A CYTOGENETIC STUDY OF ASYNAPSIS IN TOMATO

(*LYCOPERSICON ESCULENTUM* MILL.)

DISSERTATION

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INTRODUCTION

Of several environmental and genetic causes of complete or partial unfruitfulness in economic plants asynapsis is one. The term "asynapsis" has been used in literature to designate failure of expected conjugation of homologous chromosomes during the first meiotic division. Although, in a purely literal sense, this term is most appropriate to describe the initial absence of synapsis in zygotene, it is certainly a misnomer for pre-metaphase disjunction of homologues following zygotene pairing. A more appropriate term "desynapsis" has been used by some authors for the latter condition where the homologous pairs of chromosomes had synapsed in zygotene and pachytene and their dissociation occurred after pachytene. But, in the frequent instances where observations have been confined to diakinesis and/or metaphase I and it has not been possible to fully ascertain whether the lack of conjugation was due to absence of initial pairing or subsequent dissociation of homologues, neither term seems adequate. However, for lack of a more appropriate alternate term, it seems desirable to retain the more conventional usage of the term asynapsis for all such cases where observations are confined to diakinesis and/or metaphase I.

Onset of this kind of meiotic abnormality is known, in some species, to have been triggered by external conditions such as extreme temperatures, deficient moisture in soil and atmosphere, and such other factors as age of the plant (13). Most of the cases of asynapsis

studied so far, however, suggest that the phenomenon of asynapsis has a definite genetic basis (2,3,5,8,11,12,16,27,42,44).

The "asynapsis genes" may be distinguished from another group of genes referred to as "male sterile." The action spectrum of the two kinds of genes is different. The male sterile genes cause complete absence or extreme scarcity of pollen in the mutants possessing them. They are also associated with aberrant morphology of floral structures and generally without serious detriment to ovule fertility. The asynapsis genes, on the other hand, are not known to influence the morphology of floral parts and seem to affect both micro- and mega-sporogenesis and therefore cause diminished ovule fertility.

Undesirable though these male sterile and asynaptic plants may seem from a commercial standpoint, their usefulness to a geneticist or a breeder can hardly be overemphasized. The modern plant breeder is constantly looking for a better and more suitable source of male sterility for cheaper production of hybrid seed. To a plant geneticist, the mechanism of aynapsis may be invaluable for the origin of primary trisomics whose values for linkage studies is obvious. This mechanism can usefully be employed to shed more light on the mechanism and physiology of chiasma formation, the exact nature of which still belongs to the realm of speculation.

The evolutionary significance of asynapsis is multifold. Asynapsis could lead to extinction of a species in which self-pollination is the rule unless its mode of perpetuation changes to apomixis,

to speciation through outcrossing with distantly related species, to permanent heterozygosity in open-pollinated species, or to polyploidy with establishment of fertile triploids in conjunction with restitution of nuclei.

The present study concerns a case of asynapsis discovered in the Marglobe variety of tomato, Lycopersicon esculentum Mill., in the Ohio Agricultural Experiment Station Botany Greenhouse at Wooster, Ohio, during the summer of 1957. The study was undertaken to -

1. Determine what was responsible for the asynapsis.
2. Establish the linkage relationship(s) of the gene(s) if genetically controlled asynapsis turns out to be the cause.
3. Obtain primary trisomics.

REVIEW OF LITERATURE

Reviewing the literature on asynapsis, Prakken (33) described the following causes of asynapsis as indicated by decreased chromosome pairing usually observed at first metaphase as the occurrence of a variable number of univalents:

1. Asynapsis due to the action of distinct gene or genes
2. Asynapsis caused by the loss of a chromosome
3. Asynapsis in species hybrids
4. Asynapsis as a normal process in apomictic organisms
5. Asynapsis depending on mechanical chromosome conditions such as structure and number
6. Asynapsis induced by external conditions

Regardless of the cause of asynapsis he arbitrarily classified the asynaptic plants into three different categories according to what he termed "intensity series:"

1. Weak asynapsis characterized by a few univalents in some cells
2. Medium strong asynapsis characterized by many univalents in most of cells
3. Complete asynapsis characterized by univalents only or some rare bivalents in all the cells

Most of the species studied so far belong in the first two categories. However, Datura stramonium, Alopecurus myosuroides, Allium amplectens, Tradescantia, and Trifolium pratense represent the third category. These classes of asynaptic plants are generally typified by other pecularities of meiotic behaviors as well. In the case of complete asynapsis where there is also high sterility (triploid A. amplectens being an exception) there are few or no bivalents at metaphase I, defective spindles (long, bent, tripolar,etc), nonmovement of univalents to the equator, of rare splitting of univalent at anaphase I, interphase often with other than two nuclei of cells, and regular second division. In most of the species where asynapsis is medium strong these features are less pronounced. In this case there is a variable number of bivalents at metaphase I, a normal effective spindle, movement of some of the univalents toward the equator, splitting of univalents at anaphase I, interphase nuclei or cells generally two in number, irregular second division with lagging chromosomes, and

a fairly high degree of sterility. *Allium amplectens* does not belong in any of these categories. In this case there are no bivalents, yet a normal spindle is formed. According to Levan (26) telophase starts soon after anaphase, with the result that there is no separation of chromosomes and dyad pollen grains with the somatic number of chromosomes are formed. These pollen grains are balanced and therefore viable and make the triploid *A. amplectens* fertile.

Where genetic studies on asynapsis were conducted, various means of inheritance have been suggested. In the majority of cases asynapsis is controlled by a single recessive gene. Cases of this kind are reported by Beadle (2) in *Zea*; by Clausen, R.E. (11) in *Nicotiana tabacum*; by Bergner et al. (5) in Datura; by Goodspeed and Avery (16) in *Nicotiana sylvestris*; by Catcheside (8) in *Oenothera*; by Prakken (33) in *Secale cereale*; by Li *et al*. (27) in Triticum; by Soost (44) and Clayberg (12) in *Lycopersicon esculentum*.

Two recessive genes have been suggested to explain asynapsis in wheat by Smith (42); in cotton by Beasley and Brown (3). In tomato, Clayberg's data (12) point to two-gene action as well although the author favored one-gene action.

Influence of modifying genes on the expression of asynapsis has been indicated by Li *et al*. (27) in wheat and by Beasley and Brown (3) in cotton.

