and the corresponding formulas.

Trip. Grs. involved	Parameters	Formulas
1, 2.1	$(d)_i$	$\frac{1}{2}(x_{ii}-x_{jj})$
1, 2.2	$(d)_j$	$\frac{1}{2}(x_{jj}-x_{rr})$
1, 2.1	$(h)_i$	$x_{ri}(F_1) - \frac{1}{2}(x_{ii}+x_{rr})$
1, 2.2	$(h)_j$	$x_{rj}(F_1) - \frac{1}{2}(x_{jj}+x_{rr})$
1	∂_{ij}	$x_{ij}(F_1) - x_{ri(F_1)} - x_{rj(F_1)} + x_{rr}$
1	$p\Delta_{R_i}$	$\frac{1}{2}(x_{rr}+x_{ri(F_1)}) - x_{\bar{B}(R)}$
1	$p\Delta_{R_i}$	$\frac{1}{2}(x_{rr}+x_{rj(F_1)}) - x_{\bar{B}(R)}$
1	$p\Delta_{D_i}$	$\frac{1}{2}(x_{ri(F_1)}+x_{ii}) - x_{\bar{B}(L_i)}$
1	$p\Delta_{D_j}$	$\frac{1}{2}(x_{rj(F_1)}+x_{jj}) - x_{\bar{B}(L_j)}$
1	Δ_i	$x_{ri(\bar{F}_2)} - \frac{1}{4}(x_{rr}+2x_{ri(F_1)}+x_{ii}) - x_{\bar{B}(R)} - x_{\bar{B}(L_i)}$
1	Δ_j	$x_{rj(\bar{F}_2)} - \frac{1}{4}(x_{rr}+2x_{rj(F_1)}+x_{jj}) - x_{\bar{B}(R)} - x_{\bar{B}(L_j)}$
1	Δ_{ij}	$x_{ij(\bar{F}_2)} - \frac{1}{4}(x_{ij(F_1)} + x_{ri(F_1)} + x_{rj(F_1)} + x_{ii} + x_{jj} + x_{rr})$
2.1	$(d)_{k_i}$	$\frac{1}{2}(x_{D_iD_i}-x_{ii})$
2.1	$(h)_{k_i}$	$x_{D_ii(F_1)} - \frac{1}{2}(x_{D_iD_i}+x_{ii})$
2.1	$(h)_{ik_i}$	$x_{rD_i(F_1)} - \frac{1}{2}(x_{rr}+x_{D_iD_i})$
2.1	∂_{ik_i}	$x_{rD_i(F_1)} - x_{D_ii(F_1)} - x_{ri(F_1)} + x_{ii}$

Trip. Grs. involved	Parameters	Formulas
2.1	Δ_{k_i}	$x_{D_i i(\bar{F}_2)} - \frac{1}{2}(x_{D_i D_i} + 2x_{D_i i(F_1)} + x_{ii})$
2.1	Δ_{u_i}	$x_{rD_i(\bar{F}_2)} - \frac{1}{2}(x_{rr} + 2x_{rD_i(F_1)} + x_{D_i D_i})$
2.2	$(d)_{k_j}$	$\frac{1}{2}(x_{D_j D_j} - x_{jj})$
2.2	$(h)_{k_j}$	$x_{D_j j(F_1)} - \frac{1}{2}(x_{D_j D_j} + x_{jj})$
2.2	$(h)_{jk_j}$	$x_{rD_j(F_1)} - \frac{1}{2}(x_{rr} + x_{D_j D_j})$
2.2	∂_{jk_j}	$x_{rD_j(F_1)} - x_{D_j j(F_1)} - x_{rj(F_1)} + x_{jj}$
2.2	Δ_{k_j}	$x_{D_j j(\bar{F}_2)} - \frac{1}{2}(x_{D_j D_j} + 2x_{D_j j(F_1)} + x_{jj})$
2.2	Δ_{u_j}	$x_{rD_j(\bar{F}_2)} - \frac{1}{2}(x_{rr} + 2x_{rD_j(F_1)} + x_{D_j D_j})$

where x stands for a character-metric mean and the subscripts rr, ii, jj, D_iD_i, D_jD_j, ri, rj, ij, rD_i, $D_i i$, and $D_j j$ refer to R, $L(Tm)_{1B}$, $L(Th)_{4A}$, Tm, Th, R x $L(Tm)_{1B}$, R x $L(Th)_{4A}$, $L(Tm)_{1B}$ x $L(Th)_{4A}$, R x Tm, R x Th, Tm x $L(Tm)_{1B}$, and Th x $L(Th)_{4A}$, respectively.

The parameters (d) and (h) are defined generally as the algebric sums of the genotypic values of the genes in homozygous and heterozygous states, respectively, at all loci by which the two parents differ (Mather,1949; Falconer,1960).

In particular, $(d)_w$ (w=i,j) is a measure of the effect of the substitution of the $w^{\underline{th}}$ chromosome-pair of a donor variety D for its

homologue in the recipient variety R, mid-parental value taken as the origin of measurement.

The parameter $(h)_w (w=i,j)$ is a measure of the resultant effect of allelic and nonallelic interactions within the set of heterozygous loci located in the $w^{\underline{th}}$ chromosome-pair of the Recipient x Substitution line cross.

The parameter ∂_{ij} is a measure of the interaction between the $i^{\underline{th}}$ and the $j^{\underline{th}}$ chromosome-pairs when both are in heterozygous state ($R_{1B}Tm_{1B}$ and $R_{4A}Th_{4A}$, respectively, in L_w x L_w cross), the rest of the genotype being homozygous.

The parameters $p\Delta_{R_w}$ and $p\Delta_{D_w}$ $(w=i,j)$ are the measures of nonallelic interaction effects within a chromosome-pair of which one is of original and one is of recombined type. These parameters when significantly different from zero reveal the presence of recombination ($p>0$) and epistatic effects ($\Delta \neq 0$).

The parameter Δ_w $(w=i,j)$ is a compound quantity (for details see Aksel, 1967). It includes interaction between loci in homologous chromosome-pairs of which one or both are recombinants. Like $p\Delta_R$ and $p\Delta_D$, Δ_w when significantly different from zero, reveals the presence of recombination and epistasis.

The parameter Δ_{ij} involves both chromosome and gene recombination effects at the level of homologous and/or nonhomologous chromosomes, excluding that of the ∂_{ij} kind.

The parameter $(d)_{k_w}$ $(w=i,j)$ shows the deviation of the measurements of the donor variety D and the substitution line L_w $(w=i,j)$ from their mean measurement and refers to all the differential loci in the homozygous state located in chromosomes other than the $w^{\underline{th}}$ pair of homologues, which is genotypically the same in both of them.

The parameter $(h)_{k_w}$ (w=i,j) is the resultant effect of allelic and nonallelic interactions at both the intra- and interchromosomal levels and refers to chromosomes other than the $w^{\underline{th}}$ pair of homologues.

The parameter $(h)_{ik_w}$ (w=i,j) has the same meaning as $(h)_{k_w}$ but includes also the $w^{\underline{th}}$ pair of homologues.

The parameter ∂_{ik_w} (w=i,j) indicates the presence of interaction between the $w^{\underline{th}}$ pair and the set consisting of remaining pairs of homologues when all are in heterozygous state.

The parameters Δ_{k_w} (w=i,j) and Δ_{u_w} (w=i,j) are compound quantities consisting of the effects of interactions of both the homologous and nonhomologous chromosomal kinds.

The standard error (s_p) of the parameters $(d)_i$, $(d)_j$, $(h)_i$, $(h)_j$, ∂_{ij}, $p\Delta_{R_i}$, $p\Delta_{R_j}$, $p\Delta_{D_i}$, $p\Delta_{D_j}$, Δ_i, Δ_j, Δ_{ij}, $(d)_{k_i}$, $(h)_{k_i}$, $(h)_{ik_i}$, ∂_{ik_i}, Δ_{k_i}, Δ_{u_i}, $(d)_{k_j}$, $(h)_{k_j}$, $(h)_{kj_j}$, ∂_{jk_j}, Δ_{k_j}, and Δ_{u_j}, are estimated by using the formula (Cochran and Cox, 1968):

$$s_p = \pm s \left(\frac{1}{r_1} l^2 + \frac{1}{r_2} l^2 + \ldots\ldots\ldots + \frac{1}{r_n} l_n^2\right)^{\frac{1}{2}}$$

where s is the square root of the error variance obtained from the nonsegregating generations of the respective triparental group, r the number of observations (or repititions), and l the coefficient of a character-metric in a formula. The error variances of the F_2 and the backcross generations are presumed to be the same as that of the error variances estimated from the corresponding nonsegregating generations.

The row means were considered to have equal weights and were used as units of observations. The variance analyses are done according to Steel and Torrie (1960).

Dominance was considered, in a broad sense, as the resultant of the

allelic and the nonallelic interaction effects within one or several pairs of differential homologues (Aksel and Kuspira, 1968; Aksel, 1970). The relative magnitude and the direction of dominance was assessed by using Wigan-Mather potence ration (Wigan, 1944; Mather, 1949). The potence ratio was estimated in this study only when (h) [where (h) = $(h)_i$, $(h)_j$, $(h)_{k_i}$, $(h)_{k_j}$] was significantly different from zero.

IV EXPERIMENTAL RESULTS

The character-metric means ($\bar{x}$) and their corresponding standard errors ($s_{\bar{x}}$) estimated from the row means are given in Table 3. The data in Table 3 indicate high homogeniety of the row means in the parental and the F_1 generations. As mentioned before, the parents and their crosses are arranged into three triparental groups. The recipient variety Chinese Spring (R) recurs in all three groups, $L(Tm)_{1B}$ recurs in groups 1 and 2.1, and $L(Th)_{4A}$ recurs in groups 1 and 2.2. No differences were found between reciprocal crosses (Table 4) and hence they were pooled together. The pertinent parameters and their corresponding standard errors (s_p) are collected in Table 5. The parameters $(d)_i$ and $(h)_i$ pertinent to the cross R x $L(Tm)_{1B}$, and $(d)_j$ and $(h)_j$ pertinent to the cross R x $L(Th)_{4A}$ recur in the triparental groups 2.1 and 2.2 respectively.

The error variances estimated from the nonsegregating generations (parents and F_1s) with respect to the characters considered are given in Table 6 separately for the three triparental groups. All the F values estimated as the ratio between and within generation variances are highly significant, indicating that the three parents and their F_1 crosses involved in the respective triparental groups are different from one another with respect to the characters considered, although the mean measurement differences (especially with respect to days-to-heading) are not large. A similar situation is also revealed from the data presented by Kuspira and Unrau (1957). A difference of less than two days, although indicated to be highly significant by the parameter concerned, will not be considered significant in this study since heading dates were recorded on a one-day basis.

The interpretation of the experimental results, which are given in Table 5, is provided in sequence for each triparental group separately.

1. Analysis of Triparental Groups

A. Triparental Group 1

The substitution of the chromosome-pair $Tm_{1B}Tm_{1B}$ for its homologue $R_{1B}R_{1B}$ in recipient Chinese Spring increases the mean measurements of the characters days-to-head and number of kernels per spike [$(d)_i$ = 0.42** and 2.41**, respectly]. With respect to the characters, plant height, number of tillers per plant, weight per kernel and yield per plant, the chromosome substitution does not produce any significant change [$(d)_i$ not significantly different from zero].

The chromosomes R_{1B} and Tm_{1B}, acting jointly as $R_{1B}Tm_{1B}$ in the cross R x $L(Tm)_{1B}$, contribute additively to the character-metrics, days-to-head, number of kernels and weight per kernel [$(h)_i$ not significantly different from zero], whereas with respect to plant height, number of tillers and yield per plant they contribute nonadditively [$(h)_i$ = 3.64**, -2.01*, and -3.15**, respectively]. With respect to number of tillers, the set of genes contained in chromosome Tm_{1B} over dominates its allelic sets in R_{1B} [$(h)_i/(d)_i$ = 1.76 1];and with respect to plant height and yield per plant, it shows heterotic effect [$(h)_i$ = 3.64** and -3.15**, respectively, compared to $(d)_i \simeq 0$].

The homologues R_{1B} and Tm_{1B} differ by two or more loci with respect to days-to-head, plant height, number of tillers, and yield per plant ($p\Delta_{R_i}$ = -1.07**, -2.86**, 3.08**, and 1.45 $\pm$ 1.27, respectively; $p\Delta_{D_i}$ = -0.44**, -3.21**, 1.10 $\pm$ 0.96, and 2.69*, respectively). The highly significant Δ_i values for these four characters (Δ_i = -0.80**, -1.97**, 6.03*, and 4.21**, respectively) also indicate the presence of recom-

bination and nonallelic interaction.

The significant values of Δ_i thus corroborate the conclusion that two or more than two loci are controlling the above characters. With respect to number of kernels the significant value of Δ_i indicates the presence of nonallelic interaction at the level of homologous chromosomes (Δ_i = 1.80**). However, since the recombination parameters $p\Delta_{R_i}$ and $p\Delta_{D_i}$ are not significantly different from zero ($p\Delta_{R_i}$ = 0.85 $\pm$ 0.72 and $p\Delta_{R_i}$ = 1.33 $\pm$ 0.69), one would suspect that nonallelic interaction involves chromosomes in recombined form. Nothing can be said definitely about weight per kernel (Δ_i not significantly different from zero).

The substitution of the chromosome-pair $Th_{4A}Th_{4A}$ fot its homologue $R_{4A}R_{4A}$ in recipient Chinese Spring increases days-to-head and plant height but reduces yield per plant [$(d)_j$ = 1.12**, 3.64**, and -2.58**, respectively]. The remaining characters are not affected by this substitution [$(d)_j$ not significantly different from zero].

The chromosomes R_{4A} and Th_{4A} acting jointly as $R_{4A}Th_{4A}$ in the cross R x $L(Th)_{4A}$ contribute additively to the character-metrics of all the characters considered [$(h)_j$ not significantly different from zero], except for plant height and number of kernels [$(h)_j$ = 3.97** and -3.04**, respectively].

The set of genes in chromosome Th_{4A} is dominant to the set in R_{4A} with respect to plant height [$(h)_j/(d)_j$ = 1.09 1], whereas with respect to number of kernels the resultant effect of the heterozygous chromosome-pair $R_{4A}Th_{4A}$ is a significant negative heterosis [$(h)_j$ = -3.04** compared to $(d)_j \simeq 0$].

The homologues R_{4A} and Th_{4A} differ at two or more that two loci with respect to days-to-head, plant height, number of tillers and yield

per plant ($p\Delta_{R_j}$ = -0.42**, 1.03 ± 0.95, 2.73**, and 3.51**, respectively; $p\Delta_{D_j}$ = 0.57**, 2.65**, 3.42**, and 1.56 ± 1.07, respectively). Although the recombination parameters ($p\Delta_{R_j}$ and $p\Delta_{D_j}$) for number of kernels are not significantly different from zero, the significant value of Δ_j for this character (Δ_j = 1.87**) indicates the presence of nonallelic interaction at the level of homologous chromosomes. However, as mentioned before, this kind of nonallelic interaction probably involves chromosomes in recombined form and indicates that two, or more than two, loci are involved. Nothing can be said definitely about weight per kernel (Δ_j not significantly different from zero).

The heterogous chromosome-pairs $R_{1B}Tm_{1B}$ and $R_{4A}Th_{4A}$ in the cross $L(Tm)_{1B}$ x $L(Th)_{4A}$ are independent in their action for all the characters studied (∂_{ij} not significantly different from zero), except plant height (∂_{ij} = -7.18**). The fact that the parameter Δ_{ij} is highly significant for all the characters studied indicates the presence of nonallelic interaction of a kind different from that of ∂_{ij} and involving both the chromosome and gene recombinations (Δ_{ij} = 0.69**, 4.74**, 0.92**, -2.56**, -1.86**, and -1.50**, respectively). By definition (see Aksel, 1967), the parameter Δ_{ij} is equal to $\delta_{ij} - q(x_{ij} - y_{ij})$, where δ_{ij} stands for the resultant of the nonallelic interaction effects at the level of nonhomologous chromosomes within the noncrossover sub-population of the $[L(Tm)_{1B} \times L(Th)_{4A}]$ F_2 population (excluding ∂_{ij}) and $q(x_{ij} - y_{ij})$ refers to both the presence of crossing over and the nonallelic interaction at the level of homologous and/or nonhomologous chromosomes within the crossover sub-population.

B. Triparental Group 2.1

The chromosome-pair $Tm_{1B}Tm_{1B}$ involved in triparental group 1 also occurs in this group. The effects of substitution of the chromosome-pair $Tm_{1B}Tm_{1B}$ for its homologue $R_{4A}R_{4A}$ in recipient Chinese Spring, and the experimental results pertinent to this chromosome-pair, have already been discussed.

In the cross Tm x $L(Tm)_{1B}$ the pair of homologues $Tm_{1B}Tm_{1B}$ is the same in both the parents. It, therefore, involves a set of differential loci contained in some or all of the homologous pairs Tm_xR_x ($x \neq 1B$). Note that the chromosomes of $L(Tm)_{1B}$, excluding chromosome-pair $Tm_{1B}Tm_{1B}$ are those of R.

With respect to all characters studied the difference between the donor Tm and the disomic substitution line $L(Tm)_{1B}$ is highly significant. The set of twenty chromosomes of Tm contains predominantly genes which reduce days-to-head, plant height, number of tillers, number of kernels, and yield per plant but increase weight of kernel[$(d)_{k_i}$ = -8.78**, -20.14**, -6.50**, -10.11**, -4.00**, and 7.13**, respectively]. Note that the difference between R and $L(Tm)_{1B}$ with respect to days-to-head was positive, whereas for the rest of the characters it was negative or not significantly different from zero.

With respect to number of kernels, the set of differential alleles in the chromosomes of Tm and those in R contained in the substitution line $L(Tm)_{1B}$, (excepting homologues $Tm_{1B}Tm_{1B}$), contribute additively to the character-metric [$(h)_{k_i}$ not significantly different from zero]; whereas they are nonadditive with respect to the remaining five characters [$(h)_{k_i}$ =-1.71**, 4.66*, 5.72**, 6.08**, and 6.50**, respectively]. The alleles present in the set of twenty chromosomes of Tm are mostly

dominant with respect to weight per kernel and partially dominant with respect to days-to-head [$(h)_{k_i}/(d)_{k_i}$ = 0.85<1 and 0.19<1, respectively] over their allelomorphs in R, whereas alleles in R are mostly dominant with respect to yield and number of tillers per plant, and partially dominant with respect to plant height over their homologues in Tm [$(h)_{k_i}/(d)_{k_i}$ = -1.63<-1, -0.88>-1, and -0.23>-1, respectively].

The fact that the values of the parameter $\blacktriangle_{k_i}$ are significantly different from zero with respect to the characters days-to-head, plant height, number of tillers, and weight of kernel indicates that these characters are controlled by two, or more than two, differential loci ($\blacktriangle_{k_i}$ = 1.42**, 2.29*, 1.55**, and -3.00**, respectively).

For the characters number of kernels and yield per plant the parameter $\blacktriangle_{k_i}$ is not significantly different from zero. Therefore, it is not clear whether the heterozygotic set of twenty chromosomes of Tm and R consists of a single locus, or of several loci either acting independently or having balanced effects with respect ot these two characters.

The cross R x Tm involves all 21 chromosome-pairs, i.e., including also the homologous pair $R_{1B}Tm_{1B}$. The comparison of the F_1 measurements with the corresponding mid-parental values shows that on the average there is dominance with respect ot most of the characters, except plant height [$(h)_{ik_i}$ = -3.18**, 2.63**, 2.96**, 5.61**, and 6.89**, respectively]. With respect ot plant height, the $(h)_{ik_i}$ value is not significantly different from zero.

With independence of action between the set of differential loci in the $R_{1B}Tm_{1B}$ and that contained in the remaining pairs of homologues, it would be expected that $(h)_{ik_i} - (h)_i - (h)_k = \partial_{ik_i}$, such that $\partial_{ik_i} = 0$. Since, however, ∂_{ik_i} is significantly different from zero for

days-to-head (∂_{ik_i} = -1.46**) we may conclude that the involved sets of differential loci do not act independently.

The highly significant Δ_{u_i} values with respect ot days-to-head, number of tillers, and weight of kernel also indicate the presence of nonallelic interaction (Δ_{u_i} = 1.14**, 2.44**, and -11.02**, respectively). Since neither ∂_{ik_i} nor $(h)_{ik_i}$ are significantly different from zero with respect to plant height, the significant Δ_{u_i} value(Δ_{u_i} = 2.29*) indicates the presence of nonallelic interaction either within the chromosome-pair $R_{1B}Tm_{1B}$ or within the set of twenty heterozygous chromosomes or both of them, and also that two, or more than two, loci are involved.

C. Triparental Group 2.2

The chromosome-pair $Th_{4A}Th_{4A}$, involved in triparental group 1, also occur in this group. The effects of its substitution for the homologue-pair $R_{4A}R_{4A}$ in recipient Chinese Spring and the experimental results pertinent to this chromosome-pair have already been given.

In the cross Th x $L(Th)_{4A}$ the pair of homologues $Th_{4A}Th_{4A}$ is the same in both the parents. It, therefore, involves a set of differential loci contained in some or all of the homologous pairs Th_xR_x ($x \neq 4A$). Note that the chromosomes of $L(Th)_{4A}$, excluding chromosome-pair $Th_{4A}Th_{4A}$ are those of R. The difference between the donor Th and the disomic substitution line $L(Th)_{4A}$ with respect to all the characters studied, except yield per plant, is highly significant. The set of twenty chromosomes of Th contains predominantly genes which reduce days-to-head, plant height, number of tillers and number of kernels but increase weight of kernel [$(d)_{k_j}$ = -9.10**, -21.49**, -5.95**, -4.81**, and 7.70**, respectively]. Note that the difference between R and $L(Th)_{4A}$ with

respect to days-to-head is positive, whereas for the rest of the characters it is negative or not significantly different from zero.

With respect to all characters studied except for number of tillers [$(h)_{k_j}$ not significantly different from zero], the alleles contained in the set of twenty chromosomes of Th and those in R are nonadditive in their contribution towards the character-metrics [$(h)_{k_j}$ = -3.41**, -7.32**, -2.96**, 7.30**, and 3.37**, respectively]. The alleles present in the set of twenty chromosomes of Th are dominant with respect to weight per kernel [$(h)_{k_j}/(d)_{k_j}$ = 0.95 1] and partially dominant with respect to days-to-head, plant height, and number of kernels [$(h)_{k_j}/(d)_{k_j}$ = 0.37 1, 0.37 1, and 0.62 1, respectively] over their homologues in R. With respect to yield per plant, the resultant effect of the interaction between the set of twenty chromosomes of Th and that of R is a significant positive heterosis [$(h)_{k_j}$ = 3.37** as compared to $(d)_{k_j} \simeq 0$].

Significant values of Δ_{k_j} with respect to all characters studied, except yield per plant, indicate that these characters are controlled by a set of differential loci (Δ_{k_j} = 1.85**, -2.79**, -0.79**, and 1.61**, respectively. For the character yield per plant, the parameter Δ_{k_j} is not significantly different from zero. It is, therefore, not clear whether the heterozygous set of twenty chromosomes of Th and R consists of a single locus, or of several loci either acting independently or having balanced effects with respect to yield per plant.

The cross R x Th involves all 21 chromosome-pairs, i.e., including also the homologous pair $R_{4A}Th_{4A}$. The comparison of the F_1 measurements with the corresponding mid-parental values shows that on the average there is dominance with respect to characters other than

except plant height and number of kernels [$(h)_{jk_j}$ = 1.67**, 1.91*, 5.65**, and 4.62**, respectively].

Significant values of the parameter ∂_{jk_j} for days-to-head, number of tillers, and number of kernels indicate the presence of nonallelic interaction between the chromosome-pair $R_{4A}Th_{4A}$ and the set of twenty nonhomologous chromosomes with respect to these characters (∂_{jk_j} = 1.81*, 3.55**, and 6.24**, respectively).

The fact that the values of the parameter Δ_{u_j} are significant with respect to days-to-head, plant height, number of tillers, and weight per kernels (Δ_{u_j} = 1.49**, 2.11*, 2.27**, and -2.53**, respectively) indicates the presence of nonallelic interaction within and/or between the chromosome-pair $R_{4A}Th_{4A}$ and the set of twenty nonhomologous chromosomes, and also that two, or more than two, loci are involved.

2. The Analysis of Single Characters Based on Graphical Frequency Distributions.

The analytical interpretations of the frequency distributions of the data obtained from the parents (R, Tm, Th, $L(Tm)_{1B}$, and $L(Th)_{4A}$) and their corresponding crosses (F_1, F_2, and backcrosses) used in this study are given separately for the six characters considered.

A. Days-to-heading

The frequency distributions of the parents, F_1s, F_2s, and backcrosses of the crosses R x $L(Tm)_{1B}$ (Fig. 1A, 1B), R x $L(Th)_{4A}$ (Fig. 2A, 2B), and $L(Tm)_{1B}$ x $L(Th)_{4A}$ (Fig. 3A, 3B) overlap almost entirely with one another and show more or less normal, continuous distributions. This means either that the chromosomes Tm_{1B}, Th_{4A}, R_{1B}, and R_{4A} do not contain any effective genes for earliness, or that they contain identical set of genes (see also Kuspira, 1963).

The frequency distribution of F_1 of the cross Tm x $L(Tm)_{1B}$ involving all the chromosomes, of which the homologous-pair $Tm_{1B}Tm_{1B}$ is the same in both the parents, is intermediate between those of the parents (Fig. 4A). The frequency distribution graph of F_2 shows two notches (see arrows) which indicate that three collectives are present in the population (see also Weber, 1959). If ordinates are drawn through the lowest points of the notches and if the ordinates are regarded as border lines, it will be found that they divide the area under the curve into three parts in a ratio of 1:2:1 (X^2 = 4.90, P>0.05). Thus it may be assumed that the character is monogenetically controlled. However, the backcross distributions indicate that some minor genes with small effects are also involved (Fig. 4B).

The F_1, F_2, and backcross distributions for the cross R x Tm are very similar to the corresponding distributions (X^2 for F_2 = 0.55, P>0.75) for the cross Tm x $L(Tm)_{1B}$ (Fig. 5A, 5B). This indicates that one gene with major effects and one or more minor genes with small effects differentiate Tm from R with respect to earliness.

The distributions in F_1, F_2, and backcross populations of the crosses Th x $L(Th)_{4A}$ and R x Th (Fig. 6A, 6B, 7A and 7B) are very similar to those of the crosses Tm x $L(Tm)_{1B}$ and R x Tm, respectively. The F_2 segregations in both the crosses show a good fit to the 1:2:1 ratio (X^2 = 3.66 and 3.25; P>0.10 and P>0.10, respectively). These facts indicate that the donor Th and the recipient R differ by one gene with major effect and one or more minor genes with small effects with respect to earliness.

Since both the chromosomes Tm_{1B} and Th_{4A} were found to be identical for genes affecting earliness with one another and with their homologue

we may conclude that the genes (both major and minor) affecting earliness are located in chromosomes other than 1B(I) and 4A(IV).

Wehrhahn (1961) on reanalyzing the data of Kuspira and Unrau (1957) found evidence for four genes differentiating Timstein and Thatcher from Chinese Spring with respect to earliness. Tsunewaki and Jenkins (1961) found that growth habit is controlled by genes belonging to three allelic series, Sg_1, Sg_2 and Sg_3 located on chromosomes XVIII (5D), IX(5A), and XIII(2A), respectively. The Sg_1 and Sg_2 contain 3 alleles (Sg_1, Sg_1^c, and sg_1; and Sg_2, Sg_2^c, and sg_2, respectively) while Sg_3 contains two alleles (Sg_3 and sg_3). Wehrhahn and Allard (1965) found four genes with unequal effects differentiating Baart 46 and Ramona with respect to earliness. Of these four genes, one contributes about 80% of the total heritable variation and is nearly fully dominant over the lateness allele (Allard and Harding, 1963). The major gene found in this study could be analogous to the major gene referred to by Wehrhahn and Allard.

Chromosome 5D(XVIII) has often been associated with spring and winter habits of growth in wheat (Tsunewaki, 1962; Tsunewaki and Jenkins 1961). Law (1966b) suggested that this chromosome might contain the gene of large effect observed by Wehrhahn and Allard.