Suggestions of gene controlled asynapsis were offered by Clausen, J. (10) in *Viola orphanidis*; by Ramanujam and Parthasarathy (34) in rice; by Richardson (35) in Crepis; by Koller in Pisum (23);

and by Celarier (9) in *Tradescantia*. Complete sterility both as male and female parent prevented Whittington (47) from making a genetic study of asynapsis in *Trifolium pratense*.

Loss of a pair of chromosomes was found by Newton and Pellew (29) to cause asynapsis in *Primula kewensis* and by Huskins and Hearne (19) in *Triticum*. Asynapsis in the latter case was, however, caused by the loss of a specific pair. Synapsis was restored when this particular pair of chromosomes was returned to the chromosome complement and a different pair removed. This led the authors to believe that the gene or genes for synapsis were contained in that pair of chromosomes. Person (32), however, noted partial asynapsis in ten different monosomics of wheat.

Of the environmental factors, asynapsis due to high temperature has been described by Heilborn (18) in apple, by Katayama (22) in *Triticum-Aegilops* hybrids and due to low temperature by Sax (40) in *Rhoeo discolor* and Li *et al*. (27) in common wheat. Temperature changes were found to have profound influence on meiosis especially when such changes occurred at the time of meiosis in Ulmus and Populus by Johnsson (21). Noting a high degree of variation in frequency of univalents in Populus, Johnsson (21) suggested "external causes" as the most probable cause of weak asynapsis. Soost (44) seems to favor the idea that asynaptic genes may cause a shift of temperature range of optimum growth in a given plant.

Deficient soil moisture and low air humidity have been suggested to contribute to asynapsis in rye by Prakken (33). All of these plants

are in the medium strong group of Prakken's classification of intensity series. The completely asynaptic group apparently is either not influenced or the environmental range necessary to induce pairing has not been encountered in the experiments.

For failure of metaphase pairing, Beadle (2) has listed the following causes:

1. Premature chromosome division
2. Non-specific pairing between non-homologous chromosomes
3. Breakage of chiasmata
4. Deficient terminal affinity
5. Failure of chiasma formation

In all these studies on asynapsis there seems to be a general agreement that failure of chiasma formation is, if not the only, a major factor involved in asynapsis. Ehrenberg (14) advanced a fascinating hypothesis in regard to failure of chiasma formation. He suggested that crossing over may involve the breaking or reunion of protein chains in which proteolytic enzymes are involved. Thus the absence of certain enzymes may interfere with the process. This may explain how gene(s) controlling asynapsis as well as environmental factors can influence chiasma formation.

It would be presumptuous to hold that asynapsis is a single-step action of the gene(s) or of the environmental condition. On the contrary it seems probable that asynapsis is one of the consequences in a series of effects of a physiological disorder and that different erratic behaviors in the long series of steps are interrelated. Beadle (2) and

Johnsson (21) observed that asynapsis was accompanied by syncytes (plasmodial masses of microsporocytes or 'giant cells'). These giant cells are caused by failure of cell wall formation in premeiotic divisions. Similar premeiotic abnormality was also noticed by Morgan (28) in maize following X-irradiation of the pollen, a twin progeny of which suggested that asynapsis and premeiotic suppression of cytokinesis may be partially related.

No apparent macroscopic morphological abnormalities were noticed in most of the aynaptic plants, until the time of pollen formation. Roy and Jha (39) however found their "semi asynaptic" plants of Abelmosbhus esculentum (L.) Moench., having luxuriant vegetative growth, producing a large number of flowers, normal looking fruits yet devoid of seeds. Evidently fruits developed parthenocarpically.

In tomato, the first report on asynapsis appeared in Rick's (36) survey of cytogenetic causes of unfruitfulness in tomato. Later Soost (44) made a comprehensive cytogenetic study of asynapsis in tomato. He listed 5 different mendelian recessive genes, designated as as_1--------as_5 controlling asynapsis in different groups of tomato plants. In no case was there any complete asynapsis. Despite the fact that chiasma frequency was reduced at metaphase I in the asynaptic plants, no appreciable difference was noticed in genetic crossing over. This indicated that exchange of genic material had already occurred before breakage of chiasmata. A similar observation has been made by Clayberg (12) in a completely asynaptic mutant recovered in San Marzano variety of tomato.

Some trisomic plants were recovered in the progeny of asynaptic tomato plants by Soost (44) and the asynaptic pea by Koller (23). Rick and Barton (37) however expressed doubt as to the usefulness for linkage studies of trisomics obtained from asynaptics on the ground of possible segregation of asynapsis and consequent unfruitfulness in subsequent generations.

MATERIALS AND METHODS

An asynaptic plant discovered in the Marglobe variety of tomato in the Ohio Agricultural Experiment Station Botany greenhouse at Wooster in the summer of 1957 constituted the basic source of the investigation herein reported. Fruits were set on this otherwise unfruitful plant by using pollen from an inbred strain of woolly (semi-dominant lethal) having several recessive marker genes whose description is given in the following pages, or pollen from Walter-15 which is known to be immune to one strain of tobacco mosaic virus. A part of the F_1 progeny of these crosses was raised in the Ohio State University Vegetable greenhouse at Columbus during the spring of 1958 and the remainder of it was field planted at Wooster during the summer of 1958. The seed for F_2 progeny of each cross was obtained from self-pollinated diploid plants of the spring planted F_1 generation. One F_2 progeny of each cross was grown at Wooster from the seeds obtained from a single fruit set on the F_1. Seed from reciprocal backcrosses was obtained only in the case of the woolly cross. A nonwoolly plant was used as the mother plant and a woolly as the pollen parent in order to be able to determine the success of the cross by the appearance of

woolly seedlings in the resulting progeny. Six backcross progenies and two more F_2 progenies of the woolly cross were grown during fall and winter of 1958-59 in the University Vegetable greenhouse at Columbus. The greenhouse plants were raised in steam-sterilized 6-inch clay pots filled with sterilized sand-soil-peat mixture. The pots were placed on the benches in such a way as to insure adequate light to each plant. However, owing to the large size of the plant population, crowding became unavoidable especially during the fall planting. The plants were pruned to single stem and supported by means of jute twine. An electric vibrator type of pollinator was used during the flowering season.