Law (1966b) and Law and Wolfe (1966) found two genes for earliness on chromosome 7B(VII) of Hope. Crumpacker and Allard (1962) found three genes, of which two were partially dominant for earliness and one was partially dominant for lateness. Florell (1931) and Powers (1934) found earliness to be controlled by three independent genes. Nandpuri (1959) found two genes, one being more effective than the other in the induction of early heading. Still others, viz., Thompson (1921), Aamodt

(1923), Gaines and Singleton (1926), Stephens (1927), Gfeller (1937), and Torrie (1936) found evidence for multiple genes affecting earliness.

B. Plant Height

Figure 8A shows that the frequency distribution in F_1 of the cross R x $L(Tm)_{1B}$ is completely contained within the distribution of $L(Tm)_{1B}$. However, its modal class falls to the right of those of the parents. The F_2 and backcross distributions do not give any distinct grouping (Fig. 8B), but the mode of the F_2 distribution indicate increase in plant height.

The F_1 distribution of the cross R x $L(Th)_{4A}$ shows that the parent $L(Th)_{4A}$ is completely dominant over R (Fig. 9A). Figure 9A indicates that if the number of plants in F_1 population is increased to a level similar to that of $L(Th)_{4A}$, the two distributions would coincide almost entirely. The F_2 and backcross distributions suggest monogenic segregation (Fig. 9B). If the ordinates are drawn through the main notches of the F_2, B_1, and B_2 graphs, the area under them will be divided into two parts each. The ratios between the two parts were found to be 3:1, 1:1, and 1:1 for F_2, B_1, and B_2, respectively (X^2 = 3.34, $P>0.05$; 1.18, $P>0.10$; and 10.11, $P<0.005$; respectively). Thus we may conclude that the chromosome Th_{4A} which was substituted from the short variety Th ($\bar{x}$ = 81.78 cms.) contains one dominant gene for tallness. The median of the F_1 distribution falls to the right of that of the taller parent $L(Th)_{4A}$, indicating over-dominance.

The F_1 distribution of the cross $L(Tm)_{1B}$ x $L(Th)_{4A}$ shows that the parent $L(Th)_{4A}$ is completely dominant (Fig. 10A). The F_2 distribution (Fig. 10B) shows a segregation ratio of 3:1 (X^2 = 6.13, $P>0.01$), confirming the presence of a dominant gene for tallness in chromosome Th_{4A}.

However, the backcross distributions suggest that, in addition to the dominant gene referred to above, other genes are involved (Fig. 10B).

In the cross Tm x $L(Tm)_{1B}$, the F_1 distribution indicates that the parent $L(Tm)_{1B}$ is partially dominant (Fig. 11A). The F_2 and the backcross distributions do not give rise to any distinct classes (Fig.11B) and we conclude that a polygenic system is involved.

In the cross R x Tm, which involves all the 21 chromosomes, including also the homologue $R_{1B}Tm_{1B}$, the F_1 distribution indicates partial dominance by the donor parent Tm. It is, therefore, evident that chromosome Tm_{1B} contains gene(s) which increase plant height and express themselves when acting with the genetic background of the recipient R. Whereas, when the chromosome Tm_{1B} is in its original genetic background, the gene(s) for tallness do not show ant effect.

The crosses Th x $L(Th)_{4A}$ and R x Th show distributions similar to those of Tm x $L(Tm)_{1B}$ and R x Tm crosses, indicating that the chromosome Th_{4A} also contains one or more genes for tallness (Fig. 13A, 13B, 14A, and 14B).

Kuspira and Unrau (1957) found that chromosomes VIII(4B), XI(7A), and XVI(3D) of Thatcher; VIII(4B) of Timstein; and I(1B), III(3B), VII(7B), VIII(4B), IX(5A), and XII(3A) of Hope contain genes which affect plant height. They also reported that the chromosome XI(7A) of Thatcher has significantly greater effect on plant height as compared to that of Chinese Spring. Allan and Vogel (1963) working with Norin 10, Brevor 14 and the Chinese Spring series found that XIII(2A), II(2B), XX(2D), XII(3A), XVI(3D), IV(4A), VIII(4B), XV(4D), IX(5A), V(5B), and XVIII(5D) influence plant height. Ausemus, McNeal and Schmidt (1967)

reported that all chromosomes except 1A, 1B, 1D, 6D, and 7A affect culm length. Multigenic control of plant height has been reported by Freeman (1919) and Peterson (1965).

C. Number of Tillers per plant

The parents, F_1s, F_2s, and backcrosses of the crosses R x $L(Tm)_{1B}$, R x $L(Th)_{4A}$, and $L(Tm)_{1B}$ x $L(Th)_{4A}$ all show continuous distributions and are very similar to one another (Fig. 15A-B, 16A-B, 17A-B). It is, therefore, probable that the chromosomes Tm_{1B}, R_{1B}, Th_{4A} and R_{4A} are genotypically equivalent.

The F_1 distribution of the cross Tm x $L(Tm)_{1B}$ shows that the parent $L(Tm)_{1B}$ is dominant over Tm (Fig. 18A). The F_2 and the backcross distributions do not show any distinct grouping (Fig. 18B).

The mode of the F_1 distribution of the cross R x Tm is slightly to the left of that of the parent with the higher number of tillers (Fig. 19A), indicating that R contains partially dominant genes for this character. The F_2 and backcross distributions do not give any clear groupings (Fig. 19B).

The F_1 distribution of the cross Th x $L(Th)_{4A}$ falls between the two parental distributions suggesting an intermediate mode of inheritance (Fig. 20A). The F_2 and backcross distributions do not show any distinct groupings (Fig. 20B).

The F_1, F_2, and backcross distributions of R x Th cross are very similar to those of the corresponding distributions of R x Tm (Fig. 21A-B).

The graph pertaining to the character number of tillers per plant (Fig. 15A to 21B) indicate that this character, like plant height, is also controlled by a polygenic system. Sears (1954) reported that a

number of chromosomes contain genes which affect tillering. Ausemus, McNeal and Schmidt (1967) reported that chromosomes 1B, 1D, 2A, 2B, 2D, 3D, 4A, 4B, 4D, 5D, and 6A affect tillering in various ways.

D. Number of Kernels per Spike

The distribution in the F_1 of the cross R x $L(Tm)_{1B}$ shows an intermediate mode (Fig. 22A). The F_2 and the B_1 distributions do not show any clear discontinuities, but the B_2 distribution shows a notch at 57 which may be considered as an indication for discontinuity (Fig. 22B). The two groups in the B_2 distribution fit to a ratio of 1:1 ($X^2 = 0.06$, $P>0.99$) suggesting that the difference between the homologues Tm_{1B} and R_{1B} is due primarily to the effect of one major gene.

The distributions of the parents, F_1, F_2, and backcrosses of the cross R x $L(Th)_{4A}$ are more or less similar and are approximately normally distributed (Fig. 23A, 23B) indicating that chromosome Th_{4A} is genotypically identical with chromosome R_{4A} with respect to kernel number.

The mode of the F_1 distribution of the cross $L(Tm)_{1B}$ x $L(Th)_{4A}$ is slightly to the left of the lower parent (Fig. 24A). The F_2 and backcross populations do not show any clear discontinuities (Fig. 24B).

In the cross Tm x $L(Tm)_{1B}$, the F_1 distribution shows an intermediate mode (Fig. 25A). The F_2 and backcross distributions clearly indicate the presence of a partially dominant gene (Fig. 25B). The F_2 segregants show a ratio of 1:2:1 ($X^2 = 8.12$, $P>0.01$) and those of B_1 and B_2 show 1:1 ratios ($X^2 = 1.19$ and 3.86; $P>0.25$ and $P>0.05$), respectively).

In the cross R x Tm, the F_1 distribution shows an intermediate mode (Fig. 26A). The F_2 segregants do not adequately fit the expected 1:2:1 ratio

(Fig. 26B). The preponderance of the segregants with large numbers of kernels indicate that the chromosome Tm_{1B} contains one or more genes which increase kernel number (see also Fig. 25B). The backcross distributions (Fig. 26B) show a segregation ratio of 1:1 (X^2 = 0.92 and 2.95; P>0.25 and P>0.05, respectively).

The F_1, F_2 and backcross distributions of the cross Th x $L(Th)_{4A}$ show modes similar to those of the corresponding distributions in the cross Tm x $L(Tm)_{1B}$ (Fig. 27A-B), thus indicating that a partially dominant gene is involved. The F_2 segregants show a ratio of 1:2:1 and the B_1 and B_2 segregants show a ratio of 1:1 and 1:1,respectively (X^2 = 2.95, 1.00 and 1.35; P>0.20, P>0.30 and P>0.20,respectively).

The mode of the F_1 distribution of the cross R x Th is intermediate (Fig. 28A). The F_2 distribution is more or less continuous indicating that one or more minor genes are involved which obscure the grouping in F_2. The backcross distributions show a segregation ratio of 1:1 (X^2 = 0.03 and 2.27; P>0.97 and P>0.10 respectively), but for some reason or other they coincide with one another (Fig. 28B).

Ausemus et al. (1964) reported digenic control of kernel number per spike.

E. Weight per Kernel

The distributions of the parents, F_1s, F_2s, and backcross populations of the crosses R x $L(Tm)_{1B}$, R x $L(Th)_{4A}$, and $L(Tm)_{1B}$ x $L(Th)_{4A}$ are very similar to one another and all of them show continous and more or less normal distributions (Fig. 29A-B, 30A-B, 31A-B). These distributions together with the nonsignificant parameters (except Δ_{ij}) pertinent to these crosses strongly indicate the possibliity that the chromosomes Tm_{1B} and Th_{4A} are genotypically similar to each other and also to their homologues in R, with respect to weight per kernel.

The distribution in the F_1 of the crosses Tm x $L(Tm)_{1B}$ and R x Tm show that differential loci present in Tm are dominant, on the average, to their homologues in R (Fig. 32A, 33A). The distributions in the F_2 and backcrosses of the above two crosses do not show any distinct discontinuities (Fig. 32B, 33B).

The F_1 distributions of the crosses Th x $L(Th)_{4A}$ and R x Th indicate that the chromosomes of Th contain mostly dominant genes with respect to kernel weight (Fig. 34A, 35A). The F_2 and backcross distributions of these two crosses do not show any clear discontinuities (Fig. 34B, 35B). The frequency distributions, therefore, suggest the presence of polygenic control of kernel weight.

Kuspira and Unrau (1957) found that seven chromosomes I(1B), IV(4A), V(5B), VI(6A), XVI(3D), and XIX(6D) carried genes which affect kernel weight and that I(1B) had greatest effect. Worzella (1942) reported multigenic control of kernel weight, whereas Boyce (1948) reported monogenic inheritance in one cross and two or three genes in other crosses.

F. Yield of Seed per Plant

The parents, R and $L(Tm)_{1B}$, of the cross R x $L(Tm)_{1B}$ are very similar to one another. The mode of F_1 distribution shows a slight decrease in yield per plant (Fig. 36A). The F_2 population shows a segregation ratio of 9:7 ($X^2 = 3.97$, $P>0.025$) indicating the presence of two major complementary genes which reduce yield (Fig. 36B). The backcrosses do not show any distinct discontinuities which indicate that more than two interacting genes are involved.

The distributions in the parents, F_1, F_2, and backcrosses of the cross R x $L(Th)_{4A}$ are very close to one another (Fig. 37A-B) suggesting

that the genes contained in the chromosome Th_{4A} are identical to those contained in its homologue R_{4A} with respect to yield per plant.

The distribution in the F_1 of the cross $L(Tm)_{1B} \times L(Th)_{4A}$ is very close to those of the parents (Fig. 38A). The F_2 and backcrosses do not show a definite grouping (Fig. 38B). However, the fact that their modes fall to the left of parental and F_1 modes indicates nonallelic interaction having reducing effect on yield.

In the cross Tm x $L(Tm)_{1B}$, the F_1 distribution indicates complete dominance by $L(Tm)_{1B}$ (Fig. 39A). The F_2 and backcross distributions do not show any distinct grouping (Fig. 39B).

The distributions in the parents, F_1, F_2, and backcrosses of the cross R x Tm are very similar to those of the corresponding distributions in the cross Tm x $L(Tm)_{1B}$ (Fig. 40A-B). These facts suggest that some or all of the chromosomes of R contain mostly dominant genes for yield per plant and that a complex polygenic system is involved.

The F_1 distribution of the cross Th x $L(Th)_{4A}$ is very close to the parental distributions (Fig. 41A). The F_2 and backcross distributions do not show any clear grouping (Fig. 41B). However, the preponderance of the segregants having reduced yield indicates the presence of one or more genes with reducing effects on yield.

The F_1 distribution of the cross R x Th shows transgressive dominance toward higher yield (Fig. 42A). The F_2 and the backcross distributions are very similar to those of R x Tm cross indicating that a complex gene system controls yield per plant.

Kuspira and Unrau (1957), Kuspira (1958), and Peterson (1965) reported multigenic control for yield per plant. Kuspira and Unrau (1957) and Kuspira (1963) found that four chromosomes I(1B), III(3B),

VIII(4B), and XII(3A) of Thatcher and almost all chromosomes except IX(5A), XI(7A), XV(4D), and XX(2D) of Timstein contain genes which affect yield per plant.

V DISCUSSION

The experimental results obtained in this study reveal significant allelic and nonallelic within- and/or between-chromosomal interactions. The tendency of the parameters, pertinent to the respective triparental groups, to fall into two opposinf groups (+ and -), in most instances, shifts the direction of the resultant interaction effect towards some sort of equilibrium (see also Law, 1966; Aksel and Kuspira, 1968; and Aksel, 1970). Such an equilibrium, in most cases, has a blurring effect on the grouping of the individuals in the F_2 and the backcross generations, and makes it difficult to estimate the number of effective factors. The parameters pertaining to the gene recombination and nonallelic interactions, viz., $p\Delta_R$, $p\Delta_D$, Δ_i, Δ_j, and Δ_{ij}, therefore, even if nonsignificant, do not necessarily preclude the possibility of the existence of a single differential locus, or of several differential loci at which the two parents differ and which are acting either independently or with balanced effects (see also Aksel and Kuspira, 1968).

With respect to the characters considered, excepting for number of kernels and weight per kernel, the recombination parameters pertaining to triparental group 1 were found to be significant. This indicates that the substituted chromosome-pairs $Tm_{1B}Tm_{1B}$ and $Th_{4A}Th_{4A}$ contain two or more differential loci affecting these characters. The chromosome Tm_{1B} was found to contain genes which affect plant height, kernel number and yield per plant, while a major gene for tallness was found on the chromosome Th_{4A}.

The chromosome-pair $Tm_{1B}Tm_{1B}$ when in heterozygous combination $R_{1B}Tm_{1B}$ shows heterotic effects with respect to the characters plant height and yield per plant, while the chromosome-pair $Th_{4A}Th_{4A}$ in heterozygous combination $R_{4A}Th_{4A}$ shows heterotic effect on kernel

number (see also Aksel and Kuspira, 1968).

The chromosome-pairs $Tm_{1B}Tm_{1B}$ and $Th_{4A}Th_{4A}$ when in heterozygous combination $R_{1B}Tm_{1B}R_{4A}Th_{4A}$ show nonallelic interaction with respect to plant height ($\mathcal{J}_{ij}$ = -7.18**).

The differential alleles contained by the donors Timstein and Thatcher were found to be partially dominant over their allelomorphs in recipient Chinese Spring with respect to the characters days-to-head, plant height, number of kernels per spike, and weight per kernel; whereas they were partially recessive to their allelomorphs with respect to number of tillers and yield per plant.

Analysis of the frequency distributions of the parents and their filial generations indicate that the characters plant height, number of tillers, weight per kernel, and yield were polygenetically controlled; whereas earliness and number of kernels were controlled by one major gene and one or more minor genes with small effects. These results, therefore, corroborate the findings of Weber (1959) and Wehrhahn and Allard (1965) that all quantitative characters are not necessarily controlled by a large number of genes with small and similar effects. This is contradictory to the views held by various authors (e.g., Mather, 1941, 1949; Falconer,1960, etc.).

As mentioned before, the experimental method used in this study measures the direction and the magnitude of various allelic and non-allelic interactions within and between linkage groups. For complete analysis of the genetics of the quantitatively inherited characters, this method must be supplemented by the inbred backcross line method of Wehrhahn and Allard (1965) (see also Aksel, 1967). If a relatively small number of genes are involved, repeated backcrossing and

selfing with one or both parents would produce a number of pure lines. Backcrossing should be continued until each line is expected to contain no more than one differential gene for the character being studied. The magnitude of the effect of a gene should be equal to the distance of the group of lines carrying the genes from the class in which the recurrent parent falls. Once the genes are isolated, their relative position in the chromosome-map can be determined by using suitable markers (Thoday, 1961; Thoday, Gibson, and Spickett, 1964; Spickett and Thoday, 1966; and Law, 1967).

VI SUMMARY

An analysis of the effect of the genes which differentiate chromosomes 1B of Timstein and 4A of Thatcher from their homologues in Chinese Spring was conducted with respect to six quantitative characters, viz., days-to-heading, plant height, number of tillers per plant, number of kernels per spike, weight per kernel, and yield of seed per plant. The chromosome-pairs $Tm_{1B}Tm_{1B}$ and $Th_{4A}Th_{4A}$ which were substituted from the short donors Timstein and Thatcher, respectively, were found to contain genes for tallness. The chromosome-pair $Tm_{1B}Tm_{1B}$ was also found to contain genes affecting the number of kernels per spike and the yield per plant.

The substitution lines and the crosses involving them show the effect of each substituted chromosome in the genetic background of its own variety and in that of the recipient variety, by itself, and/or in combination with the remaining chromosomes.

The characters days-to-head and number of kernels per spike were found to be controlled by one gene with a major effect and one or more minor genes with small effects, whereas evidence of multigenic control was found for the characters plant height, number of tillers per plant, weight per kernel and yield per plant.

Highly significant intra- and interallelic interactions were observed for all the characters studied. Evidence was obtained that pertinent genetic parameters tend to be balanced (Law, 1966; Aksel and Kuspira, 1968; and Aksel, 1970).

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Table 3. Character-measurement means.

Item No.	Parents or Crosses	Generation	No. of rows studied	Earliness ($\bar{x} \pm s_{\bar{x}}$) (in days)	Plant Height ($\bar{x} \pm s_{\bar{x}}$) (in cms.)	No. Til Plant ($\bar{x} \pm s_{\bar{x}}$
1	R	P	48	73.21 ± 0.17	117.48 ± 1.08	28.60 ±
2	$L(Tm)_{1B}$	P	47	74.04 ± 0.15	117.97 ± 1.08	26.32 ±
3	$L(Th)_{4A}$	P	77	75.44 ± 0.14	124.76 ± 0.87	27.95 ±
4	Tm	P	37	56.48 ± 0.11	77.70 ± 0.74	13.33 ±
5	Th	P	45	57.24 ± 0.18	81.78 ± 0.62	16.05 ±
6	R x $L(Tm)_{1B}$	F_1	24	73.62 ± 0.34	121.37 ± 1.69	25.45 ±
		F_2	48	74.33 ± 0.13	123.64 ± 1.06	28.30 ±
		B_1	18	74.48 ± 0.17	122.29 ± 1.97	23.95 ±
		B_2	31	74.27 ± 0.17	122.88 ± 1.38	24.78 ±
7	R x $L(Th)_{4A}$	F_1	24	74.25 ± 0.24	125.09 ± 1.76	27.63 ±
		F_2	50	74.29 ± 0.12	122.74 ± 1.69	25.78 ±
		B_1	23	74.15 ± 0.25	120.26 ± 1.76	25.39 ±
		B_2	28	74.27 ± 0.23	122.27 ± 1.73	24.38 ±

ight	No. Tillers/ Plant ($\bar{x} \pm s_{\bar{x}}$)	No. Kernels/ Spike ($\bar{x} \pm s_{\bar{x}}$)	Wt. Kernel/ ($\bar{x} \pm s_{\bar{x}}$) (in mgs.)	Yield/Plant ($\bar{x} \pm s_{\bar{x}}$) (in gms.)	DF
)					
1.08	28.60 ± 0.62	56.64 ± 0.46	25.00 ± 2.72	21.01 ± 0.73	47
1.08	26.32 ± 0.65	61.45 ± 0.57	26.04 ± 3.21	22.77 ± 0.81	46
0.87	27.95 ± 0.58	56.52 ± 0.43	21.00 ± 1.99	15.85 ± 0.55	76
0.74	13.33 ± 0.33	41.23 ± 0.47	40.29 ± 2.25	14.78 ± 0.38	36
0.62	16.05 ± 0.41	46.71 ± 0.58	36.39 ± 2.30	16.75 ± 0.46	44
1.69	25.45 ± 0.87	59.02 ± 0.59	23.53 ± 3.97	18.74 ± 0.84	23
1.06	28.30 ± 0.84	58.66 ± 0.46	23.44 ± 2.87	20.39 ± 0.63	47
1.97	23.95 ± 0.76	56.98 ± 0.67	22.99 ± 5.20	18.43 ± 1.81	17
1.38	24.78 ± 0.82	58.91 ± 0.52	23.53 ± 3.37	18.07 ± 0.43	30
1.76	27.63 ± 0.75	53.33 ± 0.59	23.39 ± 2.87	17.15 ± 0.59	23
1.69	25.78 ± 0.62	54.47 ± 0.40	22.86 ± 2.93	17.12 ± 0.56	49
1.76	25.39 ± 0.71	53.72 ± 0.50	23.08 ± 3.71	15.57 ± 0.65	22
1.73	24.38 ± 0.67	53.85 ± 0.55	22.30 ± 2.76	14.94 ± 0.55	27

8	$L(Tm)_{1B} \times L(Th)_{4A}$	F_1	23	74.83 ± 0.22	121.80 ± 1.45	26.27 ±
		F_2	38	75.43 ± 0.22	123.11 ± 0.82	27.17 ±
		B_1	25	74.65 ± 0.34	123.44 ± 1.91	23.71 ±
		B_2	19	75.48 ± 0.28	123.97 ± 2.35	23.92 ±
9	R x Tm	F_1	23	61.66 ± 0.25	101.56 ± 1.35	23.60 ±
		F_2	48	64.39 ± 0.25	101.90 ± 1.46	24.72 ±
		B_1	32	66.73 ± 0.30	109.36 ± 0.78	26.29 ±
		B_2	27	61.65 ± 0.72	99.78 ± 1.81	16.48 ±
10	R x Th	F_1	24	63.56 ± 0.30	98.89 ± 0.83	24.24 ±
		F_2	48	65.88 ± 0.36	101.37 ± 1.46	25.55 ±
		B_1	28	68.78 ± 0.36	108.52 ± 1.30	28.15 ±
		B_2	24	62.26 ± 0.52	95.29 ± 0.99	21.16 ±
11	Tm x $L(Tm)_{1B}$	F_1	22	63.55 ± 0.31	102.50 ± 0.84	25.55 ±
		F_2	50	65.83 ± 0.26	102.46 ± 0.67	24.24 ±
		B_1	31	67.60 ± 0.34	108.27 ± 1.41	24.69
		B_2	29	61.11 ± 0.29	91.86 ± 1.12	17.80
12	Th x $L(Th)_{4A}$	F_1	19	62.93 ± 0.45	95.95 ± 0.89	21.00
		F_2	39	66.48 ± 0.39	96.83 ± 1.07	23.22
		B_1	28	69.27 ± 0.46	104.50 ± 1.04	23.97
		B_2	16	63.85 ± 0.84	93.35 ± 1.25	20.37

.45	26.27 ± 0.76	54.55 ± 0.72	25.26 ± 4.09	18.16 ± 0.60	22
.82	27.17 ± 0.53	54.48 ± 0.53	21.70 ± 3.20	16.42 ± 0.60	37
.91	23.71 ± 0.91	56.86 ± 0.86	22.27 ± 4.00	15.53 ± 0.78	24
.35	23.92 ± 0.74	53.37 ± 0.59	22.33 ± 6.19	14.10 ± 0.89	18
.35	23.60 ± 1.10	51.89 ± 0.45	38.25 ± 4.22	24.79 ± 1.26	22
.46	24.72 ± 0.47	50.97 ± 0.46	24.43 ± 2.28	21.05 ± 0.54	47
.78	26.29 ± 0.51	55.36 ± 0.63	28.97 ± 2.94	20.34 ± 0.90	31
.81	16.48 ± 0.76	47.67 ± 0.59	37.61 ± 3.73	16.88 ± 0.67	26
.83	24.24 ± 0.80	51.92 ± 0.68	36.34 ± 4.62	23.50 ± 0.98	23
.46	25.55 ± 0.50	51.27 ± 0.50	30.99 ± 2.61	20.73 ± 0.62	47
.30	28.15 ± 0.93	52.36 ± 0.60	28.15 ± 3.12	19.46 ± 0.70	27
.99	21.16 ± 0.63	50.75 ± 0.59	33.95 ± 4.36	20.01 ± 0.78	23
.84	25.55 ± 0.73	51.93 ± 0.61	39.25 ± 4.20	25.28 ± 0.66	21
.67	24.24 ± 0.41	52.31 ± 0.53	33.21 ± 2.03	21.77 ± 0.57	49
.41	24.69 ± 0.68	54.94 ± 0.94	31.60 ± 2.93	21.64 ± 0.87	30
.12	17.80 ± 0.81	46.94 ± 0.65	38.35 ± 3.03	17.79 ± 0.77	28
.89	21.00 ± 1.15	48.56 ± 0.70	36.00 ± 4.97	19.67 ± 0.97	18
.07	23.22 ± 0.88	49.25 ± 0.65	30.74 ± 3.19	17.42 ± 0.79	38
.04	23.97 ± 0.64	49.30 ± 0.62	28.70 ± 2.51	15.68 ± 0.52	27
.25	20.37 ± 0.65	49.02 ± 0.68	33.29 ± 4.86	16.52 ± 0.71	15

Table 4. Table of observed t-values for the differences between measur

F_1 crosses	Earliness	Plant Height	No. Tillers/ Plant
R x $L(Tm)_{1B}$	1.32	0.52	0.60
R x $L(Th)_{4A}$	1.52	0.35	0.47
$L(Tm)_{1B}$ x $L(Th)_{4A}$	0.39	0.67	0.27
R x Tm	1.44	1.87	1.28
R x Th	1.55	0.64	0.70
Tm x $L(Tm)_{1B}$	1.07	0.28	0.06
Th x $L(Th)_{4A}$	0.73	1.03	0.83

Significant value for 1% = 1.96

Significant value for 5% = 2.56

ween measurement means of the F_1 generations of reciprocal crosses.

. Tillers/ ant	No. Kernels/ Spike	Wt. Kernel	Yield/Plant	DF
.60	0.54	1.62	0.90	22
.47	0.40	0.55	0.39	22
.27	0.61	0.08	0.87	21
.28	1.02	0.39	0.72	21
.70	0.90	0.24	0.40	22
.06	0.56	0.74	1.04	20
.83	0.81	1.04	0.16	17

Table 5. The values of the parameters particular to individual triparental

Trip. Grs.	Parameters	Earliness	Plant Height	No. Tillers/ Plant	No. Kernel Spike
1	$(d)_i$	$0.42 \pm 0.09^{**}$	0.25 ± 0.87	-1.14 ± 0.89	$2.41 \pm$
	$(d)_j$	$1.12 \pm 0.08^{**}$	$3.64 \pm 0.76^{**}$	-0.33 ± 0.78	$-0.16 \pm$
	$(h)_i$	-0.01 ± 0.08	$3.64 \pm 0.83^{**}$	$-2.01 \pm 0.85^{*}$	$-0.03 \pm$
	$(h)_j$	-0.08 ± 0.10	$3.97 \pm 0.96^{**}$	-0.65 ± 0.76	$-3.04 \pm$
	∂_{ij}	0.17 ± 0.16	$-7.18 \pm 1.56^{**}$	1.78 ± 1.59	$-1.28 \pm$
	$p\Delta_{R_i}$	$-1.07 \pm 0.10^{**}$	$-2.86 \pm 0.97^{**}$	$3.08 \pm 0.99^{**}$	$0.85 \pm$
	$p\Delta_{R_j}$	$-0.42 \pm 0.10^{**}$	1.03 ± 0.95	$2.73 \pm 0.97^{**}$	$1.32 \pm$
	$p\Delta_{D_i}$	$-0.44 \pm 0.09^{**}$	$-3.21 \pm 0.94^{**}$	1.10 ± 0.96	$1.33 \pm$
	$p\Delta_{D_j}$	$0.57 \pm 0.08^{**}$	$2.65 \pm 0.82^{**}$	$3.42 \pm 0.83^{**}$	$1.03 \pm$
	Δ_i	$-0.80 \pm 0.04^{**}$	$-1.97 \pm 0.41^{**}$	$6.03 \pm 0.42^{**}$	$1.80 \pm$

vidual triparental groups.

ers/	No. Kernels/ Spike	Wt. Kernel	Yield/Plant
0.89	2.41 ± 0.64**	0.52 ± 1.84	0.88 ± 1.14
0.78	-0.16 ± 0.56	-2.00 ± 1.61	-2.58 ± 0.99**
0.85*	-0.03 ± 0.61	-1.99 ± 1.77	-3.15 ± 1.09**
0.76	-3.04 ± 0.55**	0.39 ± 1.57	-1.28 ± 0.97
1.59	-1.28 ± 1.15	3.34 ± 3.31	3.28 ± 2.04
0.99**	0.85 ± 0.72	1.28 ± 2.06	1.45 ± 1.27
0.97**	1.32 ± 0.70	1.12 ± 2.05	3.51 ± 1.25**
0.96	1.33 ± 0.69	1.26 ± 2.18	2.69 ± 1.23*
0.83**	1.03 ± 0.60	-0.11 ± 2.07	1.56 ± 1.07
0.42**	1.80 ± 0.30**	1.45 ± 0.74	4.21 ± 0.53**

	Δ_j	$0.16 \pm 0.04^{**}$	$3.32 \pm 0.39^{**}$	$4.97 \pm 0.36^{**}$	$1.87 \pm 0.$
	Δ_{ij}	$0.69 \pm 0.03^{**}$	$4.74 \pm 0.25^{**}$	$0.92 \pm 0.26^{**}$	$-2.56 \pm 0.$
2.1	$(d)_i$	$0.42 \pm 0.09^{**}$	0.25 ± 3.08	-1.14 ± 0.89	$2.41 \pm 0.$
	$(d)_{k_i}$	$-8.78 \pm 0.09^{**}$	$-20.14 \pm 2.25^{**}$	$-6.50 \pm 0.65^{**}$	$-10.11 \pm 0.$
	$(h)_i$	-0.01 ± 0.08	3.64 ± 2.94	$-2.01 \pm 0.85^{*}$	-0.03 ± 0
	$(h)_{k_i}$	$-1.71 \pm 0.08^{**}$	$4.66 \pm 2.16^{*}$	$5.72 \pm 0.63^{**}$	0.59 ± 0
	$(h)_{ik_i}$	$-3.18 \pm 0.08^{**}$	3.97 ± 2.18	$2.63 \pm 0.63^{**}$	2.96 ± 0
	∂_{ik_i}	$-1.46 \pm 0.15^{**}$	-4.35 ± 3.83	-1.09 ± 1.11	2.39 ± 1
	Δ_{k_i}	$1.42 \pm 0.04^{**}$	$2.29 \pm 1.03^{*}$	$1.55 \pm 0.30^{**}$	0.68 ± 0
	Δ_{u_i}	$1.14 \pm 0.04^{**}$	$2.33 \pm 1.02^{*}$	$2.44 \pm 0.30^{**}$	0.56 ± 0
2.2	$(d)_j$	$1.12 \pm 0.08^{**}$	3.64 ± 2.69	-0.33 ± 0.78	-0.16 ± 0
	$(d)_{k_j}$	$-9.10 \pm 0.11^{**}$	$-21.49 \pm 2.04^{**}$	$-5.95 \pm 0.81^{**}$	-4.81 ± 0
	$(h)_j$	-0.08 ± 0.10	3.97 ± 2.62	-0.65 ± 0.76	-3.04 ± 0
	$(h)_{k_j}$	$-3.41 \pm 0.11^{**}$	$-7.32 \pm 2.00^{**}$	-1.00 ± 0.79	$-2.96 \pm$

.36**	1.87 ± 0.26**	0.68 ± 0.67	4.41 ± 0.47**
.26**	-2.56 ± 0.19**	-1.86 ± 0.58**	-1.50 ± 0.33**
.89	2.41 ± 0.64**	0.52 ± 1.84	0.88 ± 1.14
.65**	-10.11 ± 0.84**	7.13 ± 2.11**	-4.00 ± 1.17**
.85*	-0.03 ± 0.61	-1.99 ± 1.77	-3.15 ± 1.09**
0.63**	0.59 ± 0.81	6.08 ± 2.04**	6.50 ± 1.18**
0.63**	2.96 ± 0.81**	5.61 ± 2.03**	6.89 ± 1.19**
1.11	2.39 ± 1.43	1.51 ± 3.58	3.54 ± 2.00
0.30**	0.68 ± 0.39	-3.00 ± 0.84**	-0.26 ± 0.54
0.30**	0.56 ± 0.38	-11.02 ± 0.83**	-0.30 ± 0.53
0.78	-0.16 ± 0.56	-2.00 ± 1.61	-2.58 ± 0.99**
0.81**	-4.81 ± 0.57**	7.70 ± 1.45**	0.45 ± 0.89
0.76	-3.04 ± 0.55**	0.39 ± 1.57	-1.28 ± 0.97
0.79	-2.96 ± 0.56**	7.30 ± 1.43**	3.37 ± 0.87**

$(h)_{jk_j}$	$-1.67 \pm 0.12^{**}$	-0.74 ± 2.26	$1.91 \pm 0.89^{*}$	0.24 ± 0.64
∂_{jk_j}	$1.81 \pm 0.20^{**}$	2.60 ± 3.74	$3.55 \pm 1.48^{*}$	$6.24 \pm 1.05^{**}$
Δ_{k_j}	$1.85 \pm 0.05^{**}$	$-2.79 \pm 0.96^{**}$	$1.71 \pm 0.38^{**}$	$-0.79 \pm 0.27^{**}$
Δ_{u_j}	$1.49 \pm 0.06^{**}$	$2.11 \pm 1.07^{*}$	$2.27 \pm 0.43^{**}$	-0.53 ± 0.30

19*	0.24 ± 0.64	5.65 ± 1.61**	4.62 ± 0.99**
68*	6.24 ± 1.05**	-2.05 ± 2.67	2.54 ± 1.64
38**	-0.79 ± 0.27**	-1.61 ± 0.63**	-0.56 ± 0.42
43**	-0.53 ± 0.30	-2.53 ± 0.67**	-0.46 ± 0.47

Table 6. Table of F values calculated jointly from parents and F_1 gen

Trip. Grs.	DF	Earliness	Plant Height	No. Tillers/ Plant	No. Spik
1	232	25.44**	29.23**	3.08**	29.
2.1	190	1254.07**	236.27**	1641.59**	125.
2.2	226	1025.06**	299.43**	60.19**	58.

Significance level at 5% = 2.21

Significance level at 1% = 3.02

ts and F_1 generations in the respective triparental groups.

rs/	No. Kernels/ Spike	Wt. Kernel	Yield/Plant
	29.19**	31.53**	15.44**
	125.23**	52.09**	22.59**
	58.20**	97.49**	16.60**

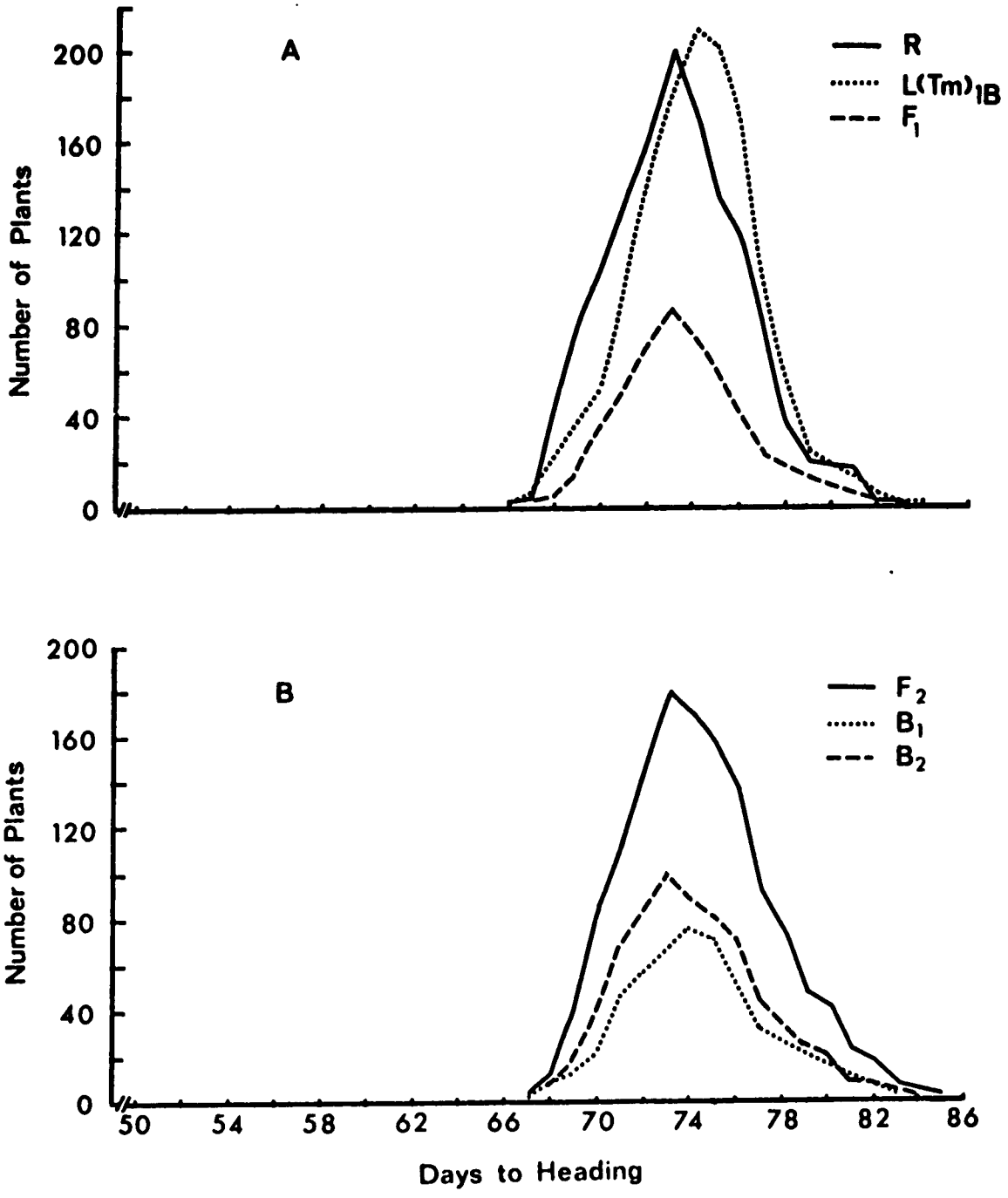

Fig.1. Frequency distribution of heading days in the cross R x $L(Tm)_{1B}$

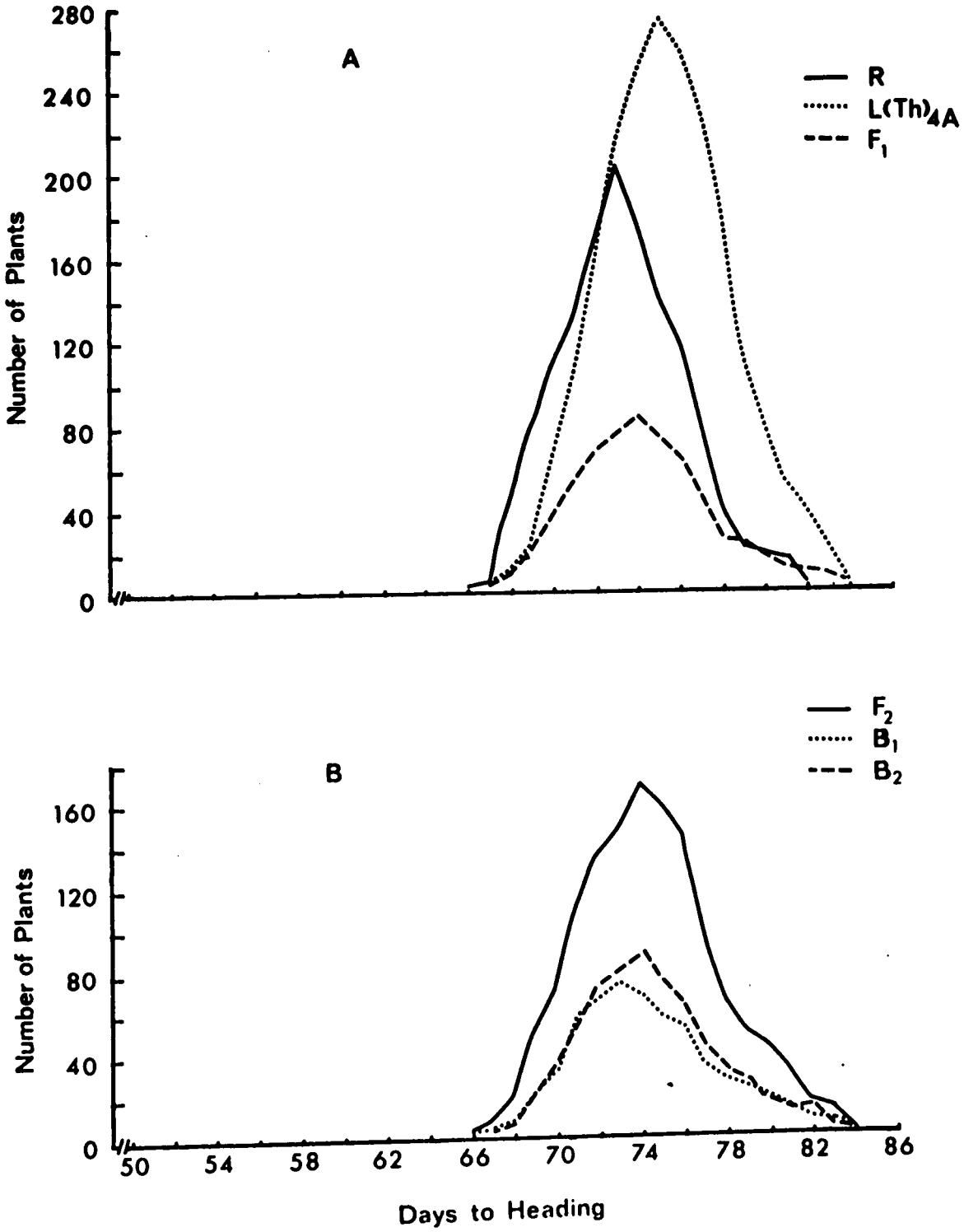

Fig.2. Frequency distribution of heading days in the cross R x $L(Th)_{4A}$

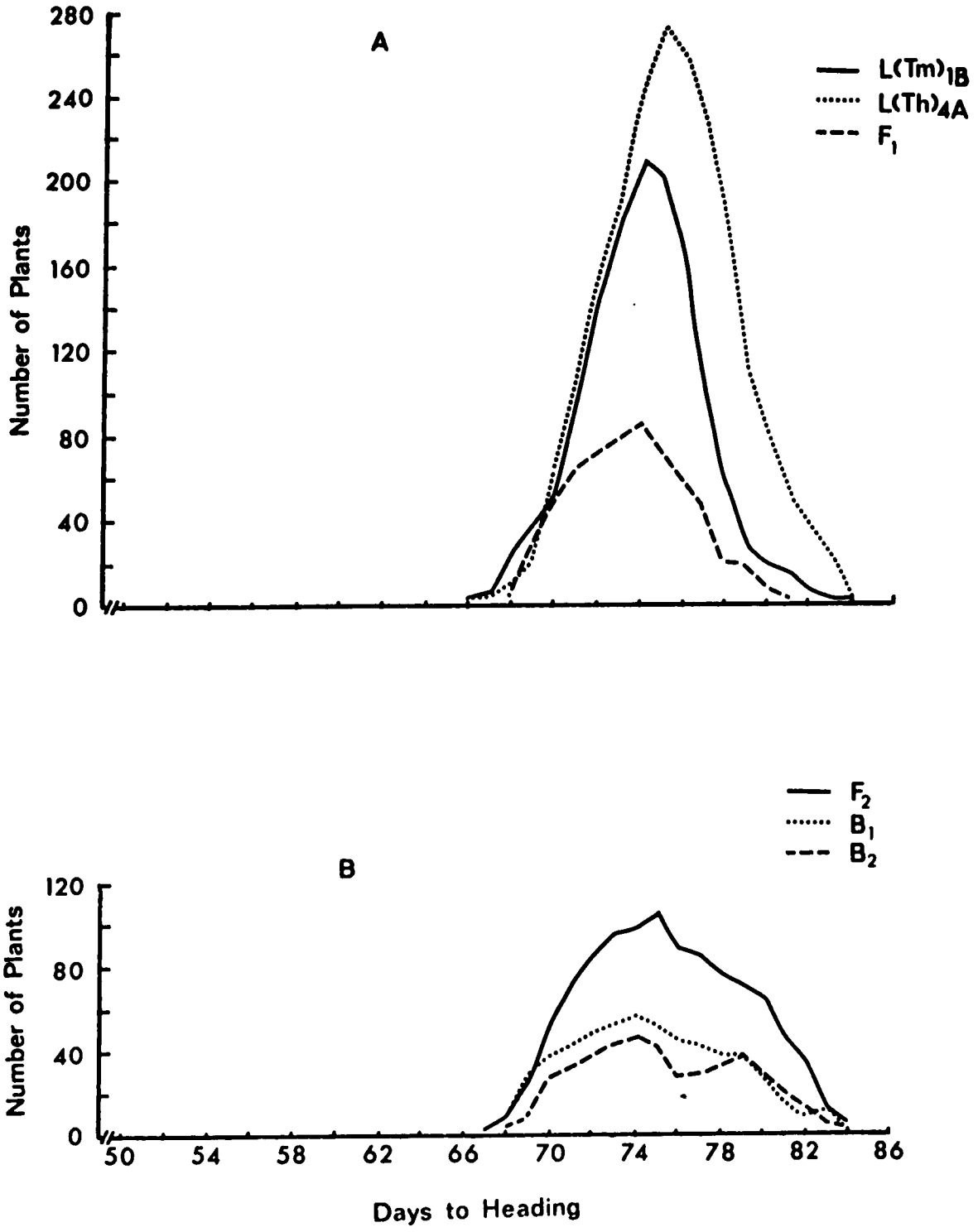

Fig.3. Frequency distribution of heading days in the cross $L(Th)_{1B} \times L(Th)_{4A}$