In the field plants were spaced 6x3 feet in rows. All plants in the greenhouse and in the field received normal cultural care. The amount of precipitation received during the summer was greater than that of past few years and so was light condition better in the greenhouse during the winter. All in all 1033 plants were used in this cytogenetic study.

The trisomic plants discovered in the F_1 generation of both the crosses were propagated from stem cuttings and brought to the University Genetics greenhouse at Columbus for future use of the trisomic material. Two plants from the F_2 generation suspected to be asynaptic were also moved to the Genetics greenhouse for getting seed from them and also to attempt backcrosses on them since the original Marglobe asynaptic plant had by that time been lost.

Careful notes were taken regarding the morphological characteristics of the plants from time to time. Each progeny number used in the text represents the progeny from a single fruit.

Description of Genes

As indicated earlier in the text, the woolly plant also carried a number of recessive marker genes. Expression and location of the genes in the linkage map of tomato as adapted from Rick and Butler (38) are described below:

1. Beaked (bk). Homozygote has a pointed beaklike process at the stylar end of the fruits. Expression of the gene is variable according to the genotypic background. Belongs to linkage group I.
2. Potato leaf (c). In homozygous condition the first true leaf is usually entire and subsequent leaves divided to lesser extent than the normal. The terminal leaflet is larger and lateral leaflets smaller and fewer than in normal tomato leaf. Identification is easy in the seedling stage as shown in Plate I, Figure 1. Linkage group IV.
3. Jointless (j). Normal pedicel joint with characteristic swelling and abscission layer is absent in the homozygote. Fruits separate from pedicel at the juncture with the calyx. Indeterminate growth of inflorescence is considered to be a pleiotropic effect of j. Classification is easy as shown in Plate II, Figure 2. Linkage group V.
4. Tangerine (t). Ripe fruit has tangerine or orange color of flesh due to replacement of lycopene by prolycopene. Pleiotropic effect on flower color causes suffusion of an orange tone over the anthers. Classification good. Linkage group VII.

5. Uniform (*u*). Absence of dark green shoulders of immature fruit in the homozygote. Entire coloration of the fruit is somewhat lighter. Classification is easy. Linkage group VII.
6. Woolly (*Wo*). Dominant gene, lethal when homozygous. In the heterozygote all vegetative parts including hypocotyl are densely tomentose. Identification is easy in the seedling stage as seen in Plate I, Figure 1. Linkage group I.
7. Colorless fruit epidermis (*y*). Yellow pigment in the epidermis of mature fruit is missing in the homozygote. Easy to identify. Linkage group III.

The Walter-15 line carries no marker gene but is immune to one strain of tobacco mosaic virus.

Assuming that the "asynapsis" gene is a mendelian recessive designated as *as*, the genotypes of the parents involved in the present crosses with respect to the marker genes are as follows:

Woolly: $Wo\,wo^{+}$ cc jj uu tt $bkbk$ yy as^{+} as^{+}
Walter-15: $wo^{+}wo^{+}$ $c^{+}c^{+}$ $j^{+}j^{+}$ $u^{+}u^{+}$ $t^{+}t^{+}$ $bk^{+}bk^{+}$ $y^{+}y^{+}$ as^{+} as^{+}
Marglobe: $wo^{+}wo^{+}$ $c^{+}c^{+}$ $j^{+}j^{+}$ $u^{+}u^{+}$ $t^{+}t^{+}$ $bk^{+}bk^{+}$ $y^{+}y^{+}$ as as

Thus the six loci namely *c*, *j*, *u*, *t*, *bk*, and *y* are in coupling phase to one another but in repulsion phase to *Wo* and *as* in the crosses involved in this study.

A summarized pedigree of the crosses is given in Figure 3.