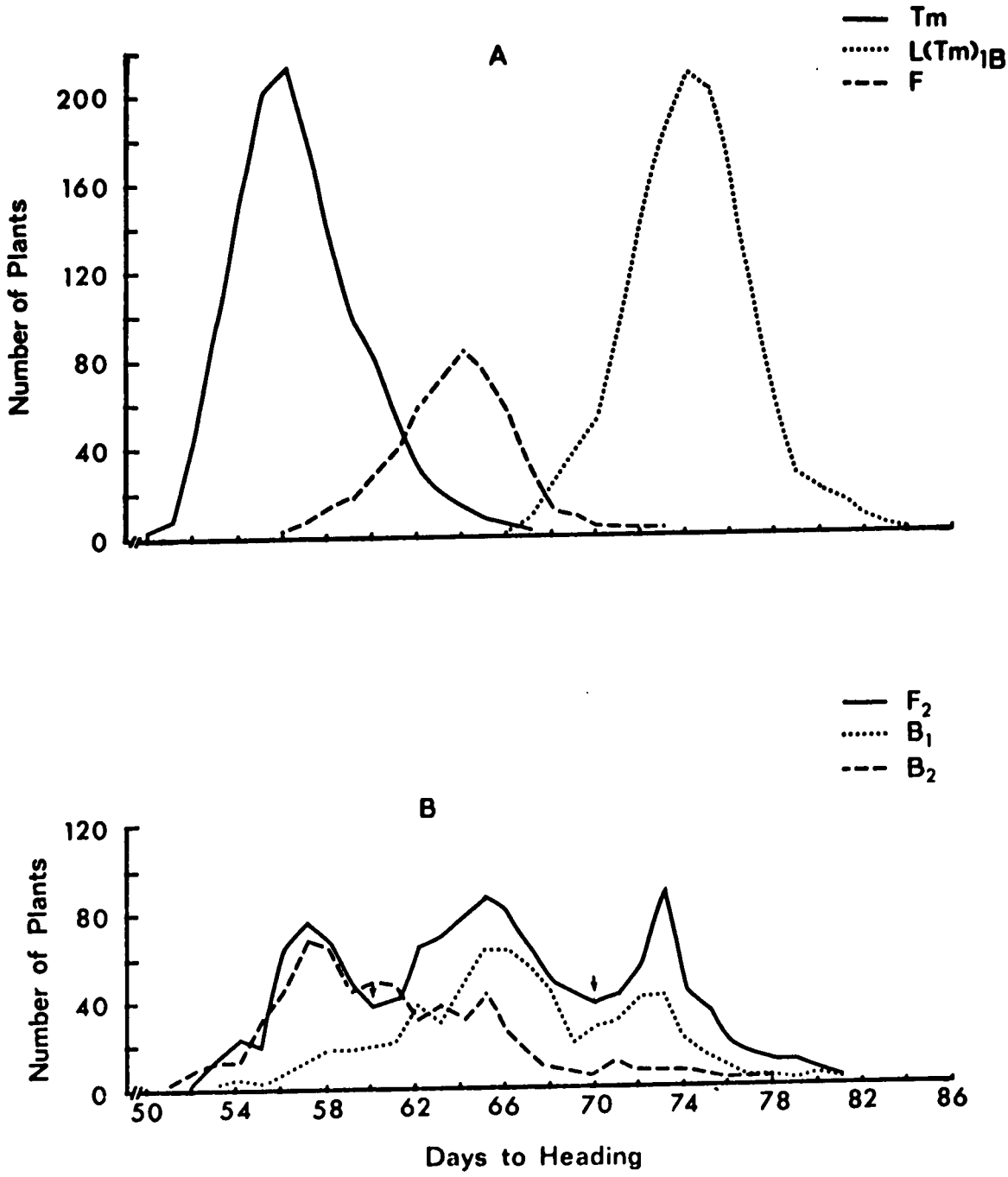

Fig.4. Frequency distribution of heading days in the cross Tm x $L(Tm)_{1B}$

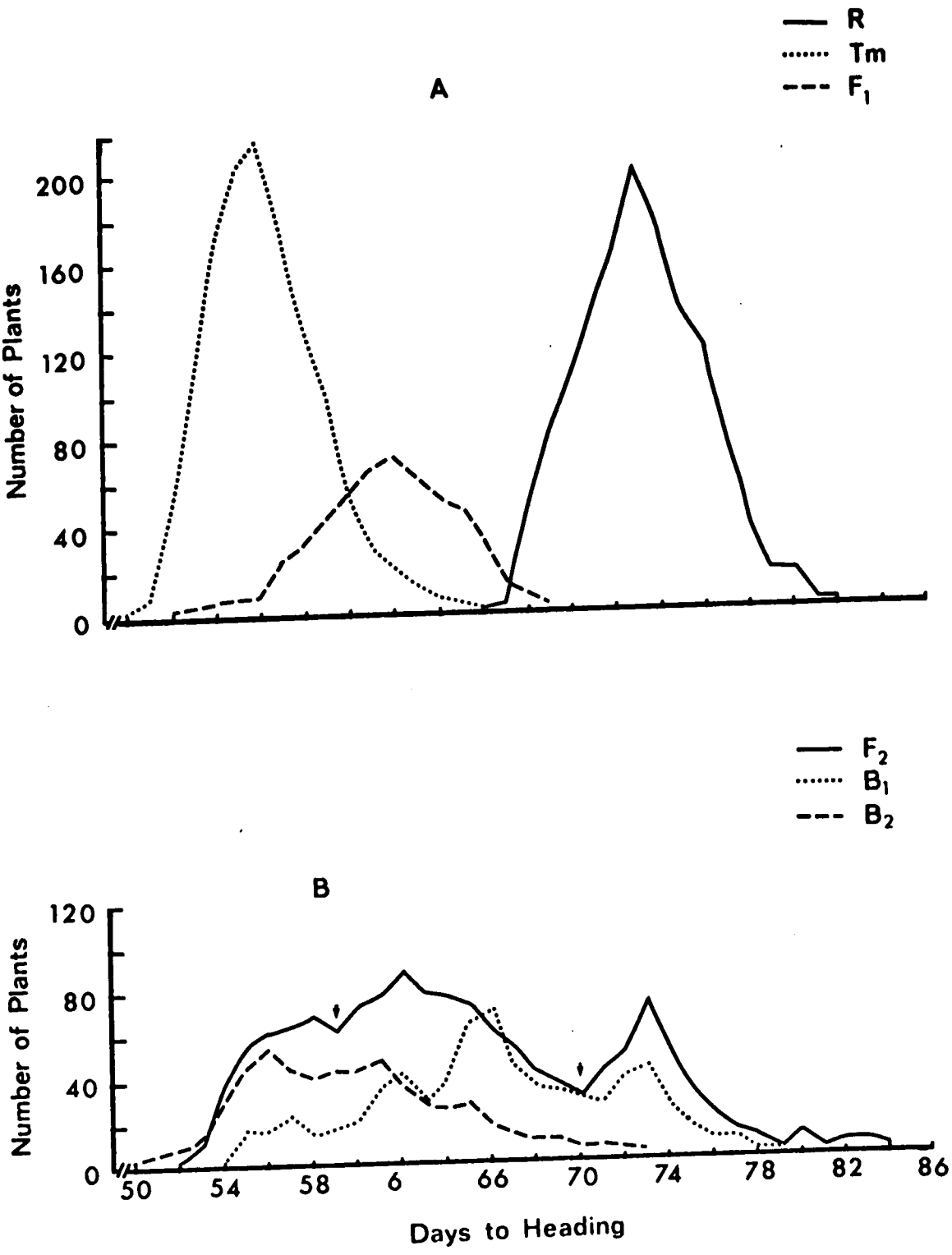

Fig.5. Frequency distribution of heading days in the cross R x Tm

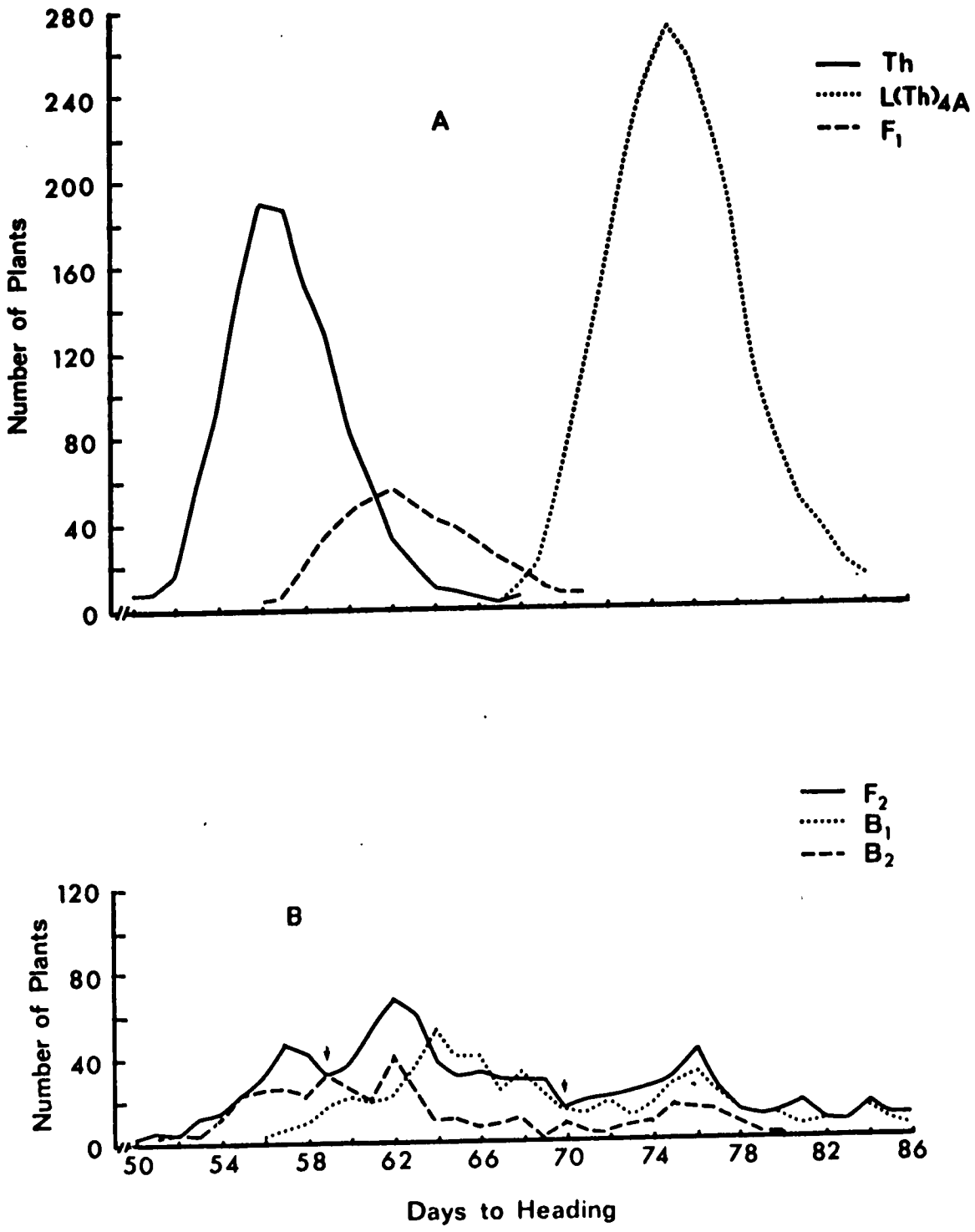

Fig.6. Frequency distribution of heading days in the cross Th x $L(Th)_{4A}$

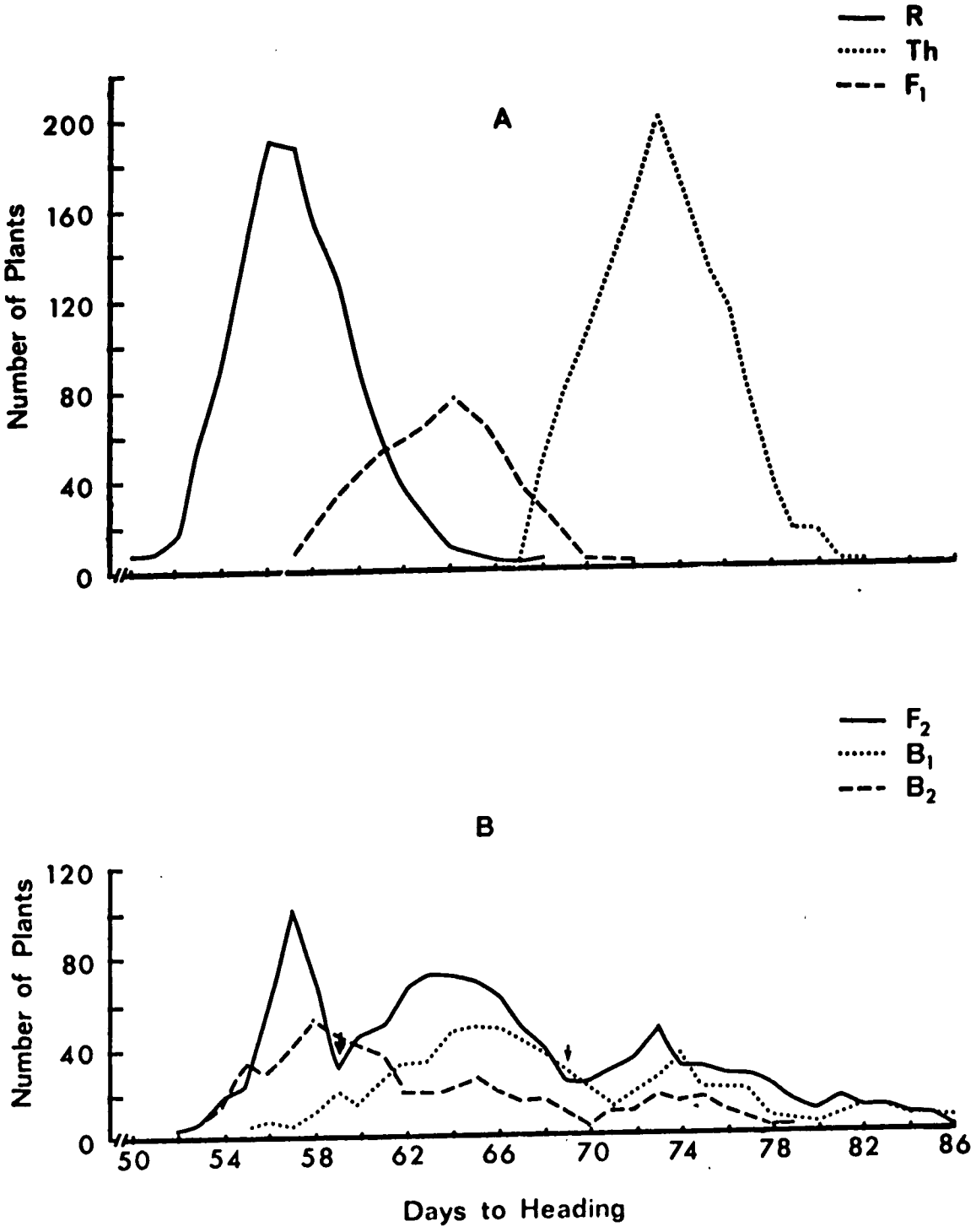

Fig.7. Frequency distribution of heading days in the cross R x Th

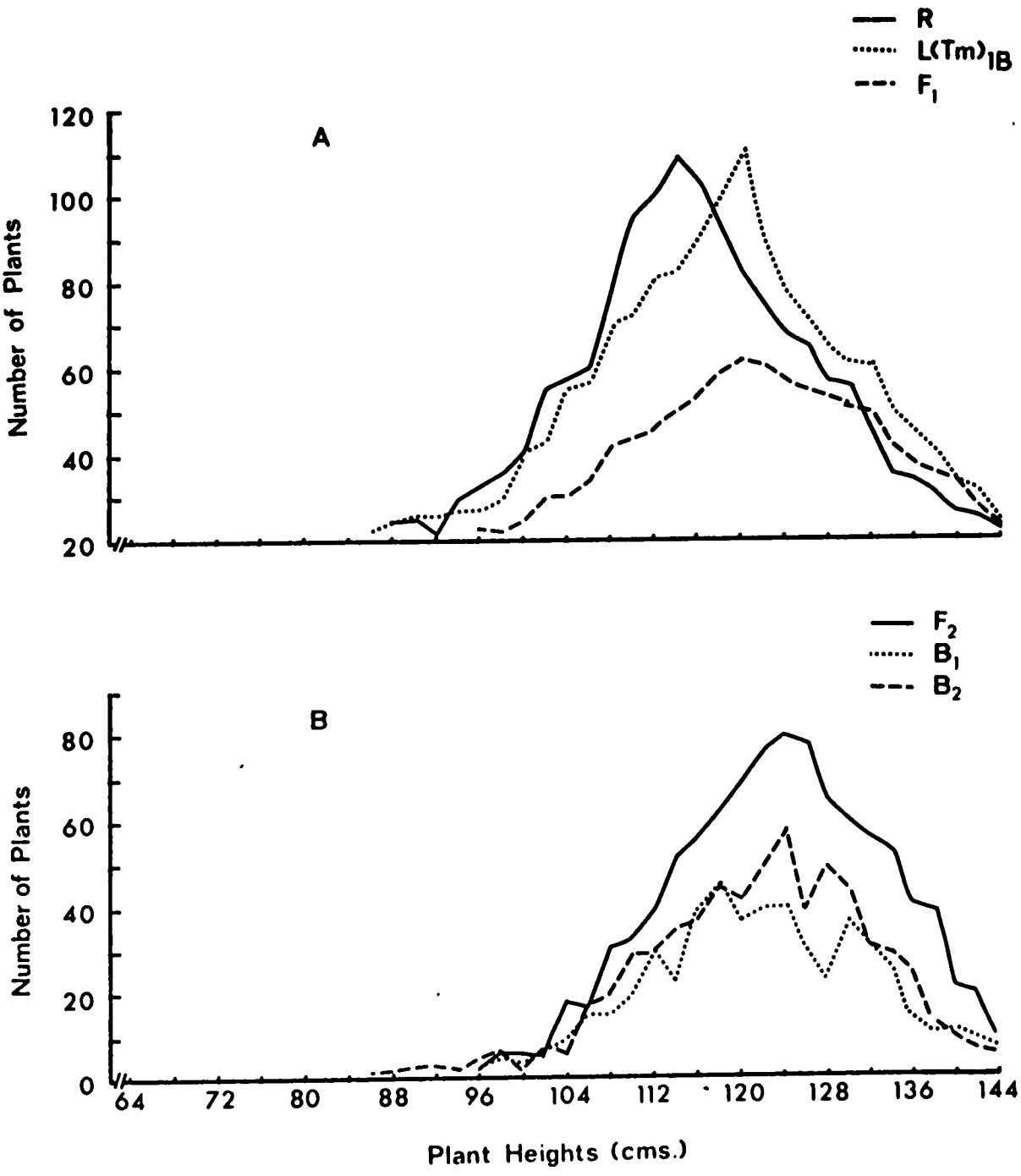

Fig.8. Frequency distribution of plant height (in cms.) in the cross R x $L(Tm)_{1B}$

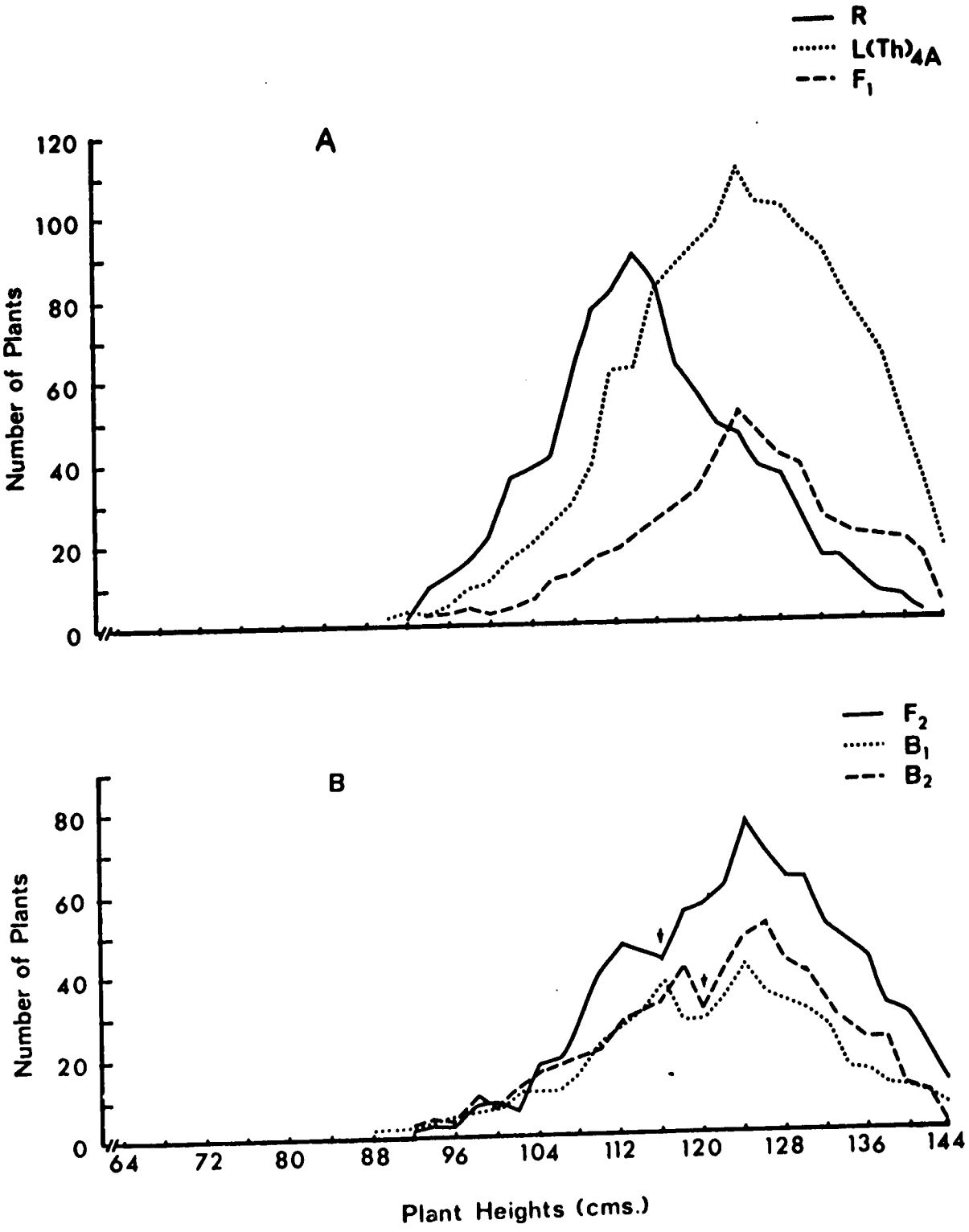

Fig.9. Frequency distribution of plant height (in cms.) in the cross R x $L(Th)_{4A}$

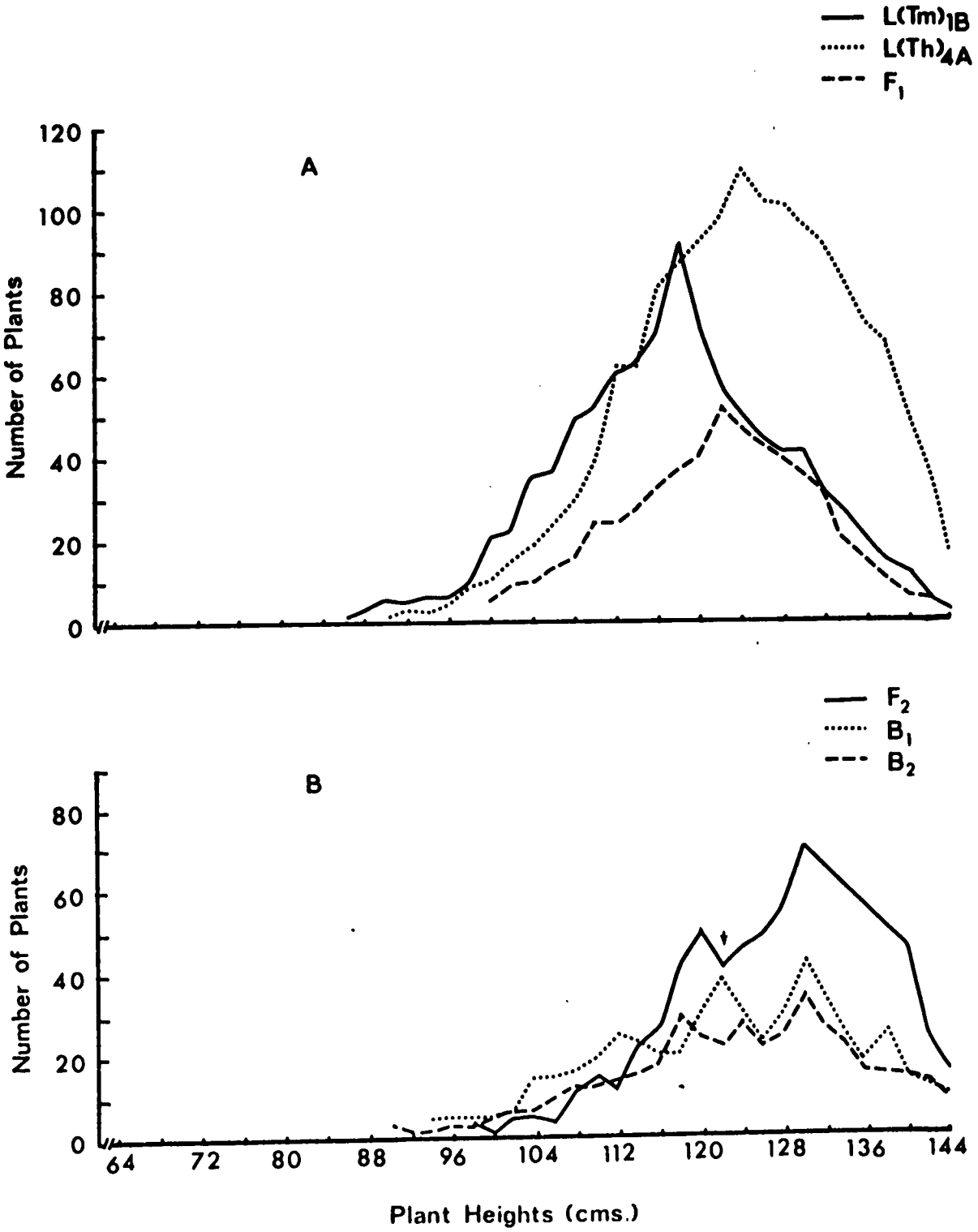

Fig.10. Frequency distribution of plant height (in cms.) in the cross $L(Tm)_{1B} \times L(Th)_{4A}$

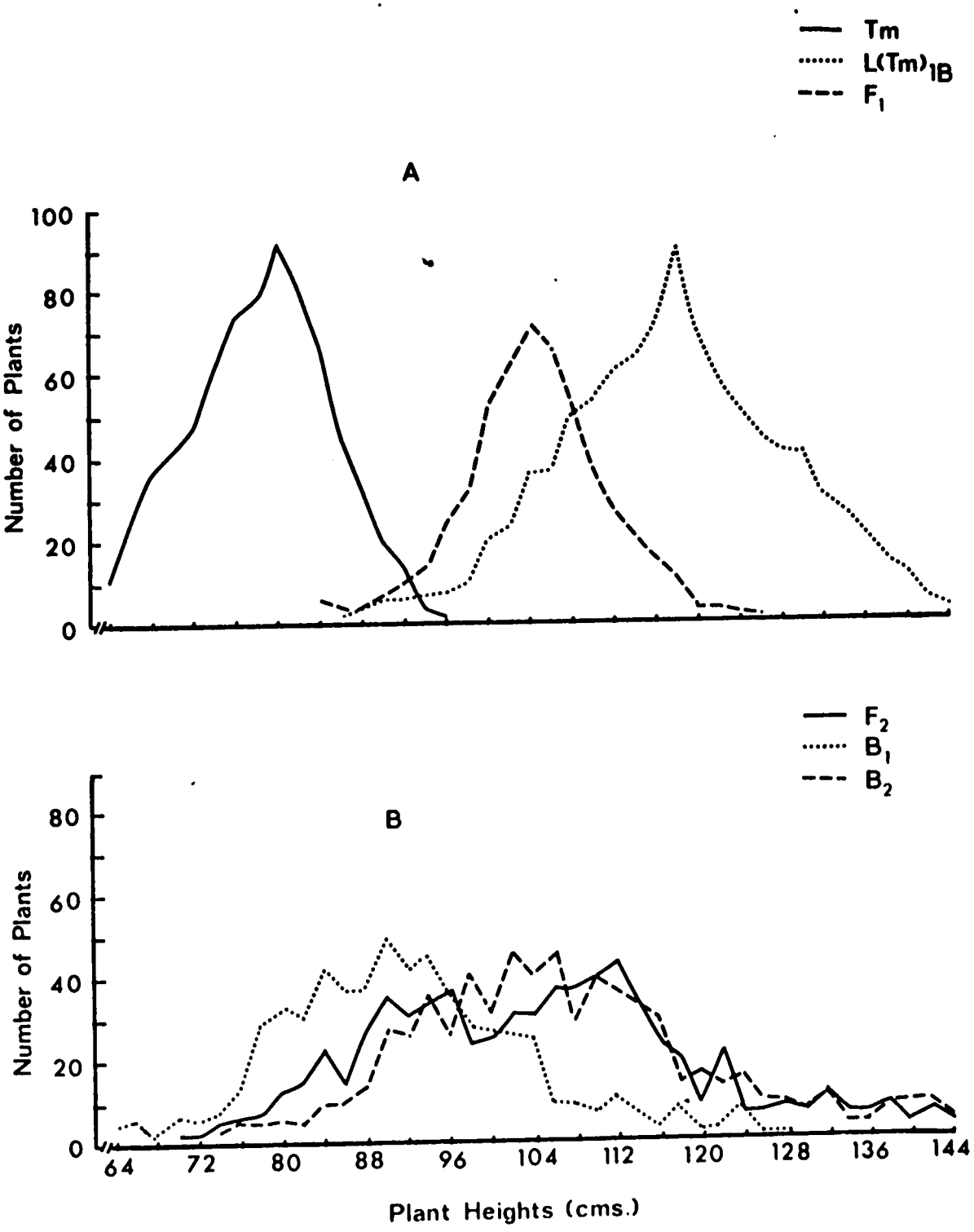

Fig.11. Frequency distribution of plant height (in cms.) in the cross Tm x $L(Tm)_{1B}$

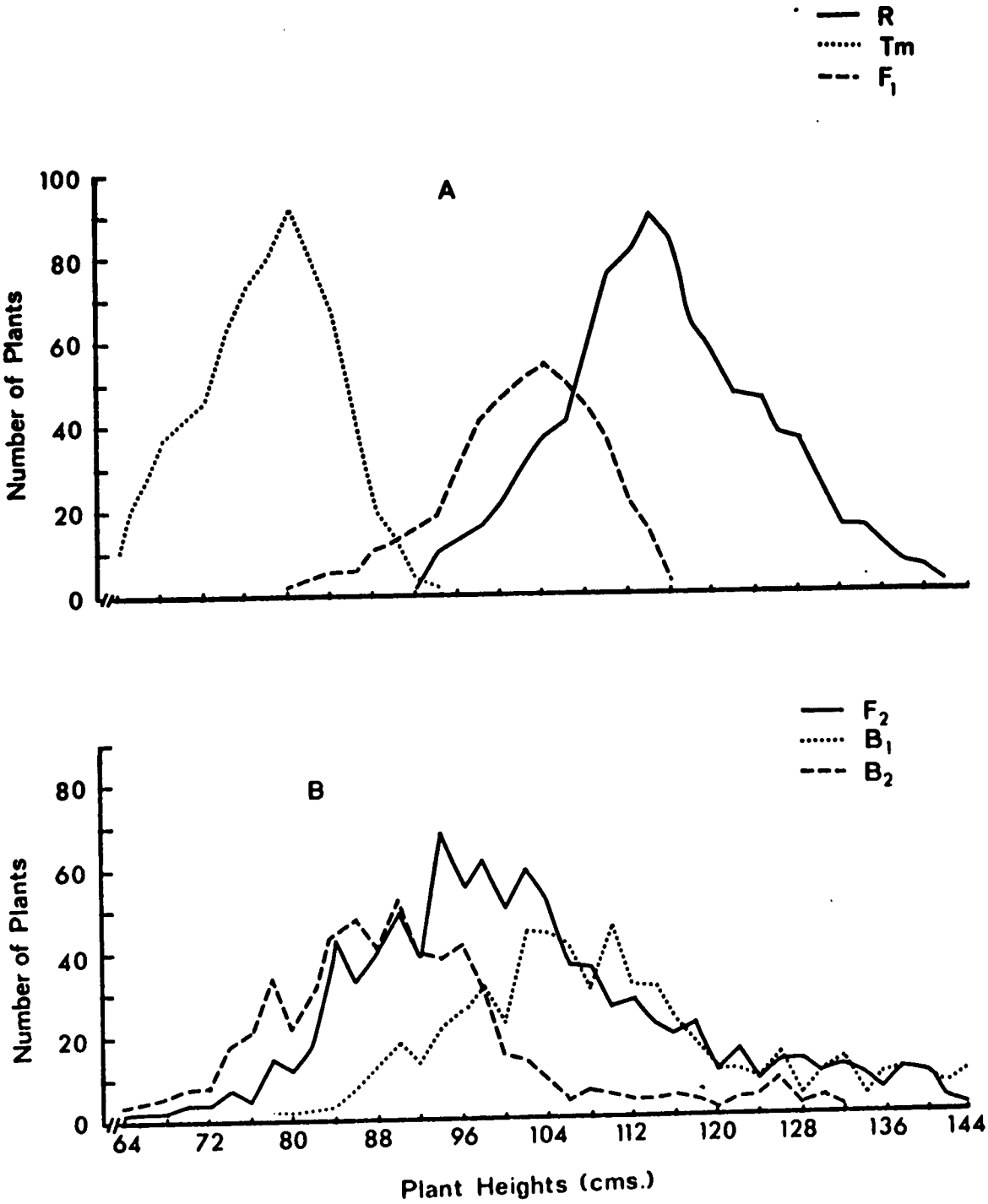

Fig.12. Frequency distribution of plant height (in cms.) in the cross R x Tm

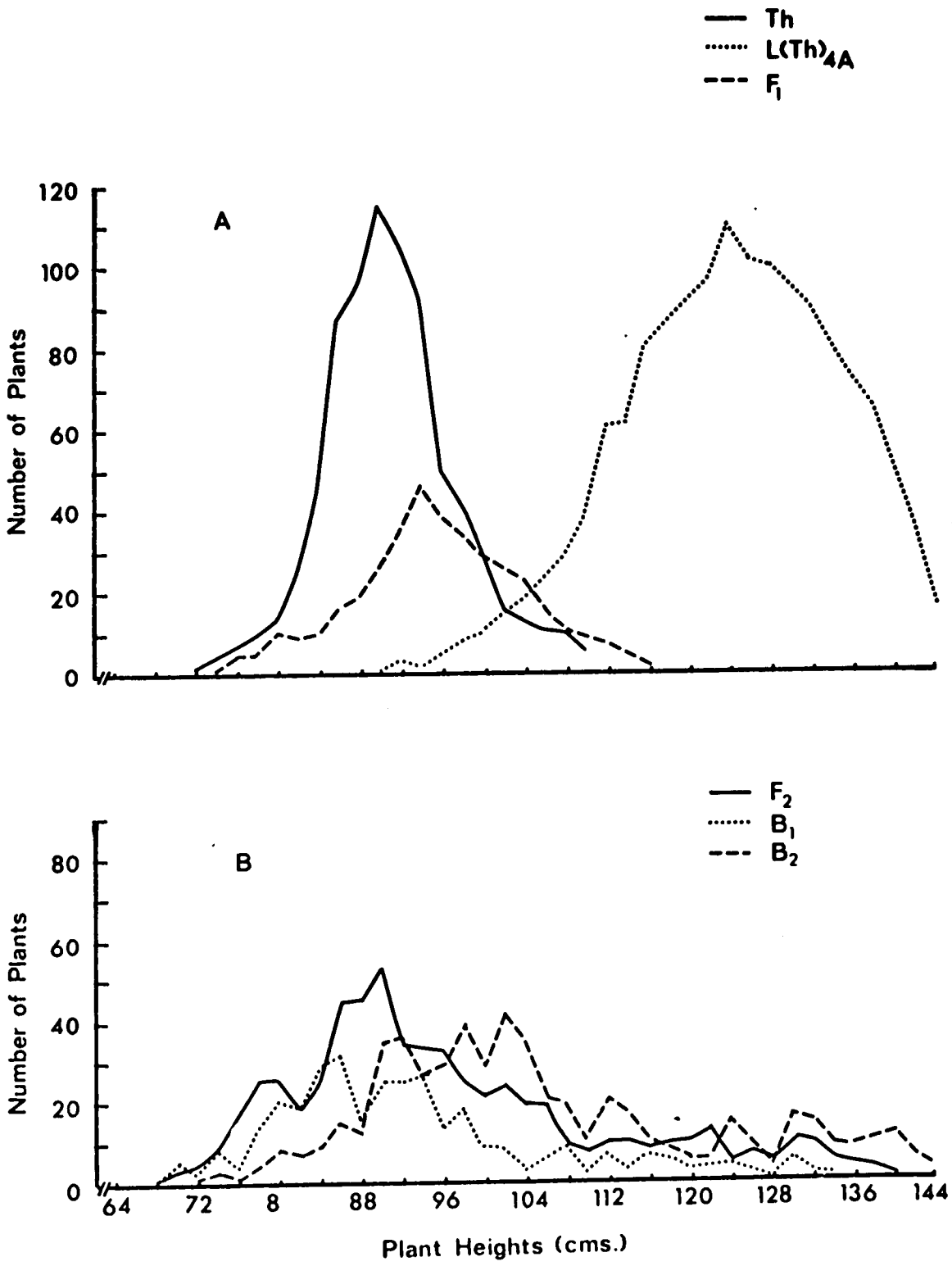

Fig.13. Frequency distribution of plant height (in cms.) in the cross Th x $L(Th)_{4A}$

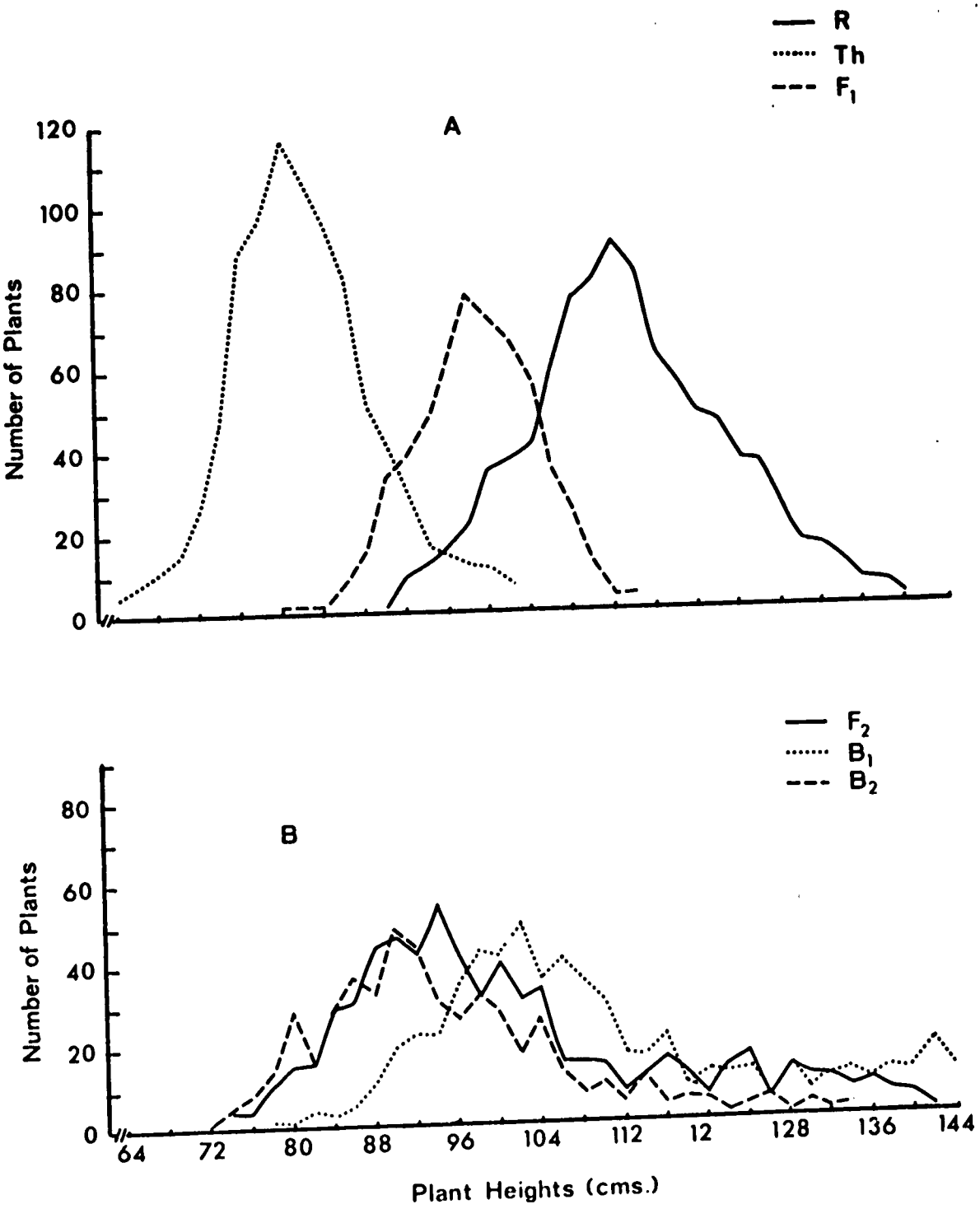

Fig.14. Frequency distribution of plant height (in cms.) in the cross R x Th

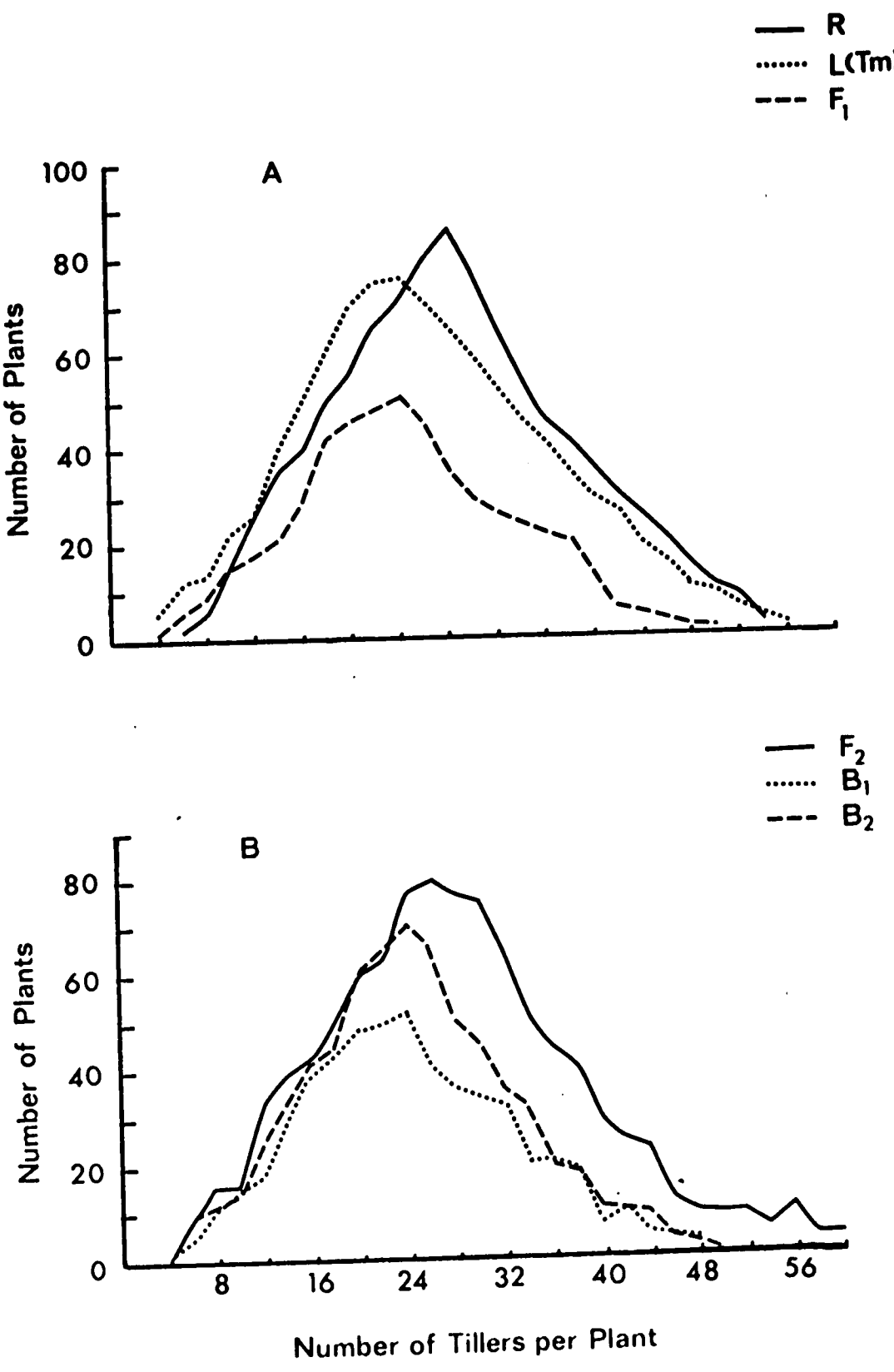

Fig.15. Frequency distribution of number of tillers in the cross R x $L(Tm)_{1B}$

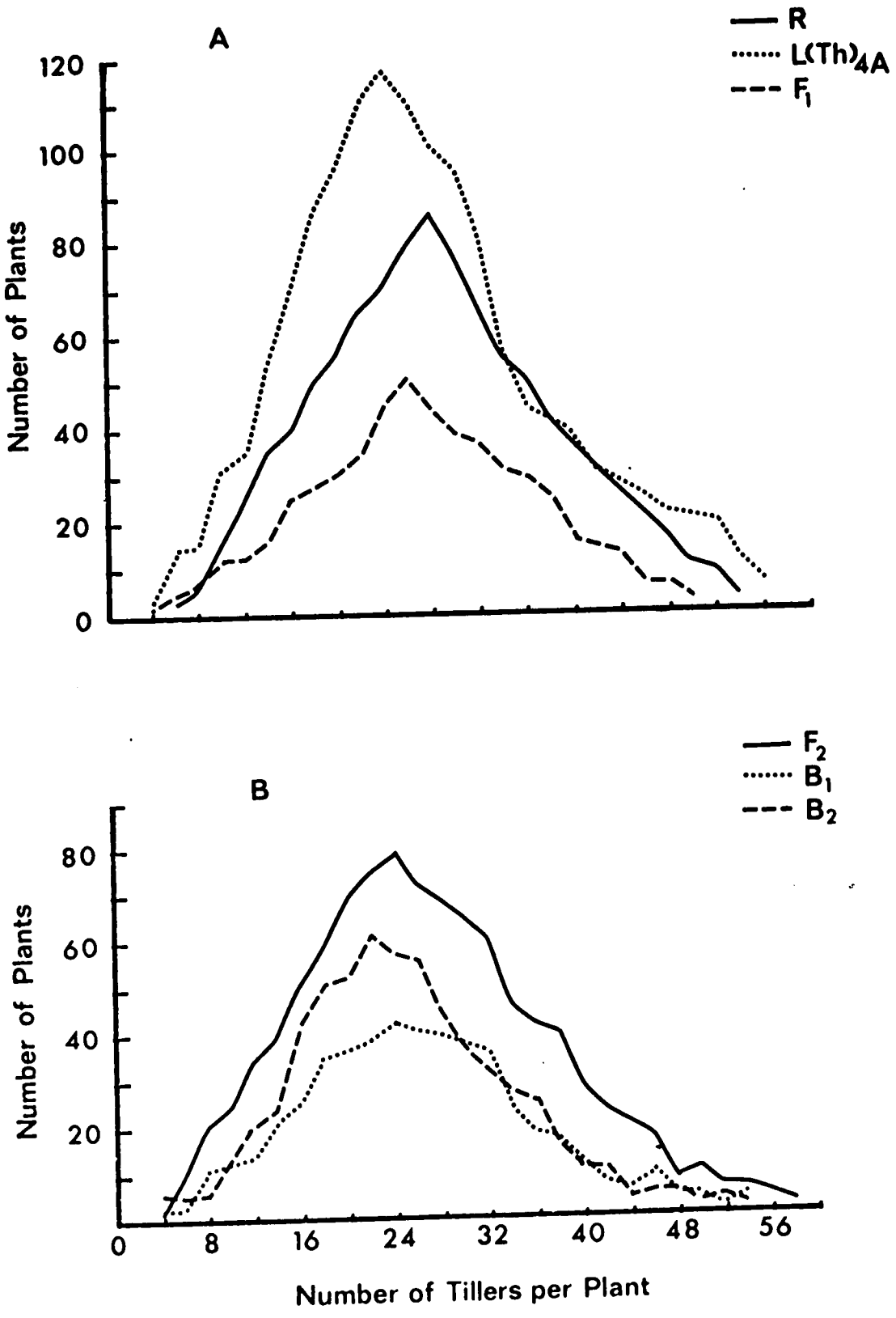

Fig.16. Frequency distribution of number of tillers in the cross R x $L(Th)_{4A}$

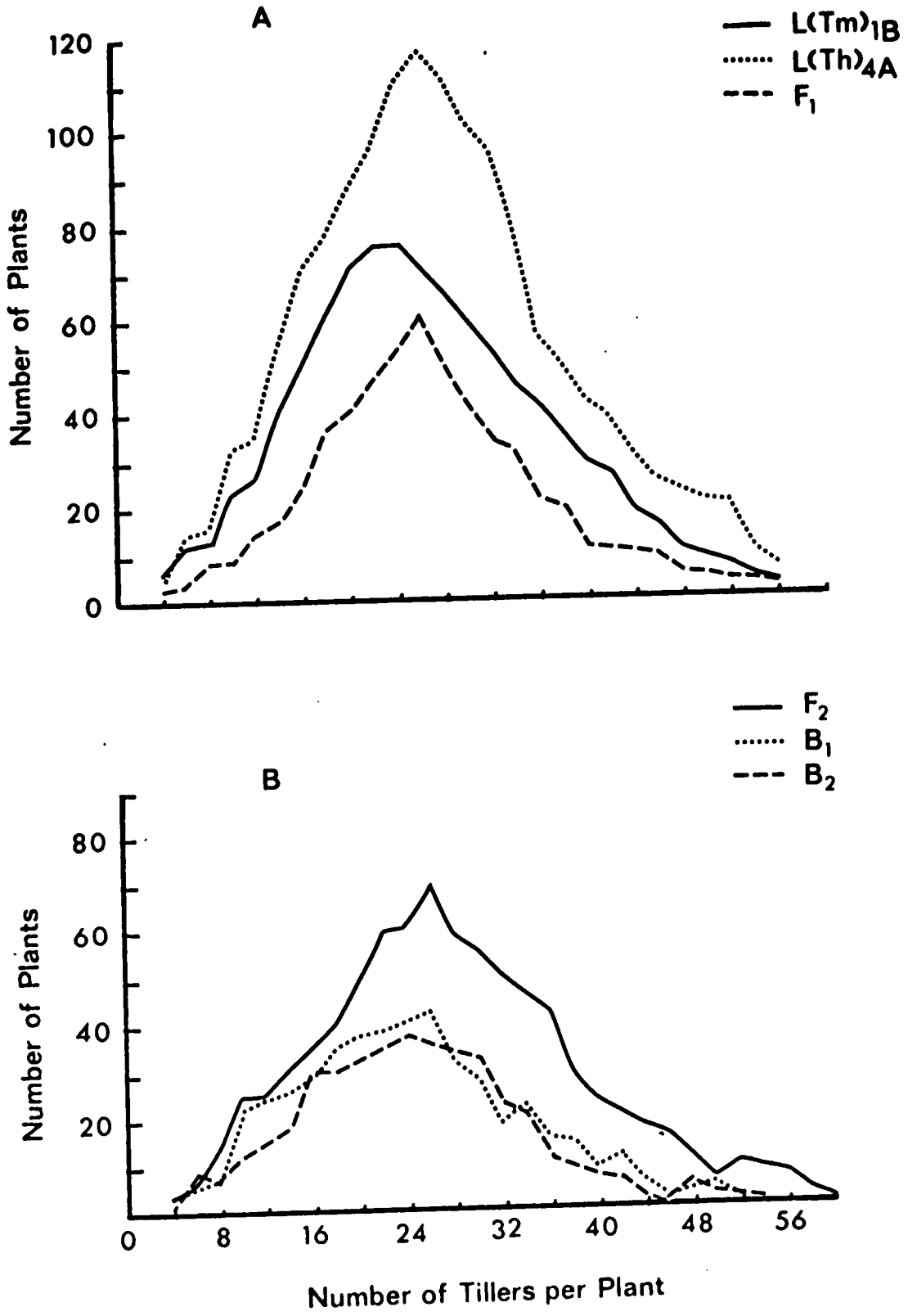

Fig.17. Frequency distribution of number of tillers in the cross $L(Tm)_{1B} \times L(Th)_{4A}$

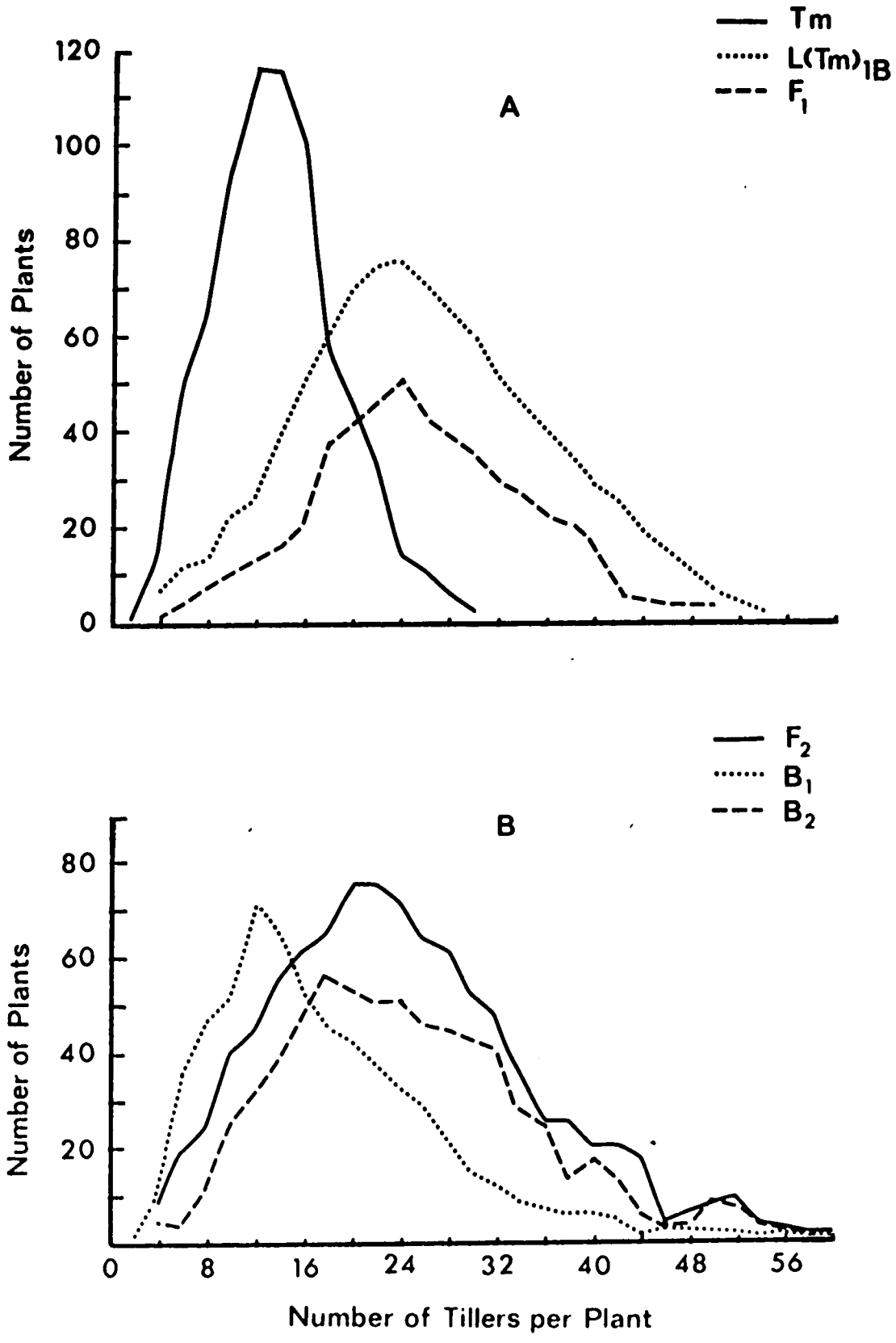

Fig.18. Frequency distribution of number of tillers in the cross Tm x $L(Tm)_{1B}$

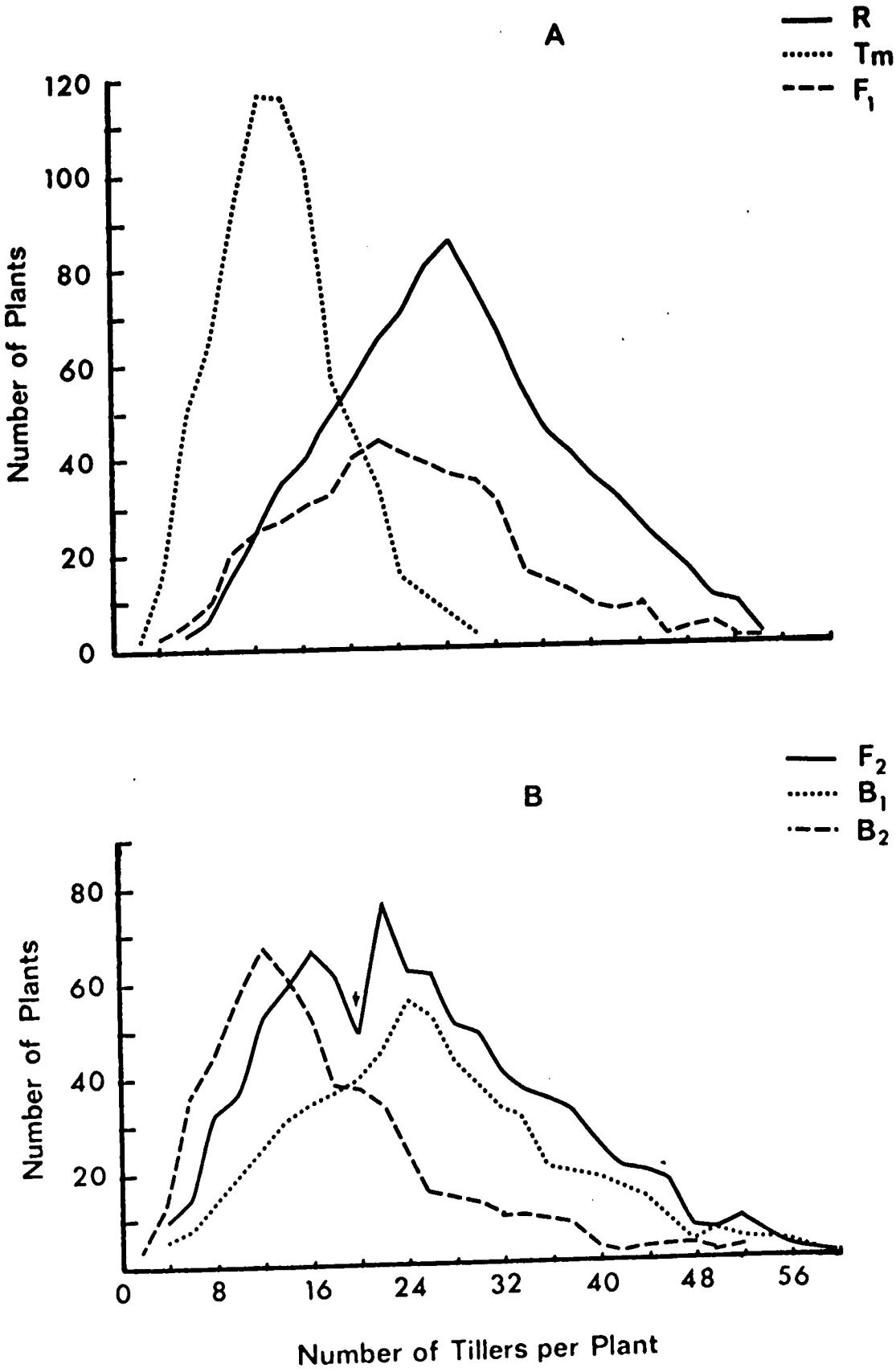

Fig.19. Frequency distribution of number of tillers in the cross R x Tm

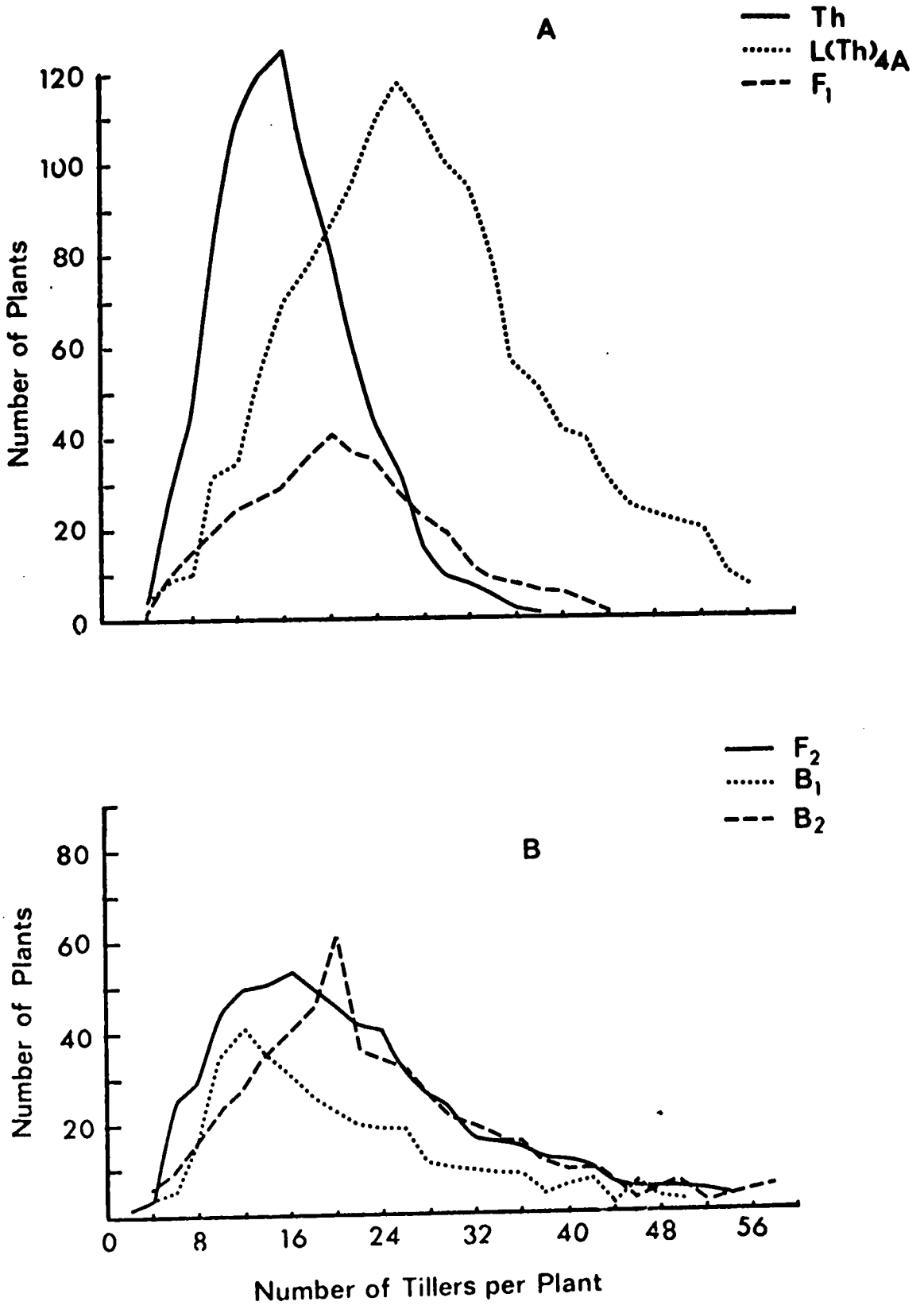

Fig.20. Frequency distribution of number of tillers in the cross Th x $L(Th)_{4A}$