Plate I

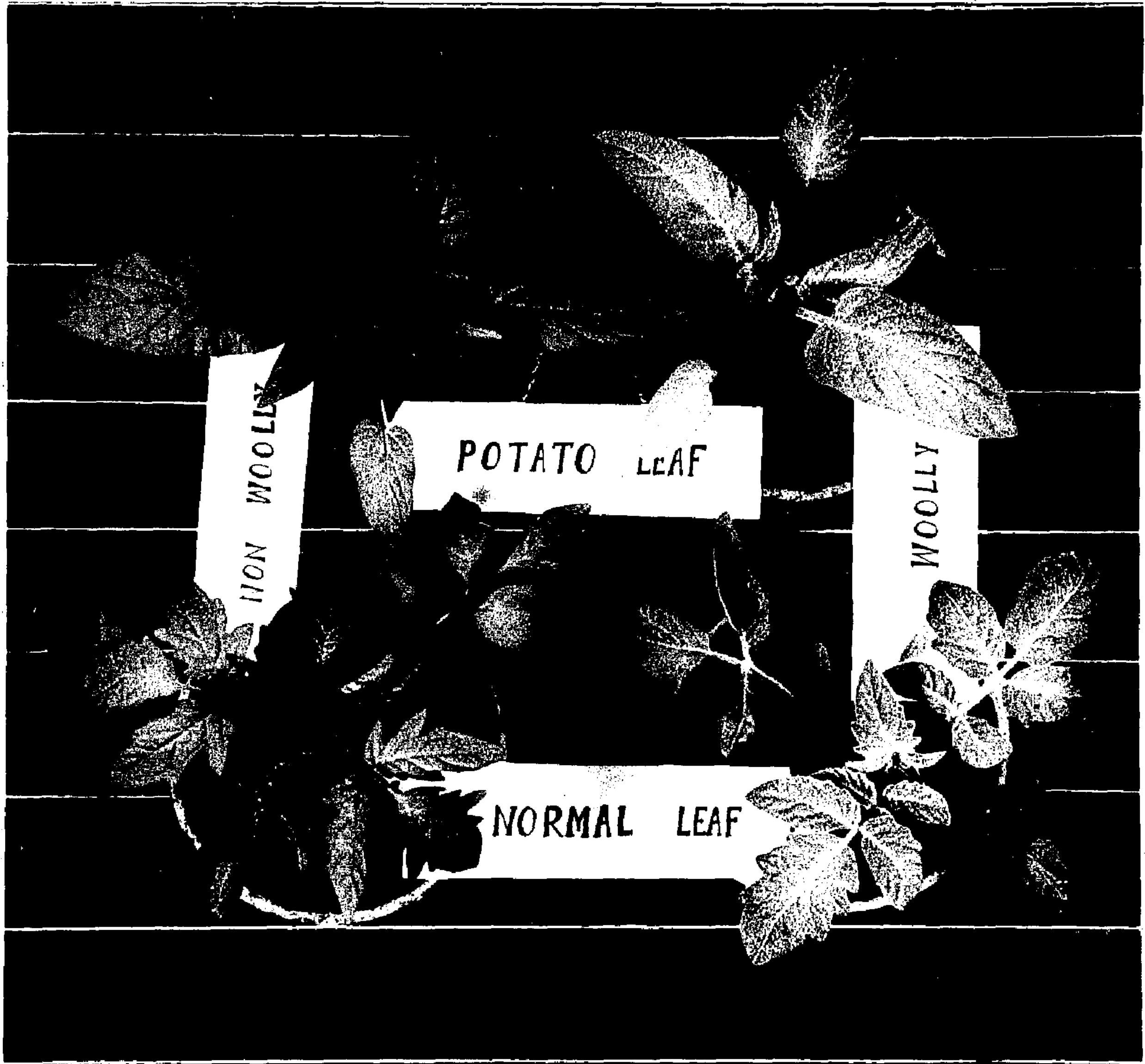


Figure 1. The two tomato seedlings on the right are woolly ($Wowo^{+}$) and the two on the left nonwoolly ($wo^{+}wo^{+}$).

The two seedlings on the top have potato leaf (cc) and the two bottom seedlings have normal cut leaf (c^{+}-).

PLATE II

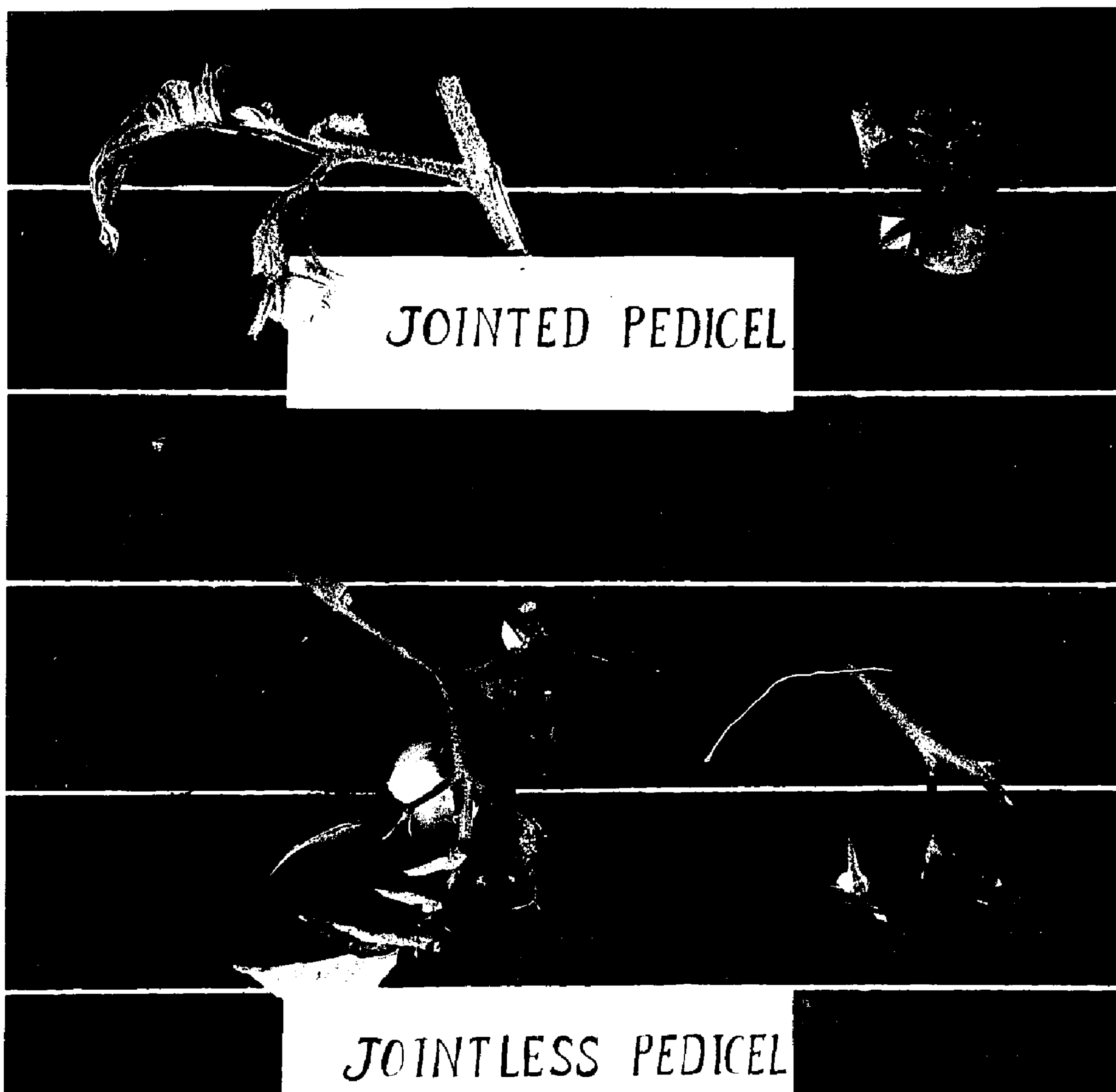
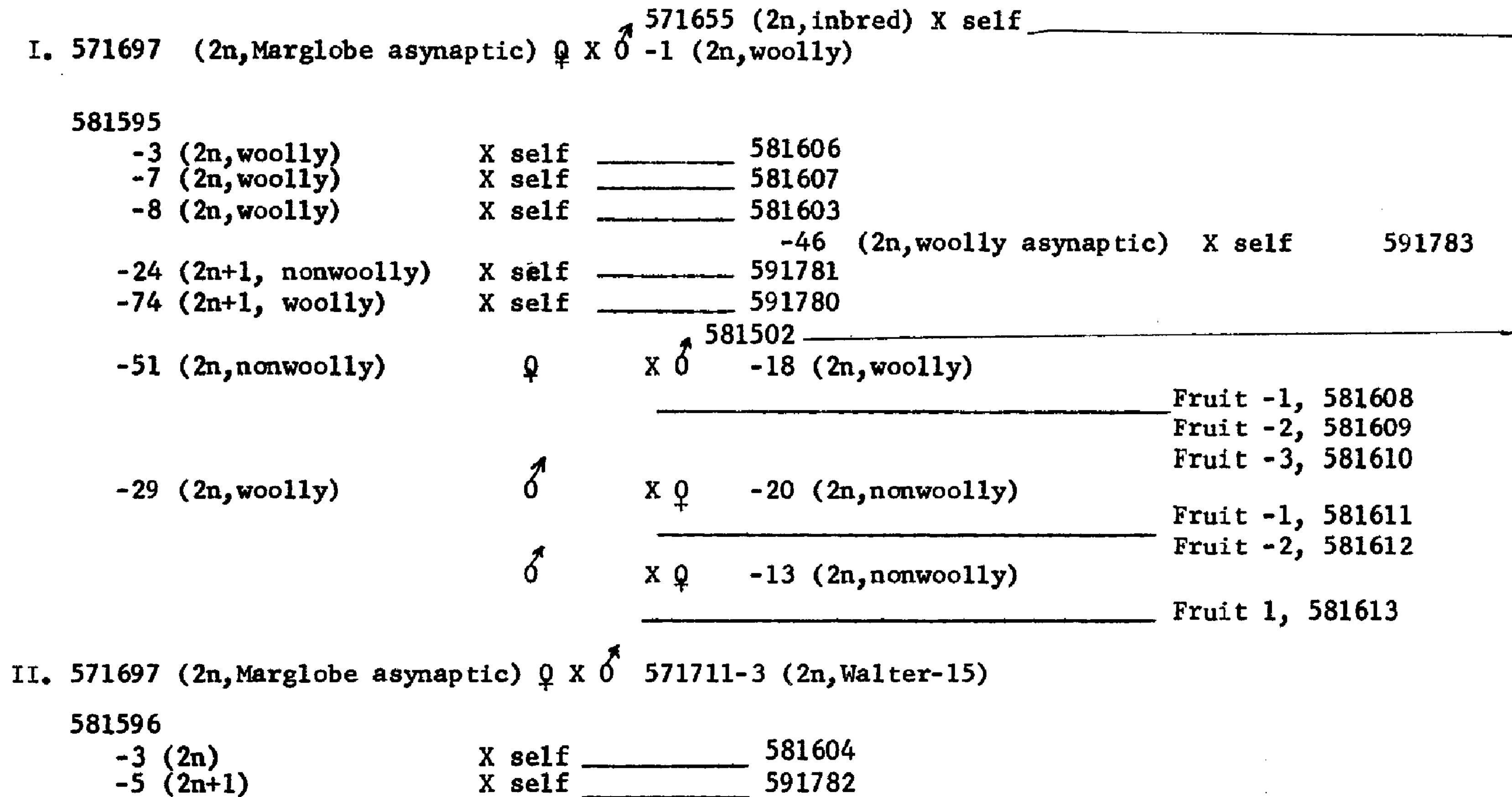