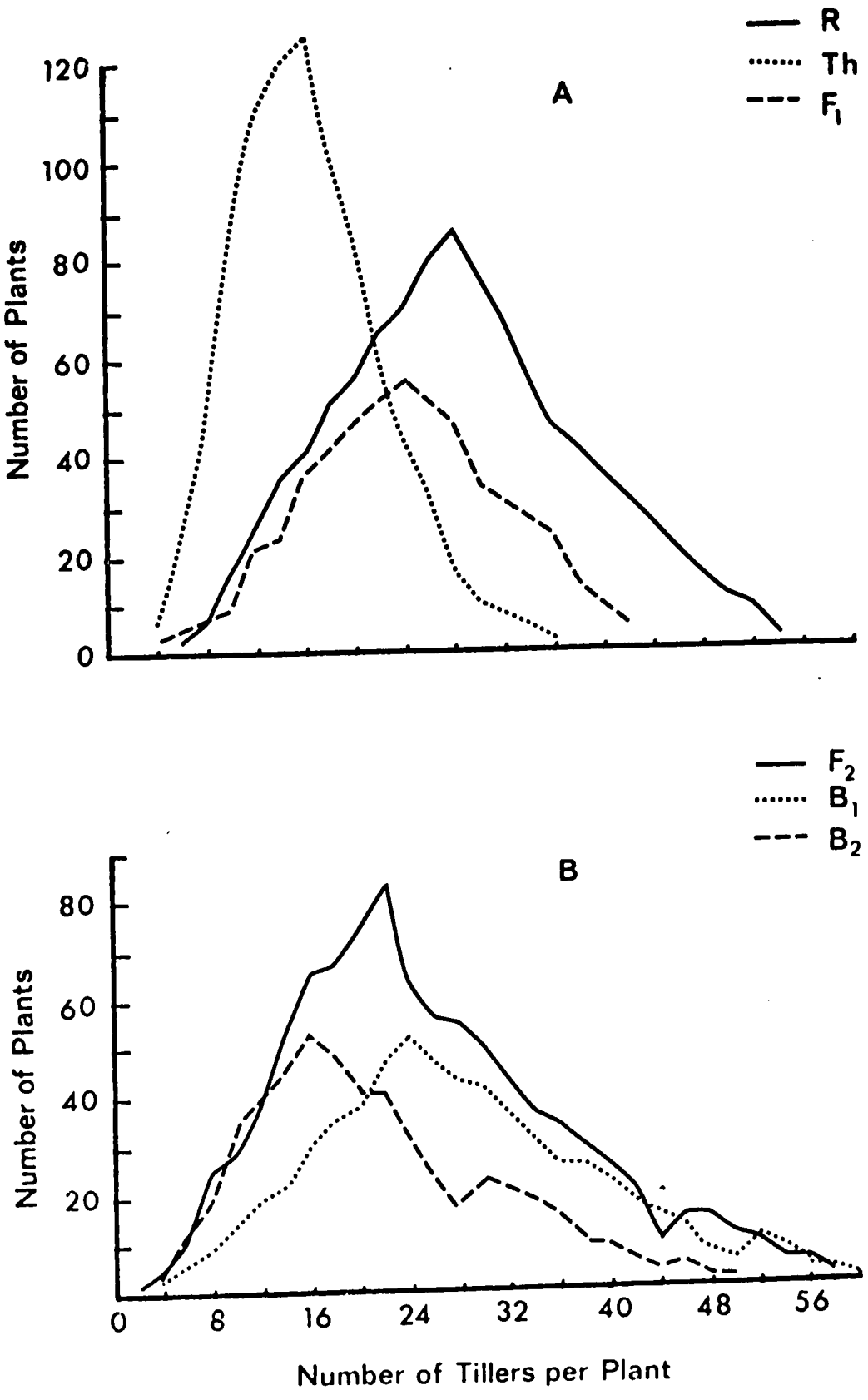

Fig.21. Frequency distribution of number of tillers in the cross R x Th

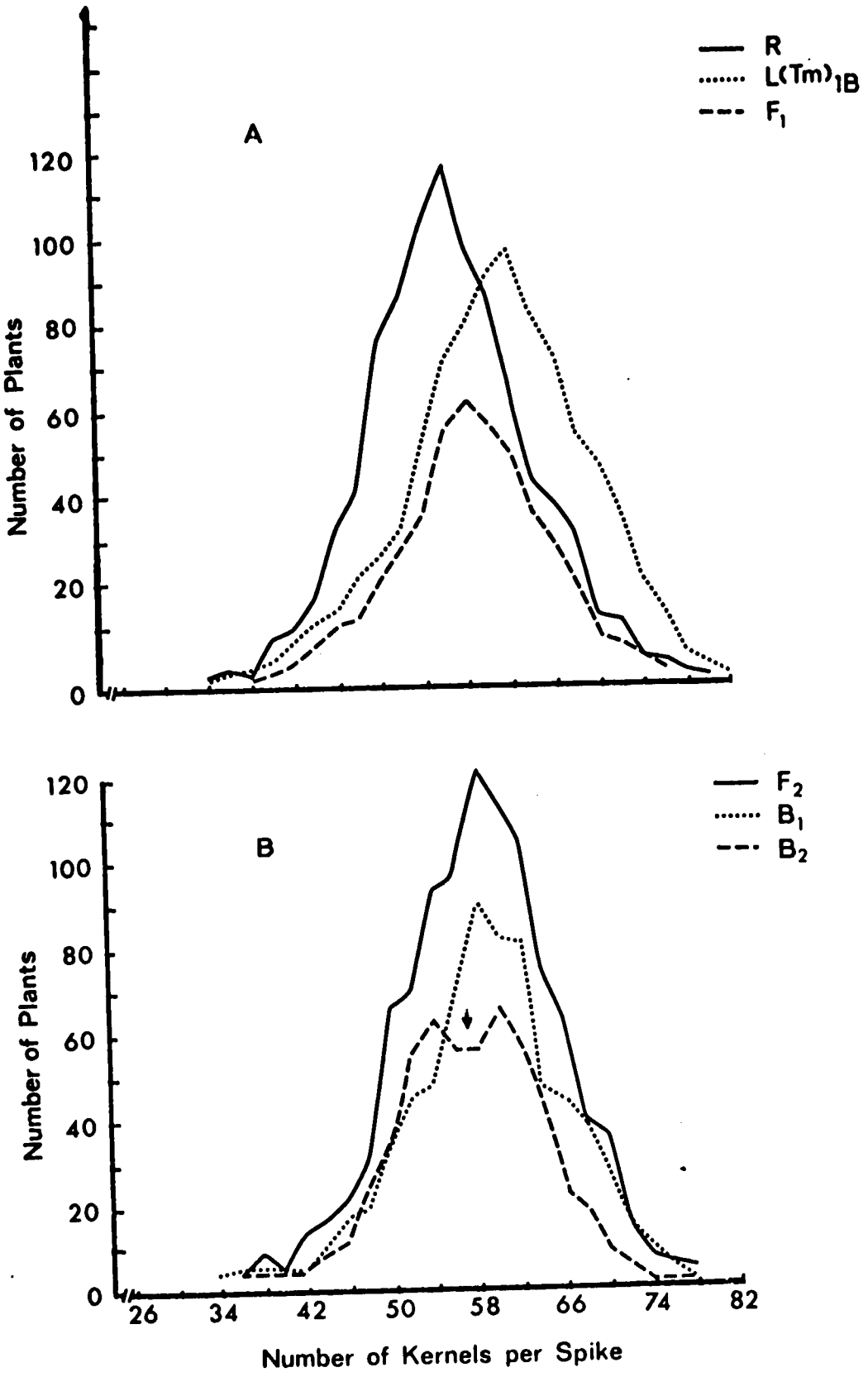

Fig.22. Frequency distribution of number of kernels per spike in the cross R x $L(Tm)_{1B}$

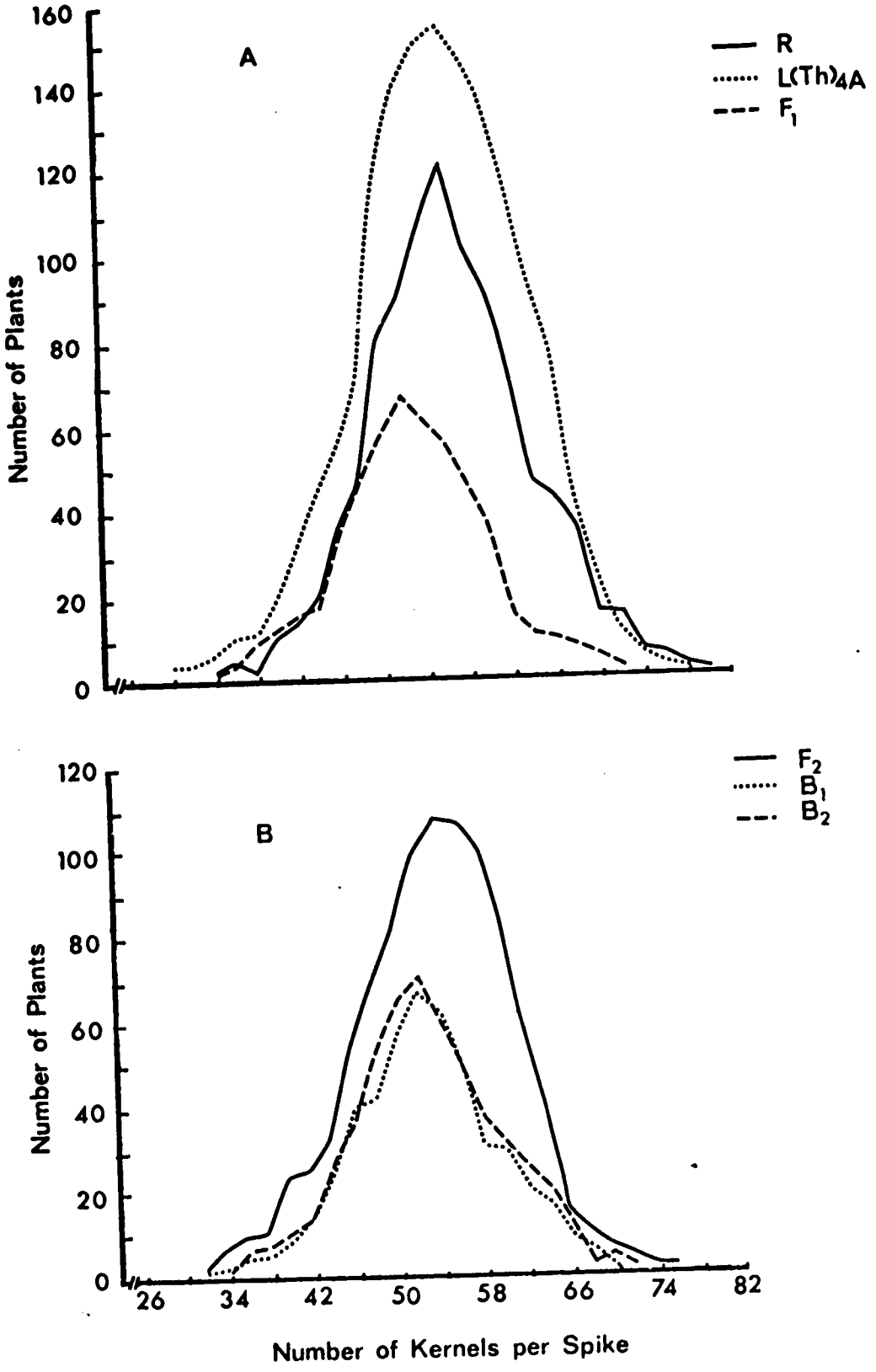

Fig.23. Frequency distribution of number of kernels per spike in the cross R x $L(Th)_{4A}$

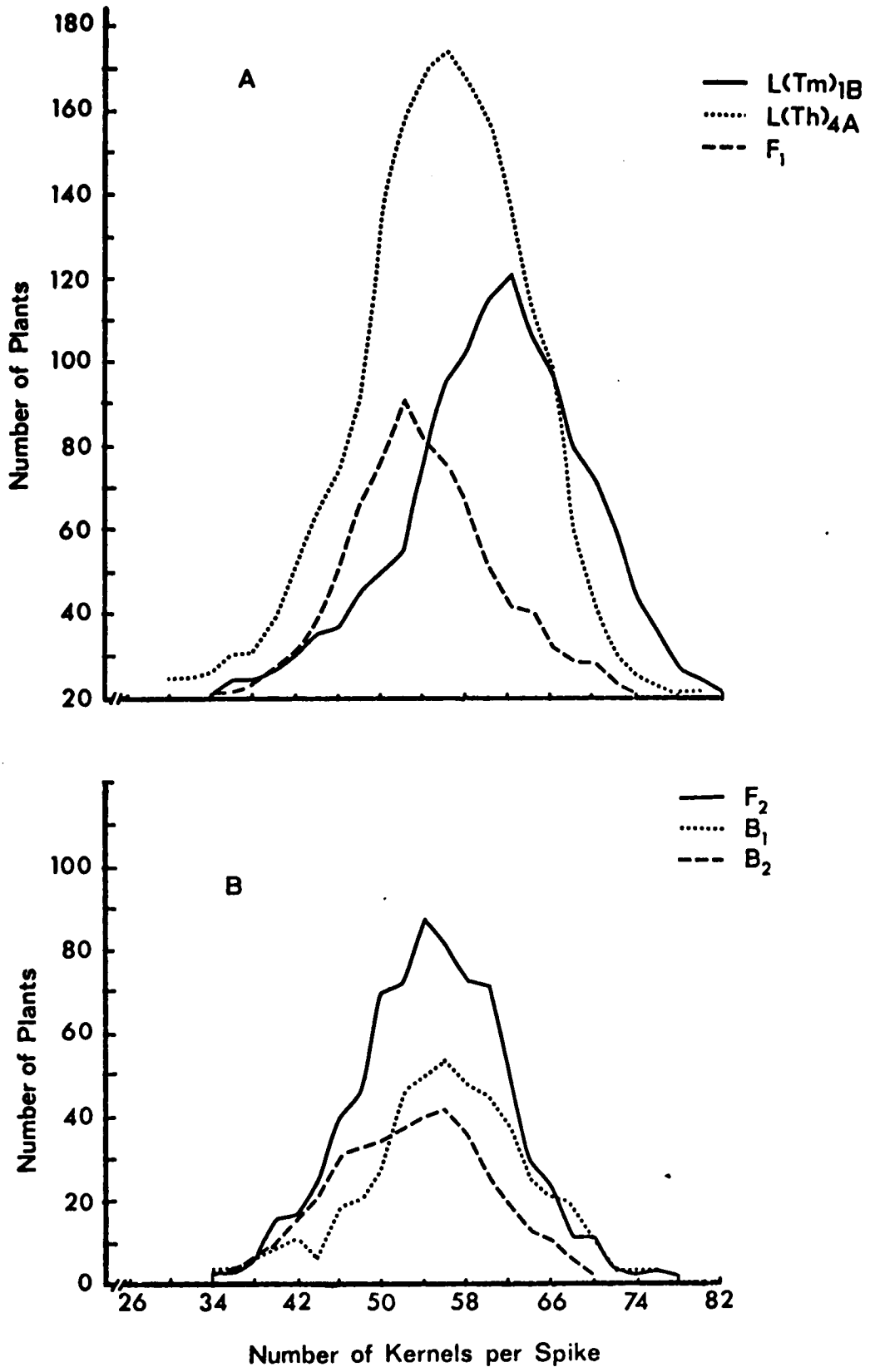

Fig.24. Frequency distribution of number of kernels per spike in the cross $L(Tm)_{1B} \times L(Th)_{4A}$

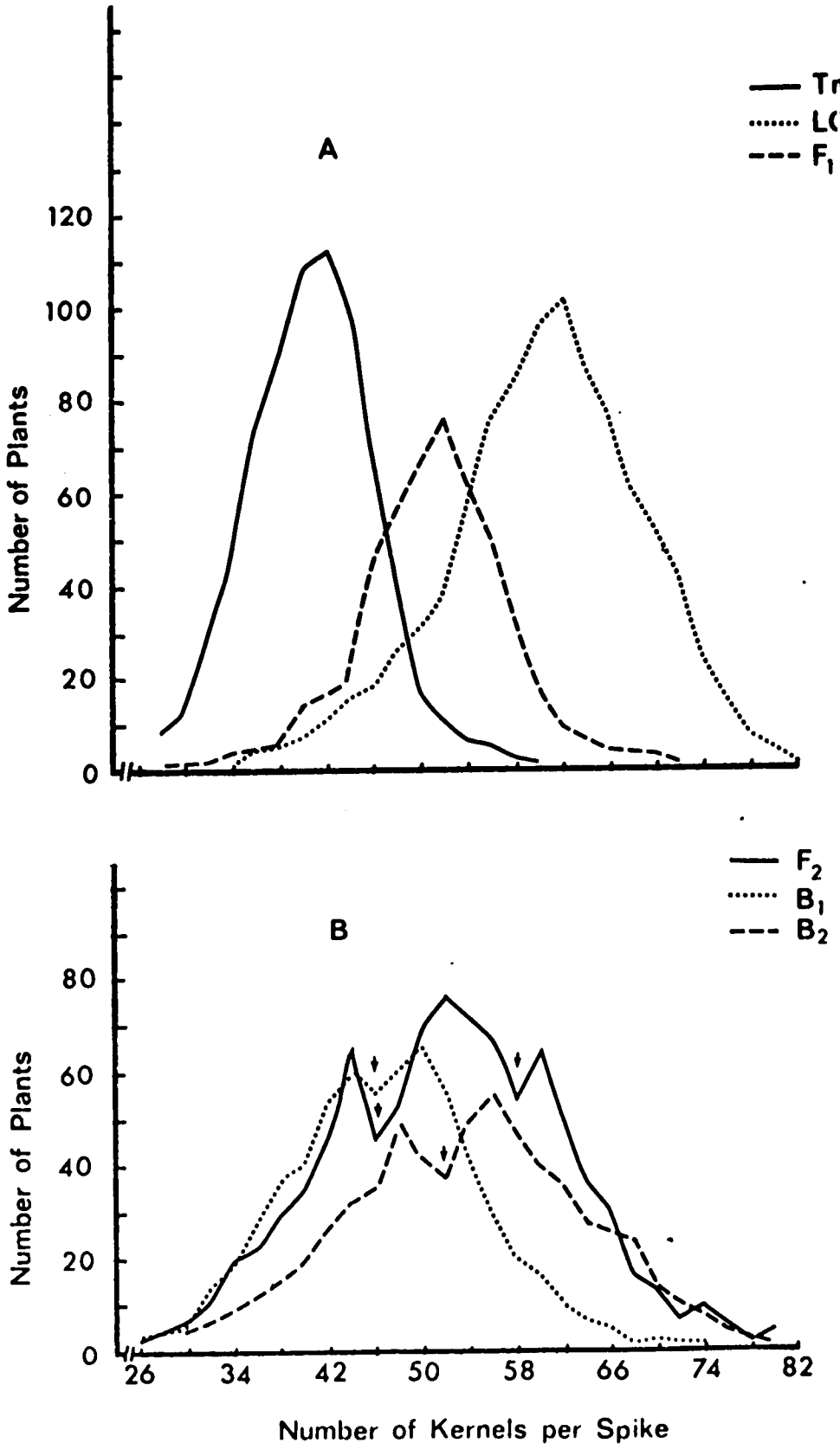

Fig.25. Frequency distribution of number of kernels per spike in the cross Tm x $L(Tm)_{1B}$

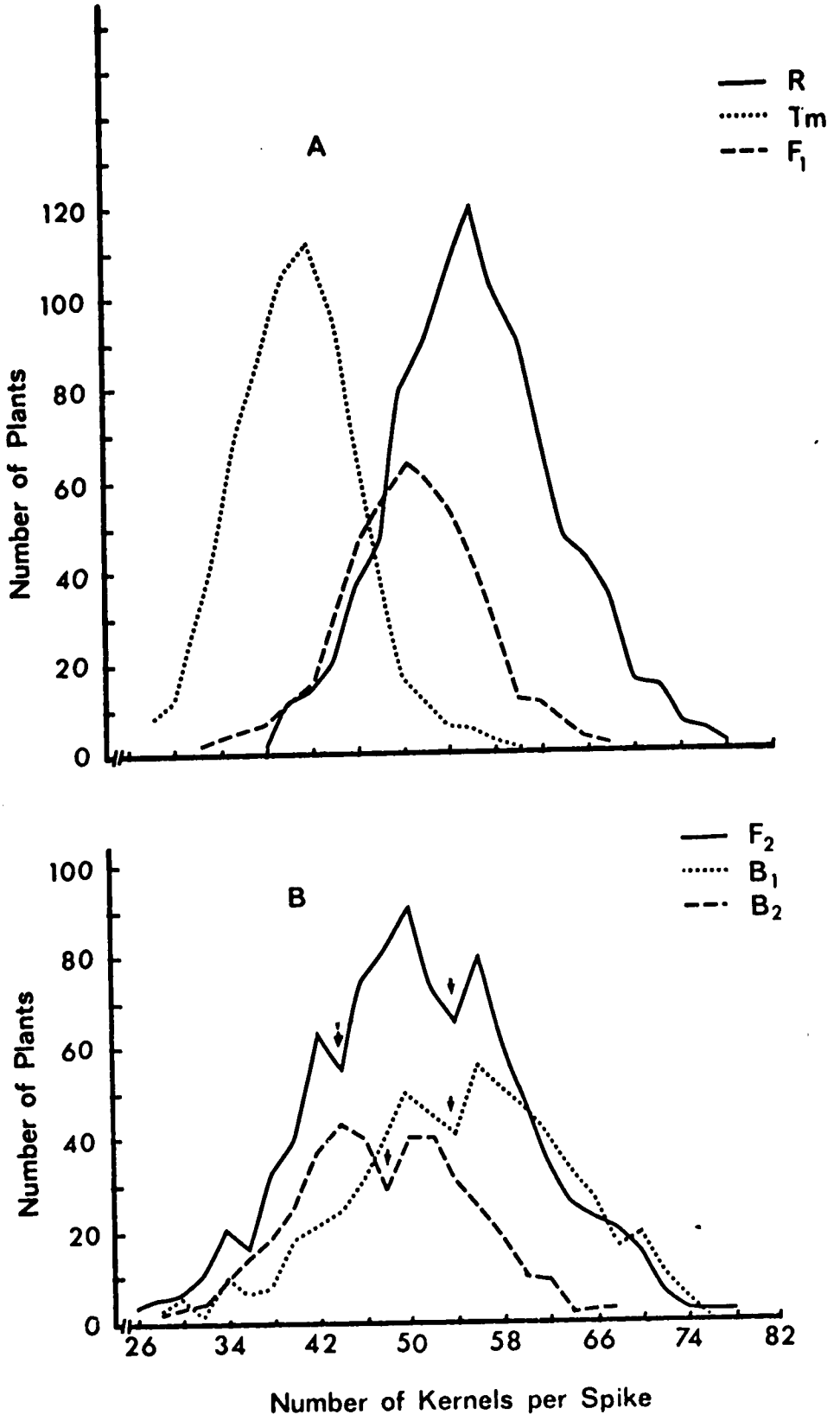

Fig.26. Frequency distribution of number of kernels per spike in the cross R x Tm

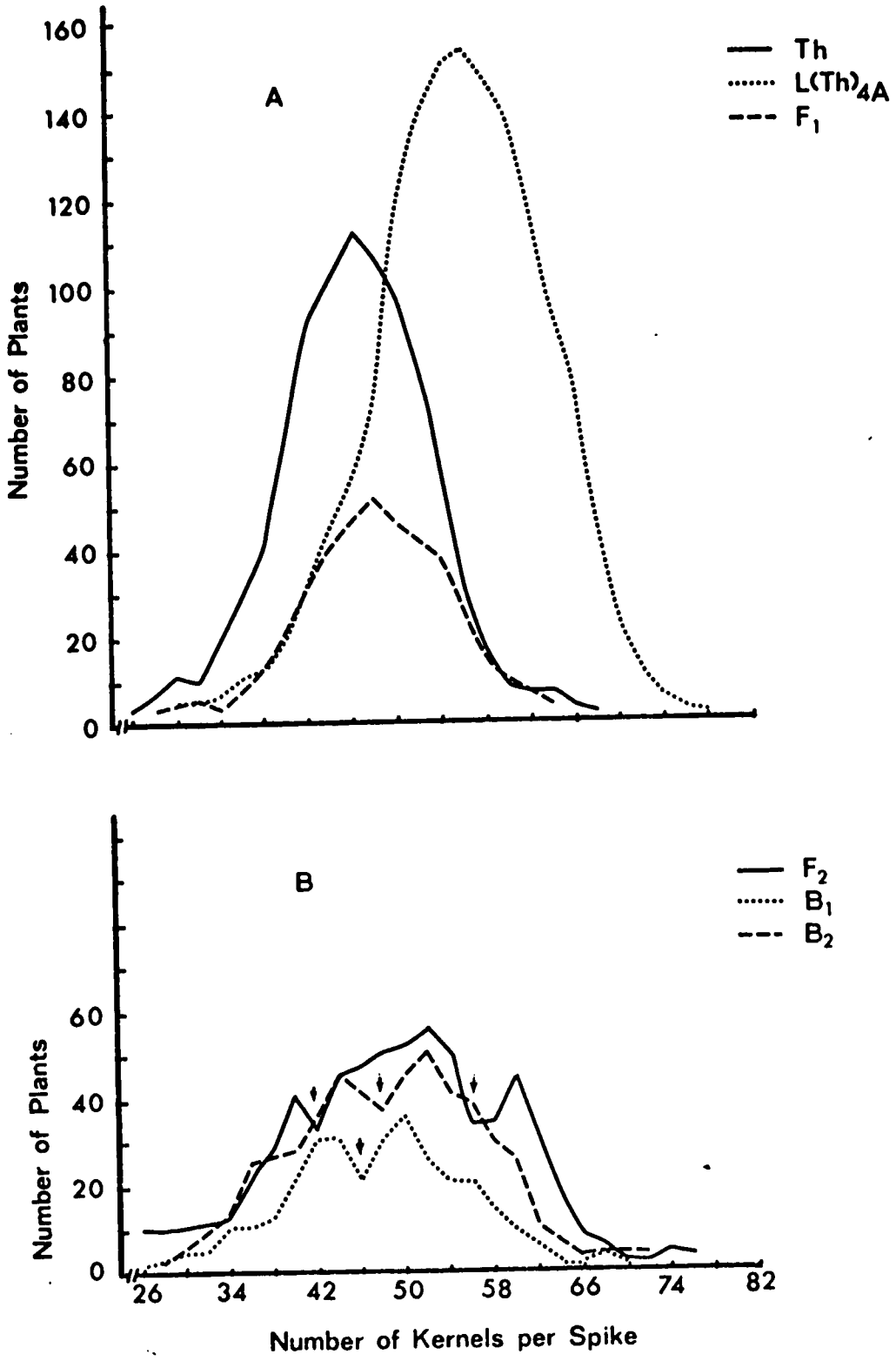

Fig.27. Frequency distribution of number of kernels per spike in the cross Th x $L(Th)_{4A}$