Figure 2. The upper two fruit clusters have jointed pedicel (j^+-) and the lower two jointless pedicel (jj)

Indeterminate inflorescence is seen in the two fruit clusters on the left.

Figure 3. Summarized Pedigree of Crosses Involved in the Present Study



Material for Cytological Study

Flower buds of appropriate age (approximately 3 to 5 days prior to anthesis) were plucked, desepalled and depetalled and fixed in freshly mixed Farmer's fluid (43) made up of three parts of 95 per cent ethyl alcohol and one part of glacial acetic acid. Buds from different plants were fixed separately in 5-7 ml. of the fixative contained in 15 ml. glass vials for about 24 hours. One or two anthers were used at a time for making smears of the pollen mother cells (PMC) in a crop of aceto-carmine by using the usual smear technique as developed by Belling (4). For temporary storage of suitable slides, sealing was done with a sediment-free mixture of equal parts of gum mastic and hard paraffin. Pickled buds were found suitable for smear preparation up to ten days or so. Three-week old material once gave quite satisfactory results when kept in cool temperature around 65° F.

For making permanent smears, Sear's (41) method was used with certain modifications. The seal of the temporary mount is gently scraped off with a sharp single-edged razor blade. The mount is then soaked in equal parts of glacial acetic acid and 95 per cent ethyl alcohol until the coverslip comes off. Placing the slide upside down and one end on a glass rod in a petri dish containing the solution is convenient. A slight push to the coverslip may hasten its separation from the slide. Both the slide and the coverslip are transferred to a Coplin staining dish containing one part of glacial acetic acid and three parts of 95 per cent ethyl alcohol keeping them in the same relative positions. A

split wooden match stick is convenient to handle the coverslip. About one minute of immersion in this solution was considered enough. The slide and the coverslip are then passed through two more one-minute baths of absolute alcohol contained in Coplin staining dishes. After the final bath, the slide and the coverslip are drained of excess alcohol by holding them edgewise on a blotter. The coverslip is then mounted back to its original position on a drop of diaphane (Euparal) of desirable consistency. The mount usually sets in an hour or so, but it is advisable to wait overnight for examination of the slide. Experience showed that the final two baths in absolute alcohol were absolutely necessary to get a clear mount with diaphane. The slightest moisture on the coverslip or on the slide will produce a milky precipitate with diaphane and render the mount cloudy. Blowing air from one's mouth in an attempt to dry the slide produces a similar undesirable milkiness on the slide and should therefore be avoided.

Sealing of slides can be eliminated if the slides are made permanent within three to four hours of staining.

An Ernst Leitz binocular Labolux microscope was used for examination of the slides.

Photomicrographs were taken from the permanent slides under oil immersion using apochromat objective lens (oil 2 ml., 1:30 N.A. X 90) combined with X 10 compensating eye piece. Watten No. 58 green filter was used.

Aceto-carmine stain was used for the study of pollen as well.

PRESENTATION OF RESULTS

F_1 Generation

The F_1 plants of the cross between the asynaptic Marglobe and the inbred woolly, hereafter referred to as No. 581595, were classified into woolly and nonwoolly phenotypes. Cytological examination of the PMC revealed diploids and aneuploids in each of the two phenotypes. The relevant data are given in the following table:

TABLE 1

Genomic classification of F_1 plants of the cross between asynaptic Marglobe and inbred woolly (581595)

Pheno-type	Number of plants					X^2	df	P
	Diploid	Aneuploid		Total	Expected 1:1			
		Tri-somic	Poly-somic					
Woolly	44	15	0	59	51	2.51	1	0.12
Nonwoolly	34	8	1*	43	51			
Total	78	23	1	102	102			

*As many as 33-34 chromosomes were counted in some cells of this polysomic plant.

The observed frequency of woolly and nonwoolly plants fits the hypothetical 1:1 ratio within an acceptable range.

The appearance of aneuploids in the F_1 generation provides an indirect measure of the extent of asynapsis in the megasporocytes of the asynaptic plant used as the maternal parent in this cross. The data revealed that the hypersomic megaspores were being produced at the rate of 23.5 per cent (24/102) on account of asynapsis operative

in megasporogenesis. Absence of monosomic or nullisomic plants in the progeny under reference was indicative of non-survival of hyposomic megaspores and/or the deficient zygotes resulting from them.

One of the anuploids among nonwoolly plants was weak and stunted with light green foliage, Plate IV, Figure 6. In its PMC as many as 33 or 34 chromosomes (2n + 9 or 10) were counted at diakinesis, metaphase I, and Anaphase I of some cells, Plate IX, Figures 20-23. The upper limit of extra chromosomes that can be tolerated by tomato plants was reported to be three by Lesley (24). Recently Soost (45) reported aneuploids from sesquidiploid F_1 hybrids of _Lycopersicon esculentum_ and _Lycopersicon peruvianum_ with two to ten extra chromosomes. He attributed the ability of the _Lycopersicon_ aneuploids to carry the new limit of extra chromosomes to either their hybrid constitution or the _peruvianum_ portion of their complement. This explanation, however, does not hold for the _esculentum_ aneuploid reported here. An explanation for this situation may be found in the genic balance, pointing to the possibility of survival of near-diploid gamets and consequently near-triploid zygote.

Formation of such hypermegaspores further suggest that asynapsis occurred in as many as 9 or 10 pairs of chromosomes in certain megaspore mother cells.

A similar study of the F_1 generation of the cross between Marglobe and Walter-15, hereafter referred to as No. 581596, yielded the data given in Table 2.

TABLE 2

Genomic classification of F_1 plants of the cross between asynaptic Marglobe and Walter-15 (No. 581596)

Phenotype	Number of plants			Total
	Diploid	Aneuploid		
		Trisomic	Polysomic	
Normal	41	5	0	46

The extent of hypersomic gametes produced in this cross works out to 10.9 per cent (5/46) which is approximately one half that of No. 581595. Cytological examination of PMC brought to light an additional feature of this cross. It was noted that this cross had a heteromorphic pair of chromosomes which apparently was other than the nucleolar pair of chromosomes, Plate VII, Figure 16.

The appearance of aneuploids in both the crosses indicates that asynapsis was fairly extensive in the megasporocytes of the asynaptic Marglobe plant.

Morphology of Aneuploids

The effect of an extra chromosome was markedly reflected through the morphology of the trisomics, Plate III, Figure 4. Differences among aneuploid plants became manifest in the early stages of the vegetative growth and continued through flowering and fruiting stages. The aneuploids were easily distinguished from their sister diploids. Without exception, all aneuploids were slow in growth and looked

stunted when full grown. A wide array was found among the trisomicswith respect to the pattern of growth, structural variation of stems, shape and color of foliage, size and shape of flower buds and flowers, size and shape of fruits, and variability in fertility ranging from complete unfruitfulness to near-normal fruitfulness. This is similar to the progenies of triploid tomatoes studied by Lesley (24,25) and by Rick and Barton (37). No attempt was made to classify the trisomics on the basis of the extra chromosome as Rick and Barton (37) did.

On the basis of the wide diversity in morphology and fertility among the present trisomics it is obvious that different chromosomes were involved in the formation of the respective trisomic individuals, and that asynapsis was general rather than specific with respect to any pair or pairs of chromosomes.

Plate III

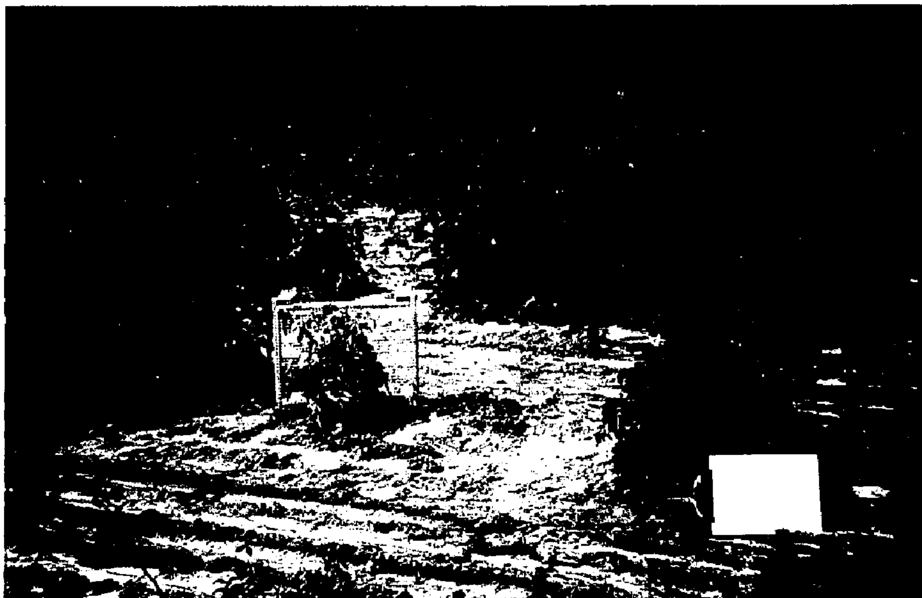


Figure 4. A comparative view of two aneuploid tomato plants of F_1 in the field. Sister diploid plants are seen in the back row as well as on the left end of the front row. Plant No. 1595-55 is a nonwoolly polysomic and the one to its left is a nonwoolly trisomic. The meshwork on the screen board behind the trisomic plant measures 43x29 cm. The meshes are 1 cm square. This screen board also appears in Figures 5-8 inclusive.

Plate IV

Figure 5. Close-up of nonwoolly trisomic plant No. 1595-54 in Figure 4.