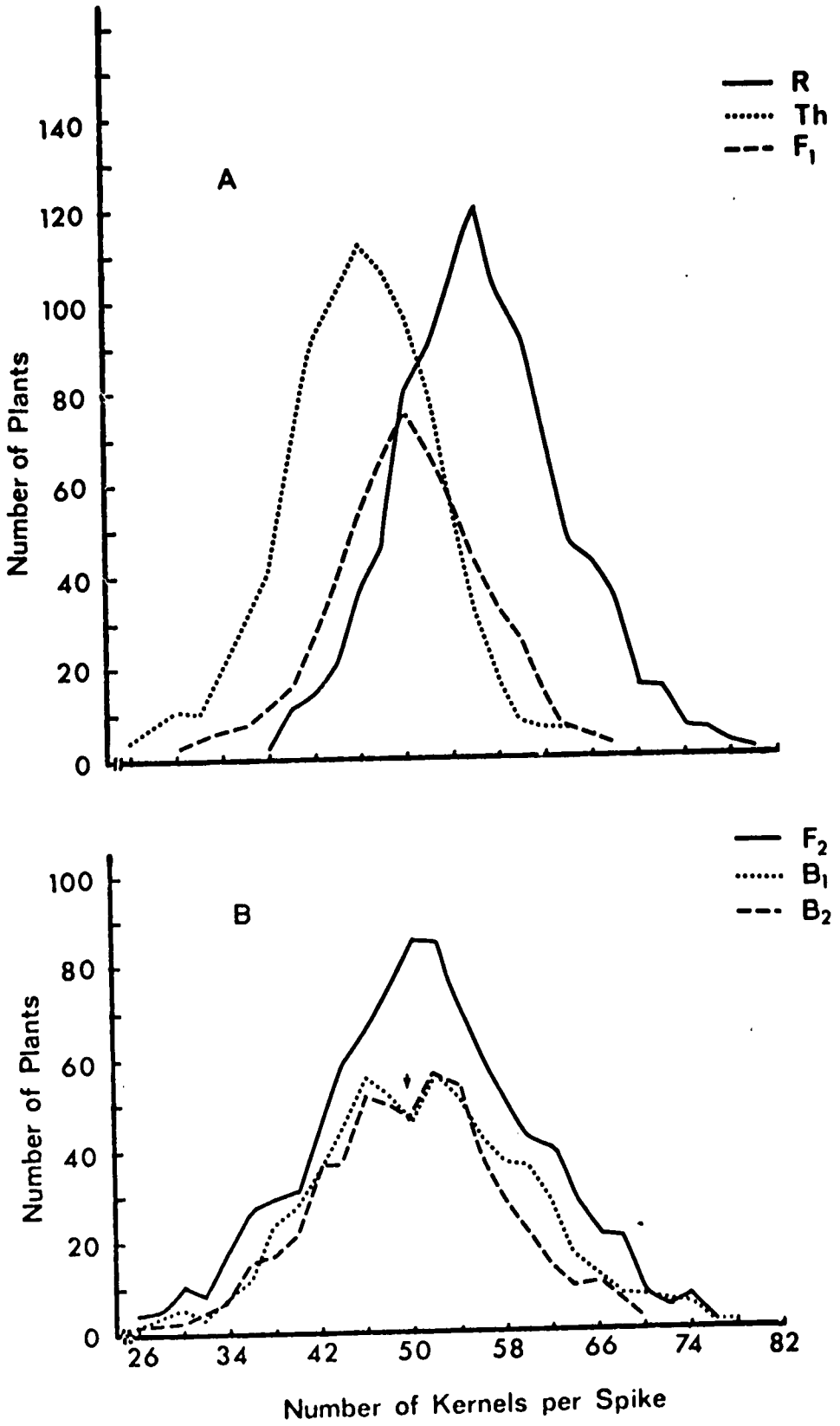

Fig.28. Frequency distribution of number of kernels per spike in the cross R x Th

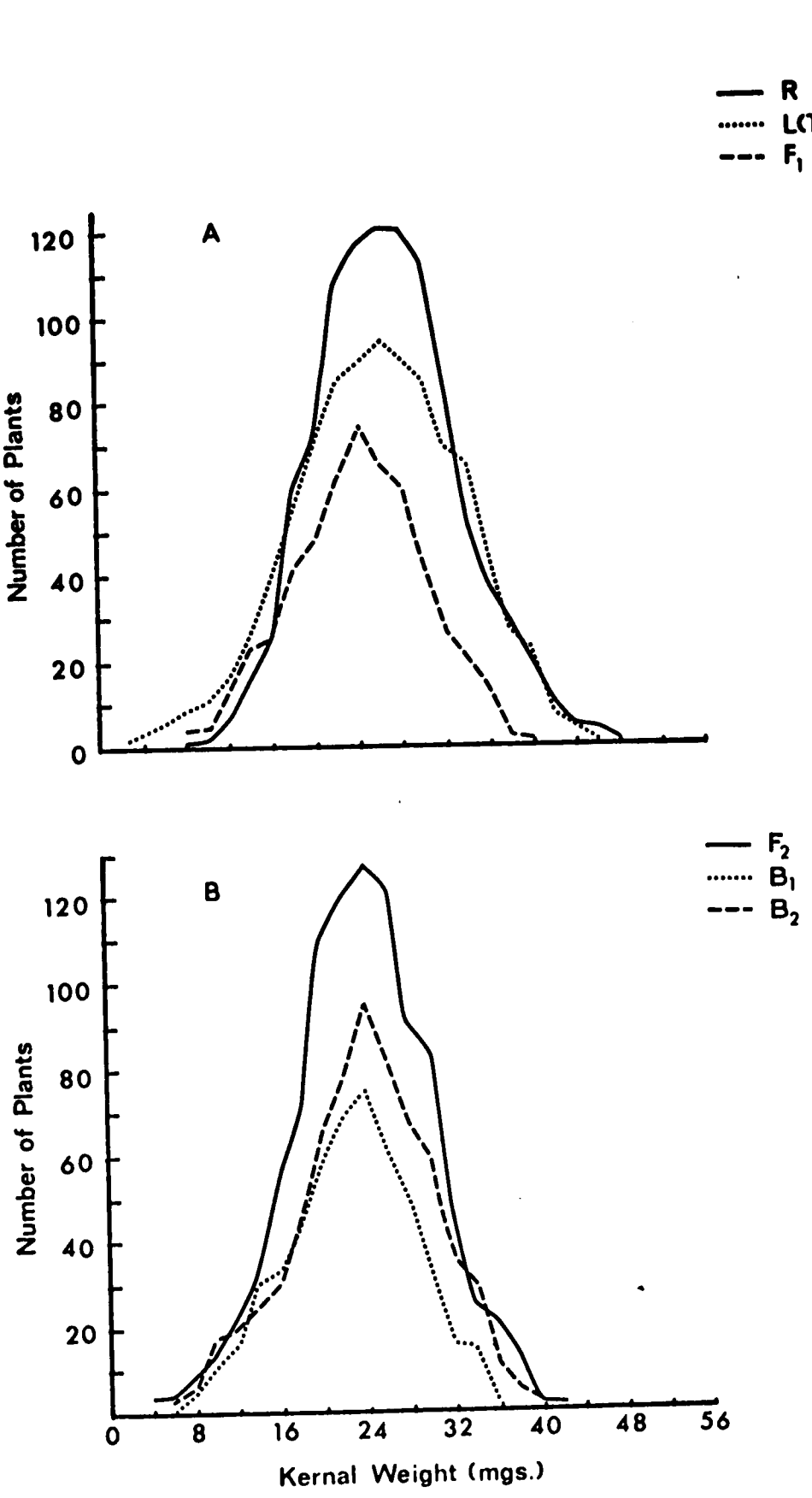

Fig.29. Frequency distribution of kernel weight (in mgs.) in the cross R x $L(Tm)_{1B}$

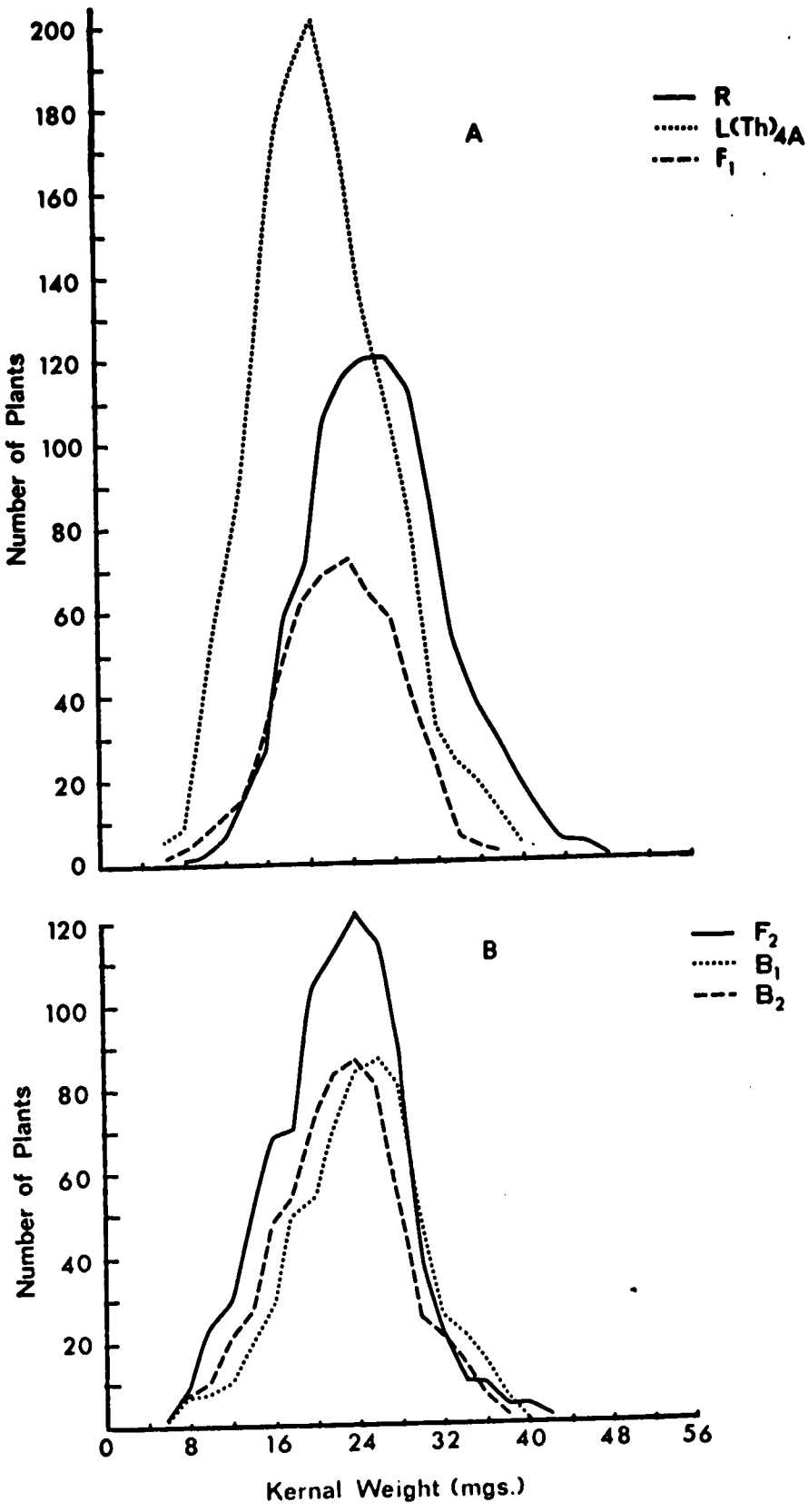

Fig.30. Frequency distribution of kernel weight (in mgs.) in the cross R x $L(Th)_{4A}$

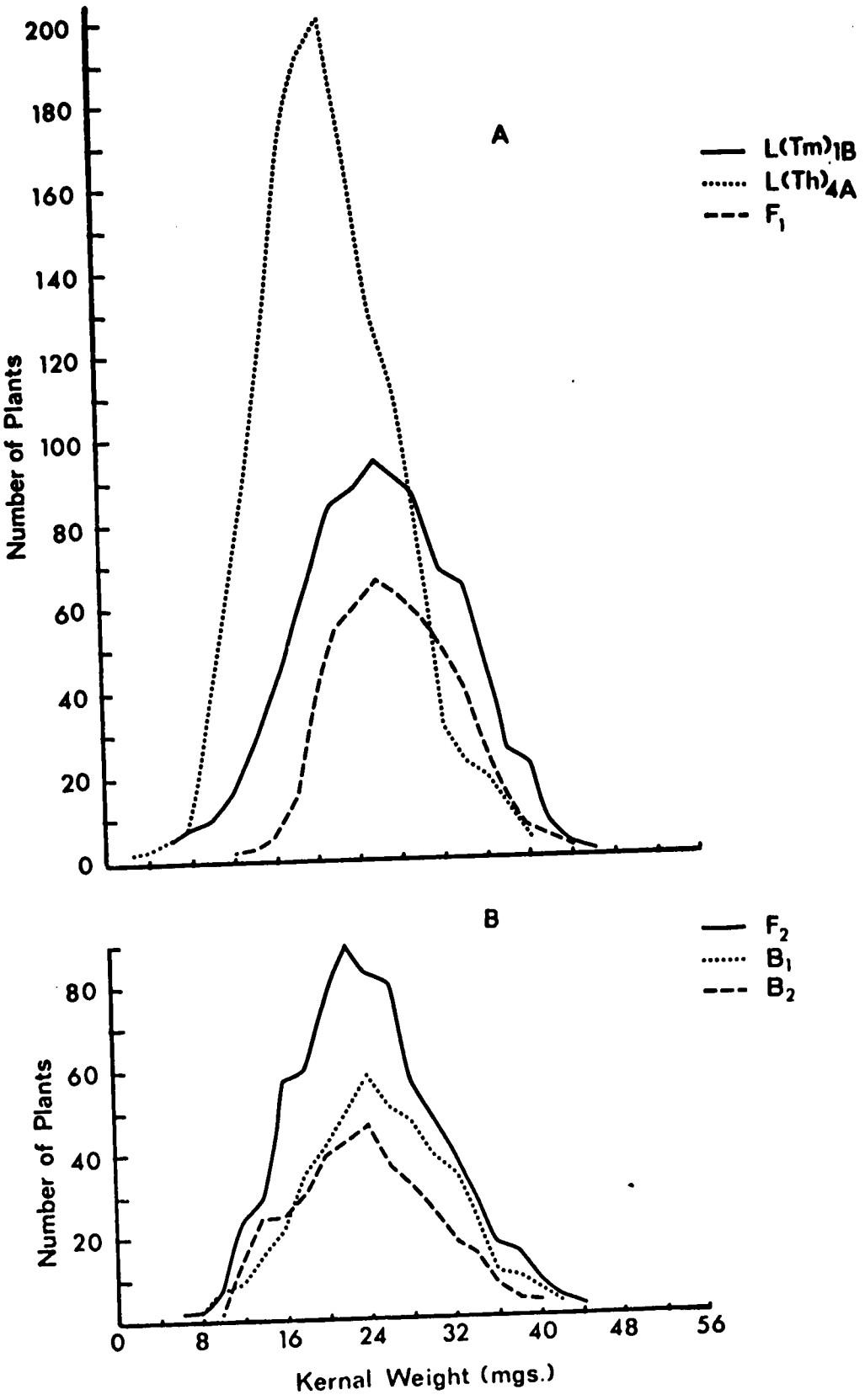

Fig.31. Frequency distribution of kernel weight (in mgs.) in the cross $L(Tm)_{1B} \times L(Th)_{4A}$

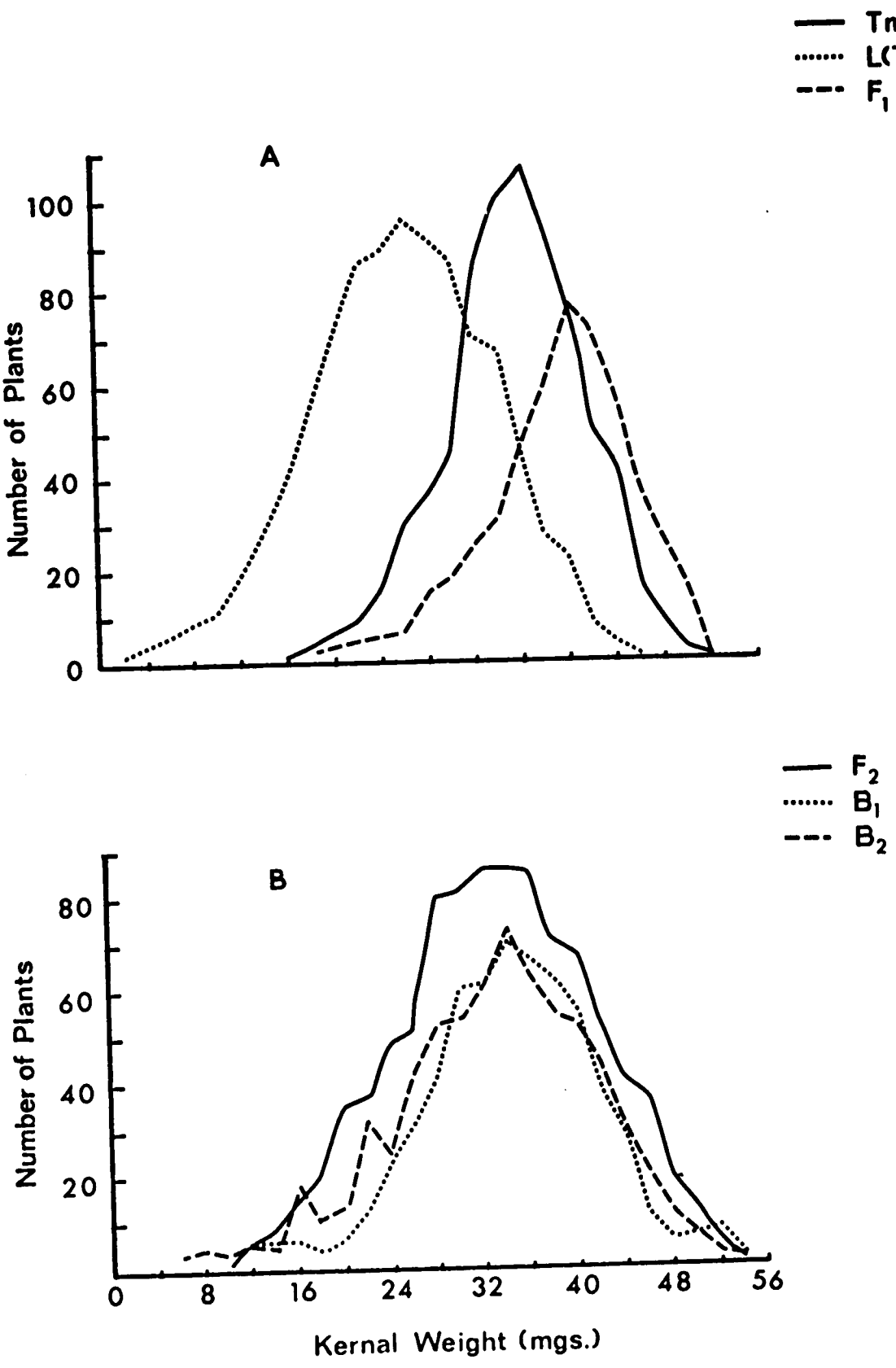

Fig.32. Frequency distribution of kernel weight (in mgs.) in the cross Tm x $L(Tm)_{1B}$

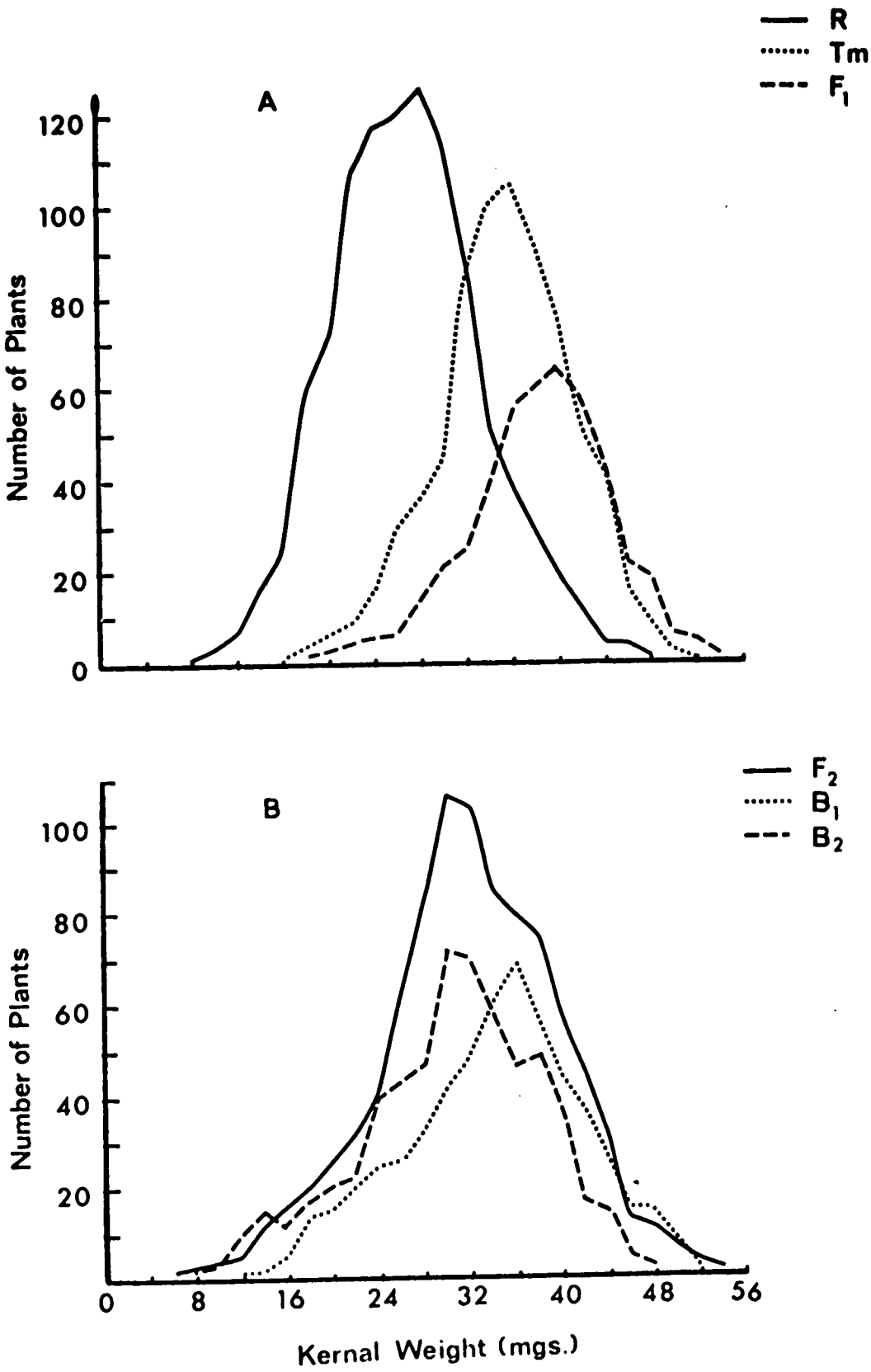

Fig.33. Frequency distribution of kernel weight (in mgs.) in the cross R x Tm

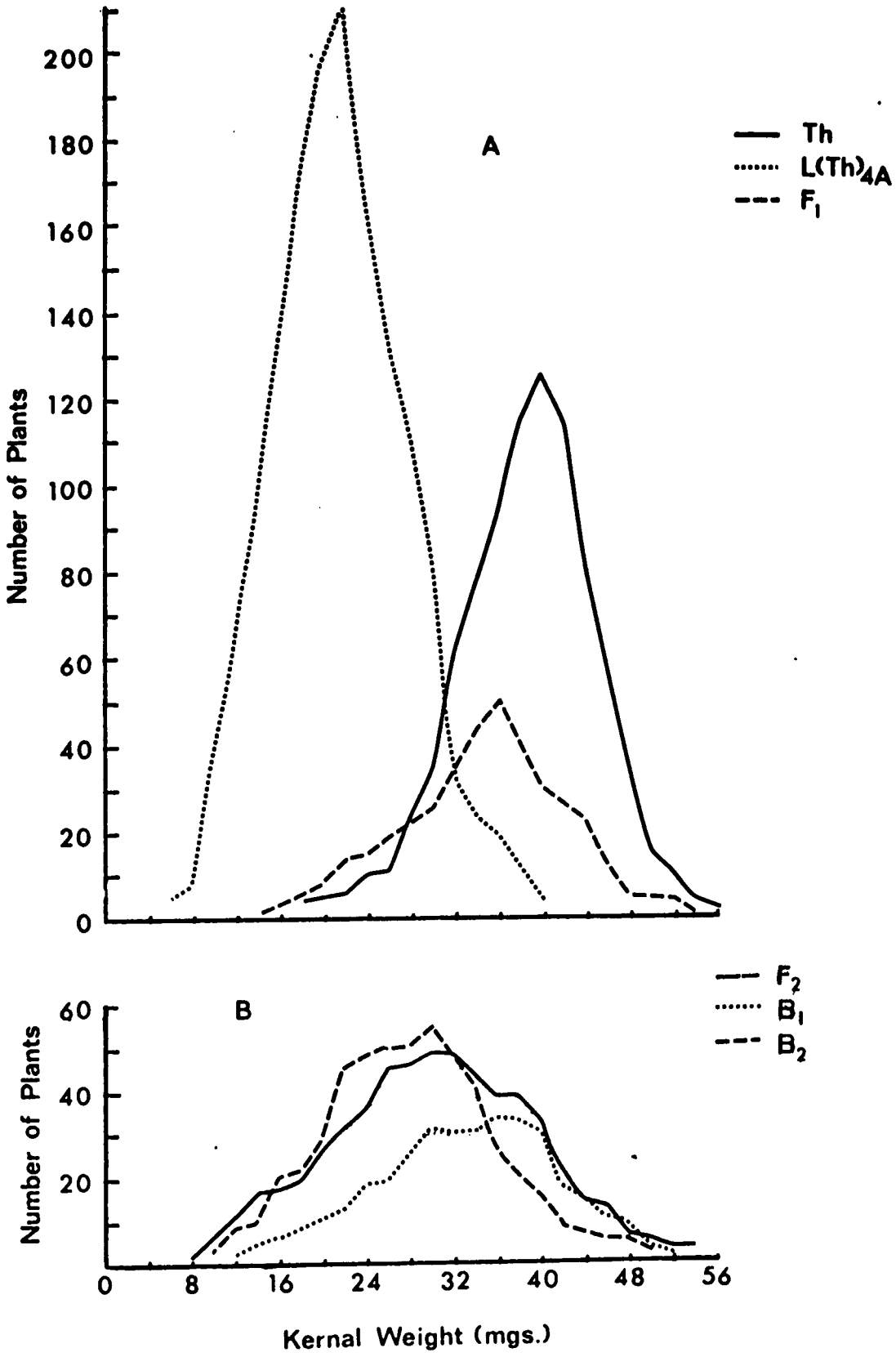

Fig.34. Frequency distribution of kernel weight (in mgs.) in the cross Th x $L(Th)_{4A}$