Figure 6. Close-up of nonwoolly polysomic plant No. 1595-55 (with 9-10 extra chromosomes) in Figure 4.

Plate V

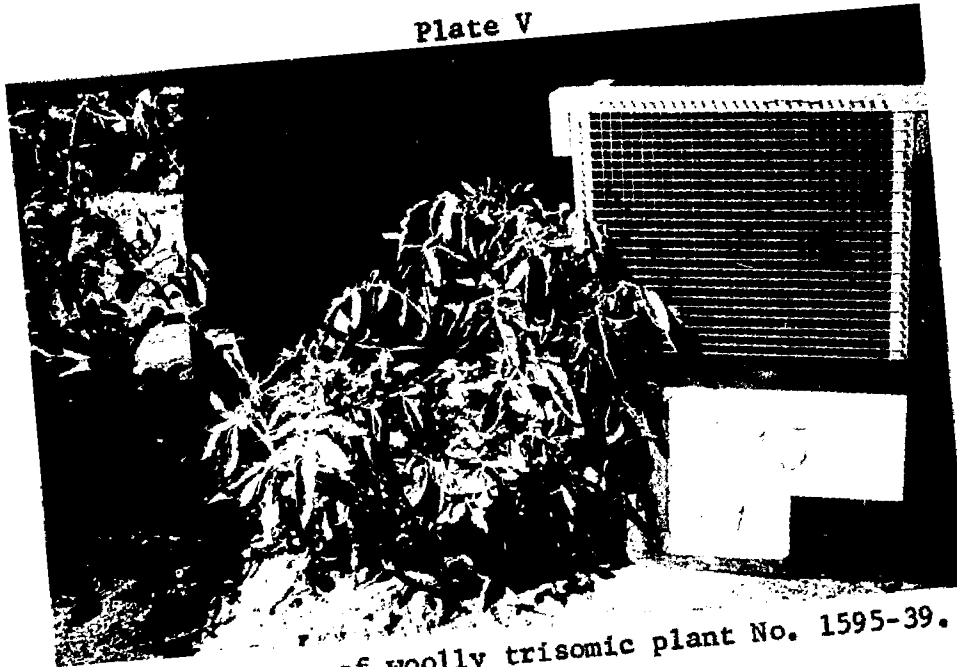


Figure 7. Close-up of woolly trisomic plant No. 1595-39.

Figure 8. Close-up of woolly trisomic plant No. 1595-40.

Cytology of Trisomics

Although the aceto-carmine smears of PMC were made for the primary purpose of chromosome count at diakinesis or metaphase I, it was possible to study other meiotic phases as well. Presence of other phases in many cases greatly helped to confirm or substantiate interpretations based on the study of diakinesis or metaphase I alone. The study of chromosome morphology at pachytene was not pursued, although it would have been highly desirable to determine which extra chromosome was responsible for the structural variation or fertility differences observed among the trisomics. It was not possible to ascertain the exact kind of a trisomic from a given trivalent configuration at such a highly contracted stage of the chromosomes as in diakinesis or metaphase I. Classification of trisomics with respect to nucleolar or non-nucleolar chromosome was, however, possible, although this identification was not feasible when the extra chromosome appeared in the form of a univalent. The cytological behavior of the extra chromosome was carefully studied. Occasionally three univalents, most probably homologues, were also seen.

Prophase I

Behavior of the extra chromosome in the trisomics was similar to that of the trisomics obtained by Lesley (24) from triploid and diploid parents. The smear preparations of PMC were not clear enough to permit critical study of early prophase stages. A lone

univalent and 12 bivalents, and one trivalent with 11 bivalents as seen in Plate VII, Figures 13 and 14, were more common formations in late diplotene or early diakinesis. Occurrence of 12 bivalents and a lone univalent was, however, by far the more frequent. In rare instances the univalent was precocious in division. Such precociously divided chromatids were less darkly stained and were smaller in size than the neighboring bivalents. Presence of more than one univalent, usually three, was interpreted as simultaneous disjunction of the members of the same trivalent. Because of fewer chiasmata per chromosome in a trivalent the falling apart of members of a trivalent under stress of diplotene repulsion is but natural. This sort of asynapsis in PMC of some trisomics was therefore considered to be due to mechanical interference in synapsis caused by the extra chromosome during competition among the homologues or due to smear pressure acting more effectively on such partially synapsed chromosomes. Occurrence of this sort of synapsis was sporadic and not a consistent feature of all other adjoining cells. Whether there was any specificity of the pattern of the presence of a trivalent, lone univalent or three univalents in different trisomics could not be ascertained on account of paucity of cells of the proper stage. Such specificity in the behavior of the extra chromosome is to be expected due to different chromosomes being involved in the make-up of various trisomics. For example it is reasonable to expect more trivalent configurations until late diakinesis or metaphase I if the longer chromosomes are involved so there is greater contact length

available for each of the three homologues. Contrariwise, univalents should fall apart often early in diplotene when short chromosomes are involved in a trisome.

Metaphase I

The metaphasic orientation of chromosomes on the equatorial plate was scarcely disturbed in the trisomics. Presence of an extra chromosome as a univalent as seen in Plate VII, Figure 15, or as a member of a trivalent as shown in Plate VII, Figure 16, was easily detectable in this stage. Univalents were found in one or two characteristic positions. Either they were on the equatorial plate or between equator and pole as pictured in Plate VII, Figures 15 and 16. In the latter position there is greater possibility of the chromosome being included in the resulting dyad at the end of the first division. Consequently two of the tetrad of spores would have n+1 chromosomes. In the former case the univalent, more often, would be a laggard in the first meiotic division and eventually end as a micro-nucleus which may or may not be included in one of the spores of the final tetrad. Split chromatids usually stay close for lack of a spindle organization with respect to the laggard. This affords a greater chance of production of normal gametes. This might perhaps be the reason why certain trisomics are more fruitful than others, although the nature of genes carried by the extra chromosome may also cause differences in fruitfulness. Whether or not the positioning of the extra chromosome is a matter of mere chance or is an established condition in a given trisomic

was left out of the scope of the present investigation. However, this aspect of correlation between positioning of the extra chromosome and the fertility of a trisomic poses an interesting study.