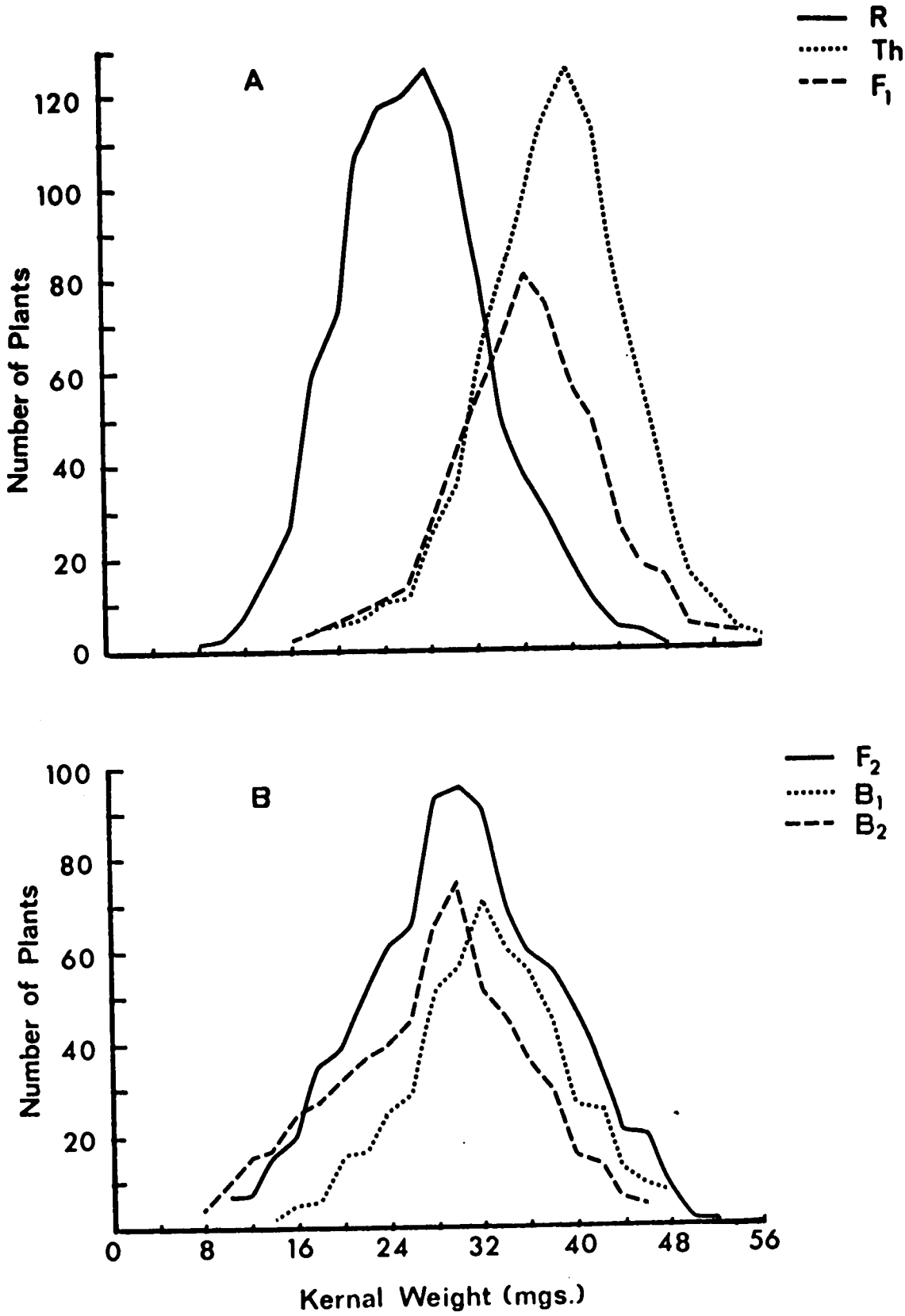

Fig.35. Frequency distribution of kernel weight (in mgs.) in the cross R x Th

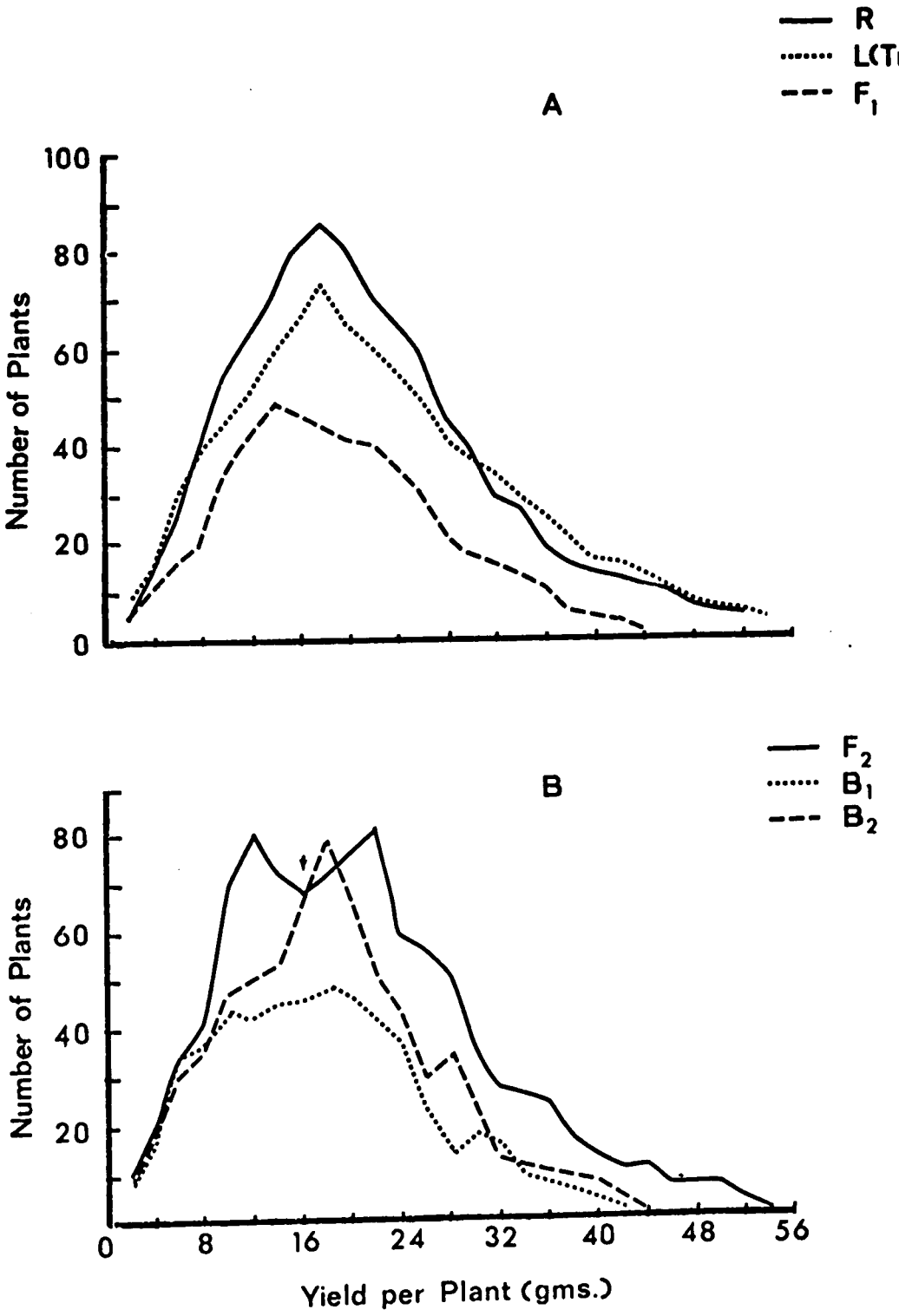

Fig.36. Frequency distribution of yield per plant (in gms.) in the cross R x $L(Tm)_{1B}$

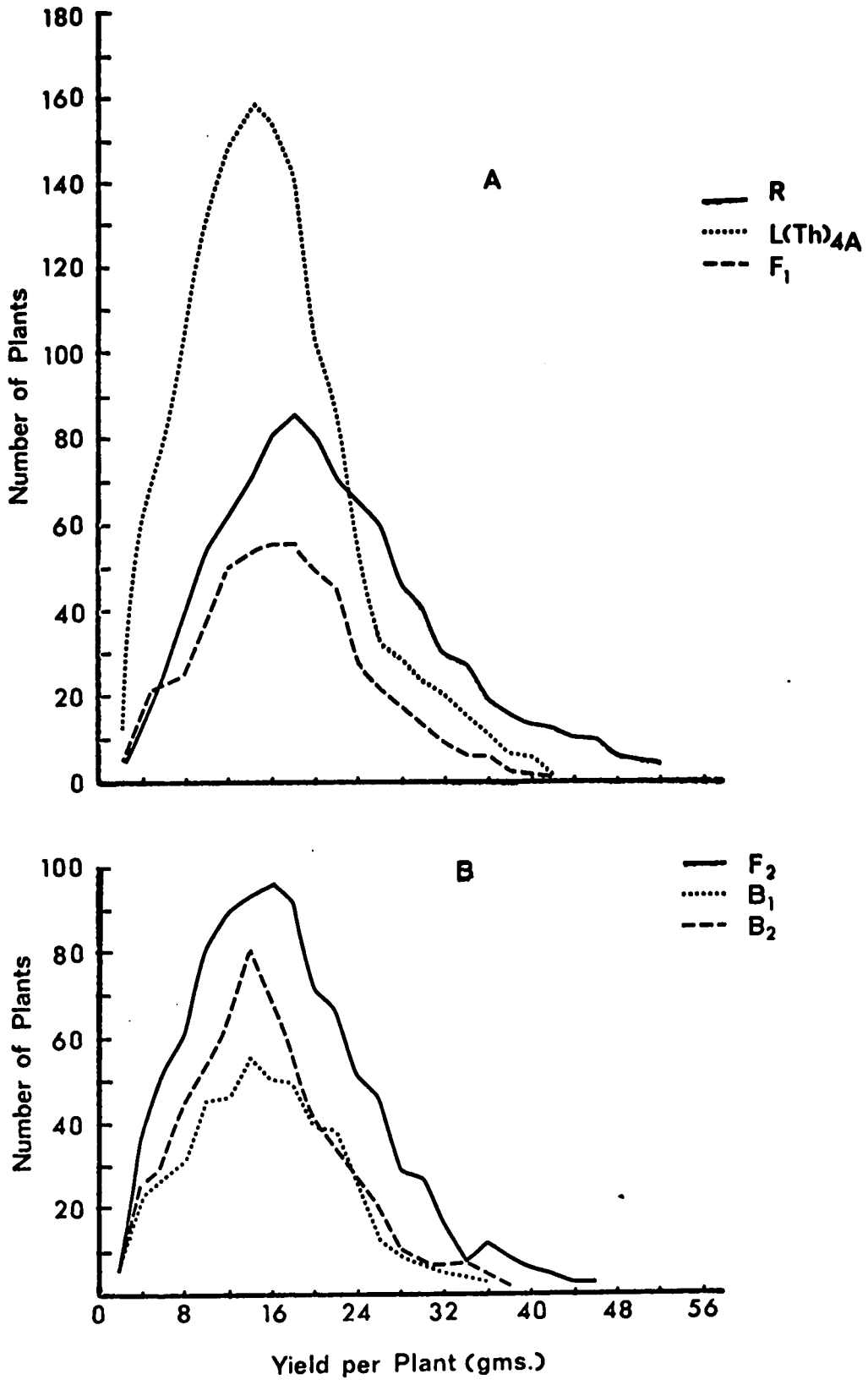

Fig.37. Frequency distribution of yield per plant (in gms.) in the cross R x $L(Th)_{4A}$

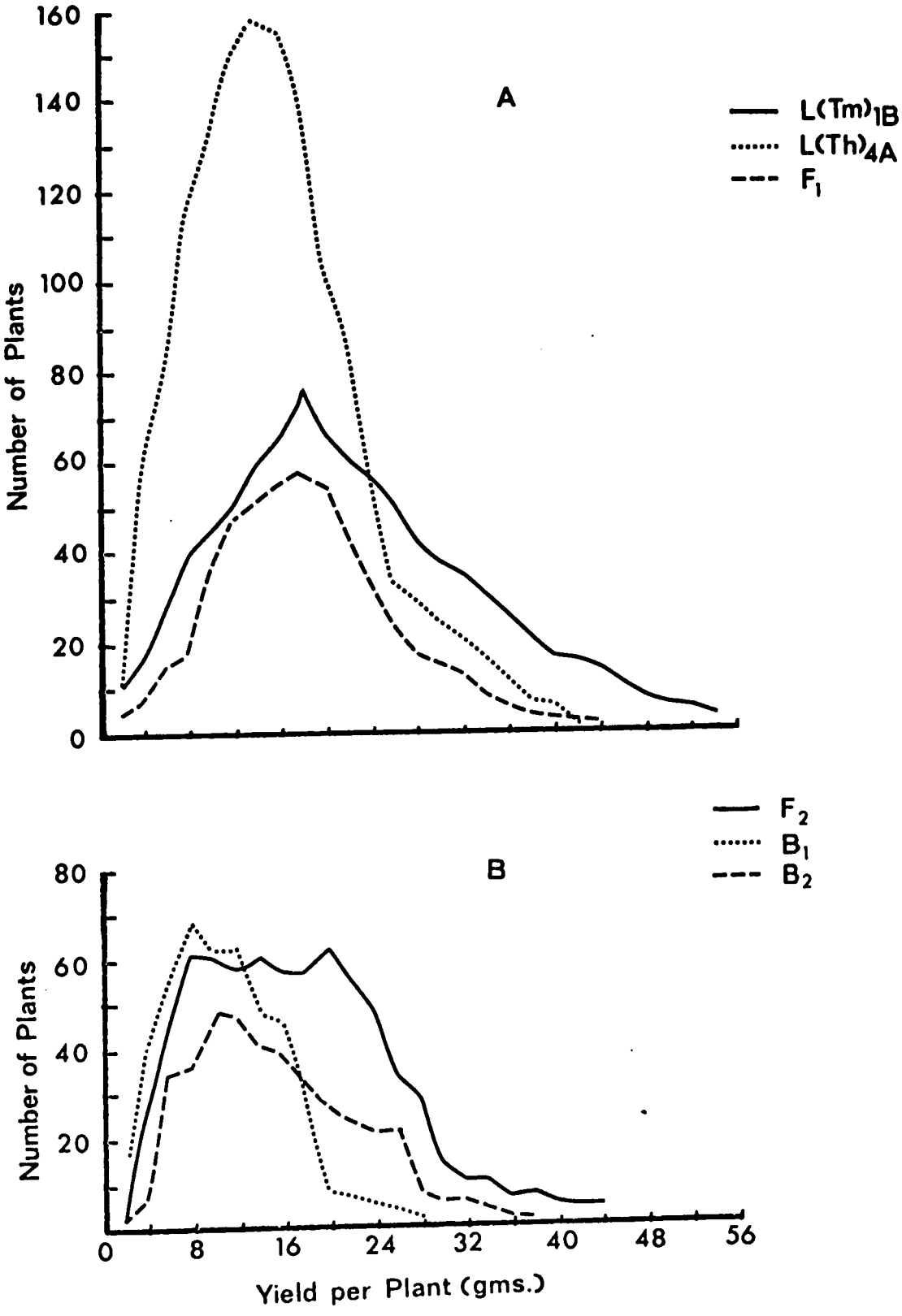

Fig.38. Frequency distribution of yield per plant (in gms.) in the cross $L(Tm)_{1B} \times L(Th)_{4A}$

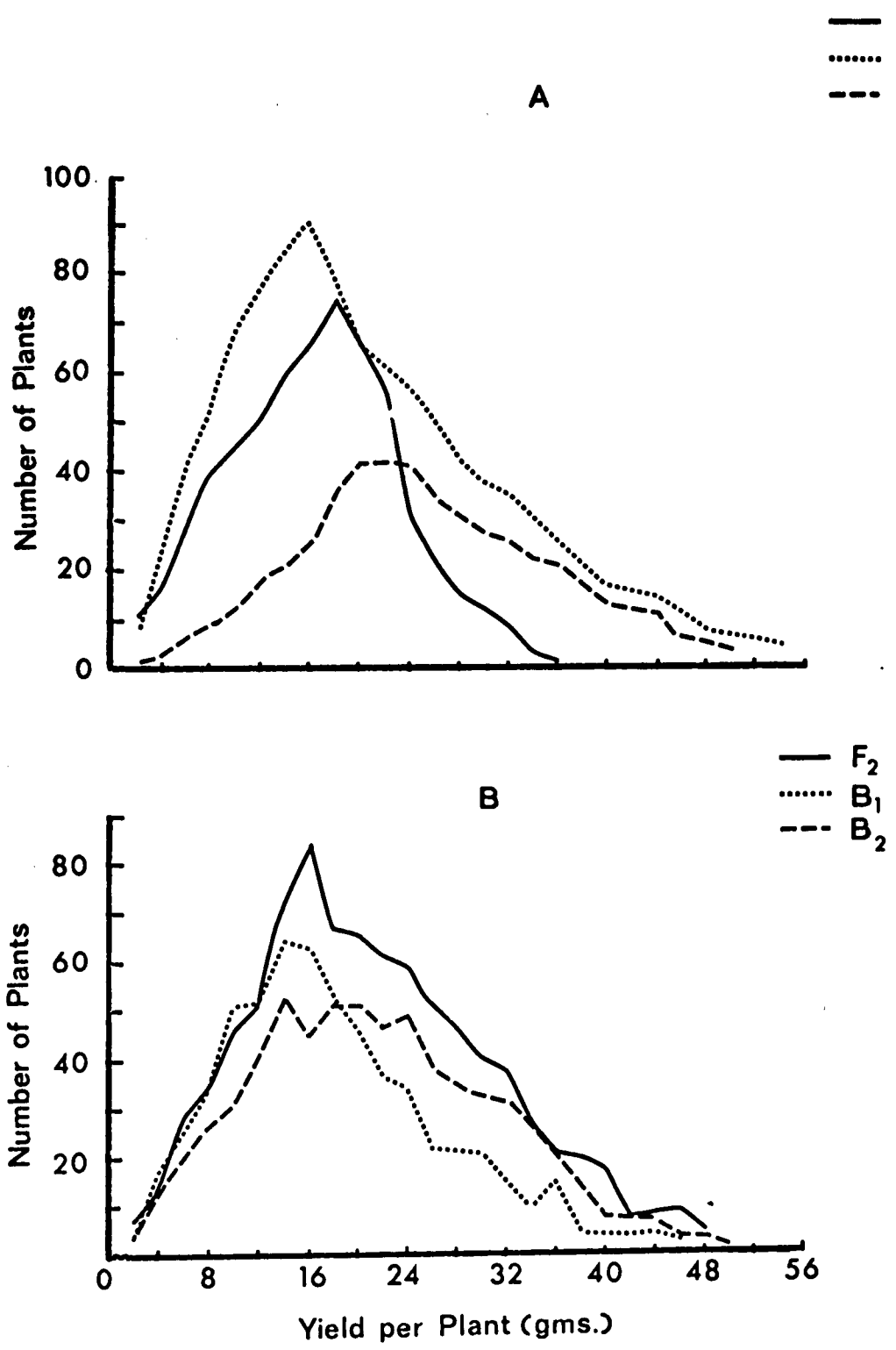

Fig.39. Frequency distribution of yield per plant (in gms.) in the cross Tm x $L(Tm)_{1B}$

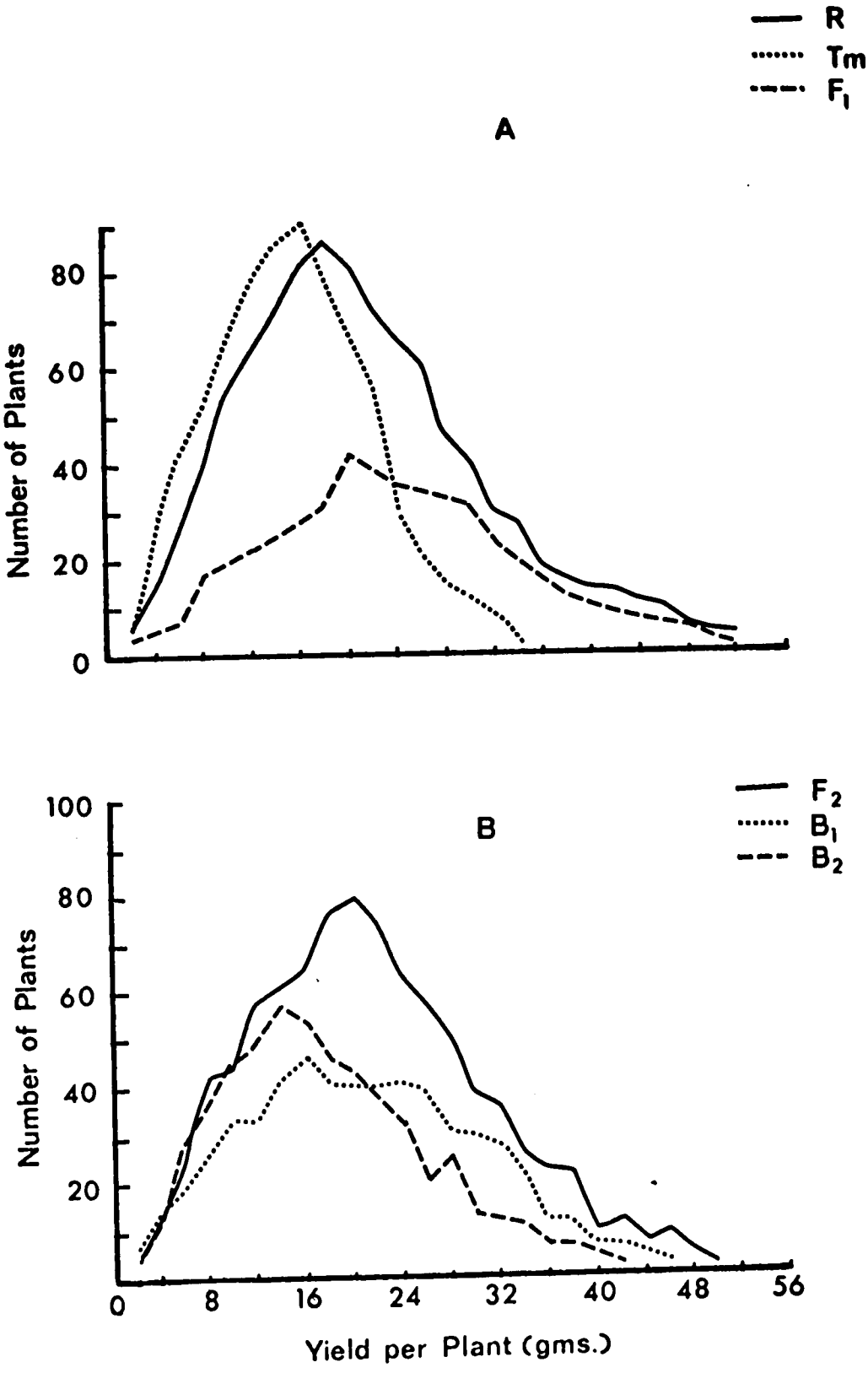

Fig.40. Frequency distribution of yield per plant (in gms.) in the cross R x Tm

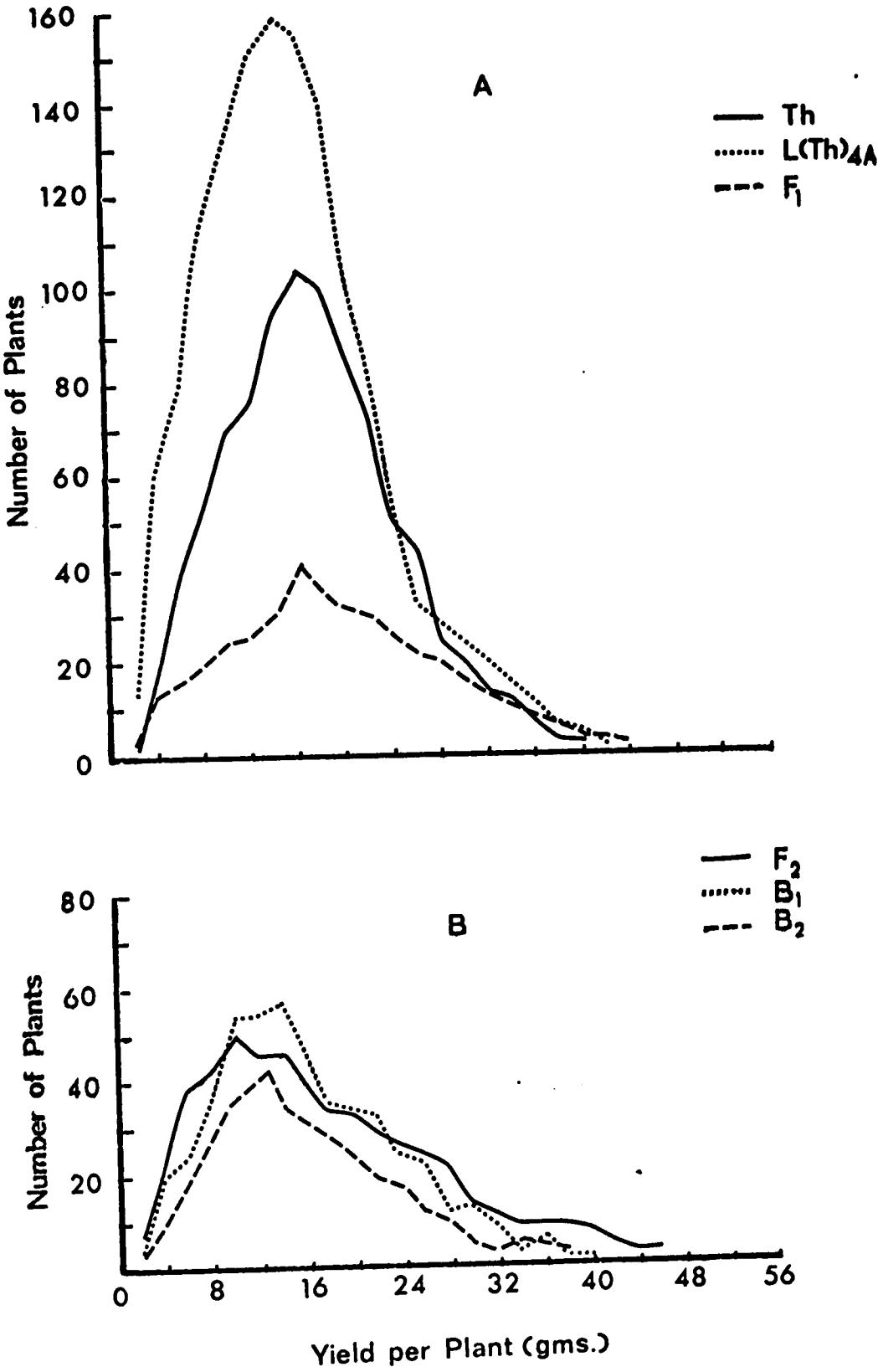

Fig.41. Frequency distribution of yield per plant (in gms.) in the cross Th x $L(Th)_{4A}$

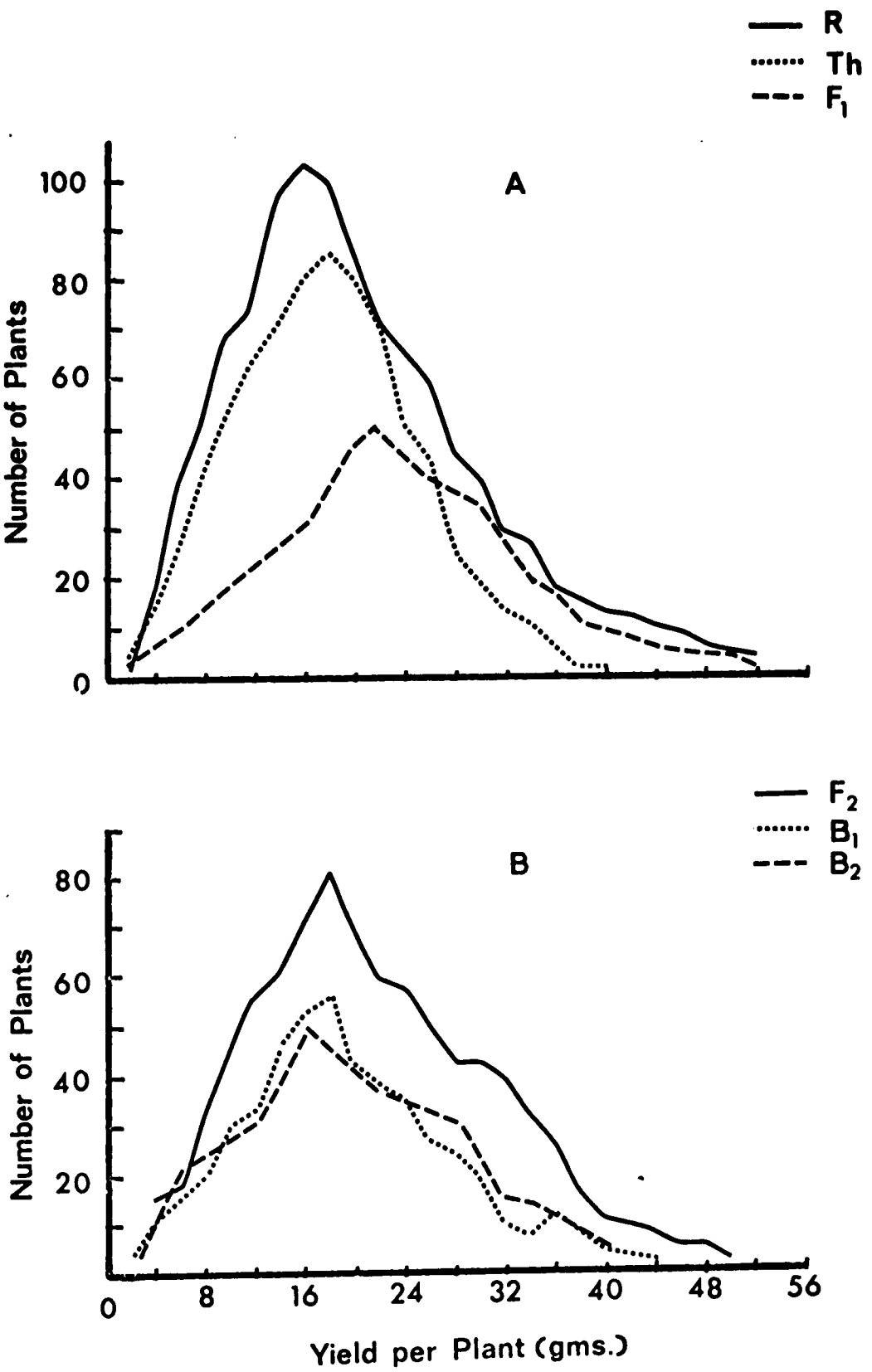

Fig.42. Frequency distribution of yield per plant (in gms.) in the cross R x Th