Anaphase I

The greatest interest in anaphase I also centered around the behavior of the extra chromosome. It was seen that the extra chromosome did not disturb the spindle organization. The movement of the chromosome complement to the respective poles was normal. The thirteen and twelve chromosome distribution in anaphase I was the most common. Where the extra chromosome was left out of the polebound chromosome complement and stayed in the middle of the spindle as a laggard, 12 and 12 chromosome distribution was the result as pictured in Plate VIII, Figure 17. Infrequently the extra chromosome was precociously divided in such a manner that each pole received one chromatid as seen in the Plate VIII, Figure 18, and therefore 12 chromosomes and one chromatid (monad) were present in each pole. The chromtid was easily recognizable being small and less darkly stained.

Second Meiotic Division

No critical study of the second division was pursued. However, full use was made of any opportunity that came forth. No striking irregularity was observed in this division. In fact the regularity with which this division was apparently proceeding in PMC of trisomics helped to confirm the identification of certain plants with respect

to their genomic make-up, especially in such cases where the smear preparations of early phases were either not clear or unavailable. The chromatids of the lagging chromosome were often seen in certain cells as micronuclei beside the tetrads as seen in Plate VIII, Figure 19.

Occasionally syncytes with as many as four nuclei were seen in early propase of some trisomics. Binucleate cells were, however, more common. The two nuclei were never seen in the same stage of meiosis. Such cells were not observed after diakinesis. Most probably the two nuclei separated or the cell as a whole degenerated. Presence of syncytes was observed by Beadle (2) in asynaptic Zea, by Johnsson (21) in asynaptic *Alopecurus myosuroides*, and by Ramanujam and Parthasarathy (34) in asynaptic rice. They are supposed to arise by failure of cytokinesis in pre-meiotic divisions.

EXPLANATION OF PLATE VI

Figure 9. Diakinesis in PMC of normal diploid tomato showing 12 bivalents. 1440 X.

Figure 10. Metaphase I in normal diploid. All twelve bivalents are oriented at the equatorial plate. 1440 X.

Figure 11. Prophase II in PMC from normal diploid. 1440 X.

Figure 12. Telophase II in PMC from normal diploid. 1440 X.

EXPLANATION OF PLATE VII

Figure 13. Diakinesis in PMC of a trisomic showing 12 bivalents and one univalent. Arrow indicates the univalent. 1440 X.

Figure 14. Prometaphase in PMC of a trisomic showing a trivalent and 11 bivalents. Arrow indicates the trivalent. 1440 X.

Figure 15. Metaphase I in PMC of trisomic. The extra chromosome is seen on the way to the pole while the remaining 12 bivalents are still on the equator. A dark speck on the edge is of a dust particle and not chromatin material. 1440 X.

Figure 16. Metaphase I in PMC of trisomic. One trivalent and 11 bivalents are seen on the equator. The bivalent on the extreme right is heteromorphic. 1440 X.

EXPLANATION OF PLATE VIII

Figure 17. Anaphase I in PMC from trisomic. Note 12 dyads in each pole and a laggard in the middle of the nucleus. The dark speck mn the edge is a dust particle. 1440 X.

Figure 18. Prophase II in PMC from trisomic showing 12 dyads and a monad in each pole. Arrows indicate the monads. 720 X.

Figure 19. Telophase II in PMC from trisomic showing the equationally divided laggard resulting in 2 micro-nuclei seen on the edge of the cell. 776 X.

EXPLANATION OF PLATE IX

Figure 20. Diakinesis in PMC of a polysomic. At least 33 chromosomes can be counted in the field. 1440 X.

Figure 21. Diakinesis in another PMC of a polysomic. At least 33 chromosomes can be counted in the field. 1440 X.

Figure 22. Metaphase I in PMC of polysomic. At least 33 chromosomes can be counted. 1440 X.

Figure 23. Anaphase I in PMC of polysomic. At least 33 chromosomes, 20 in one pole and 13 in the other, can be counted. 1440 X.

EXPLANATION OF PLATE X

Figure 24. Metaphase I in PMC of asynaptic Marglobe showing 8 bivalents and 8 univalents. 1440 X.

Figure 25. Metaphase I in PMC from F_2 asynaptic diploid showing 6 bivalents and 12 univalents. 1440 X.

Figure 26. Metaphase II in PMC from asynaptic F_2 diploid showing 3 laggards. 1440 X.

Figure 27. Early telophase II with 11-11 in the right spindle and 12-12 in the left spindle, in PMC from asynaptic diploid showing chromatids of a laggard which divided equationally at anaphase I. 1440 X.

Plate VI

Figure 9

Figure 10

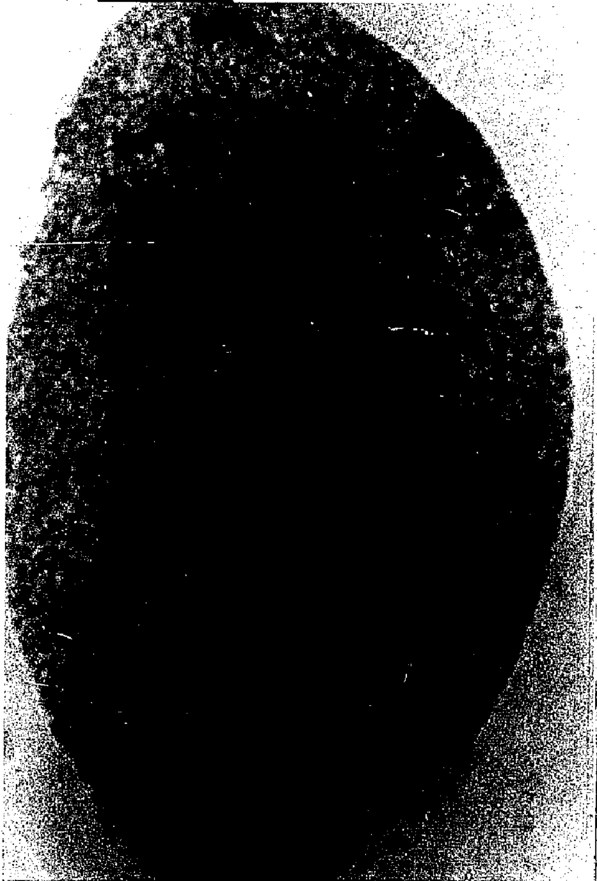


Figure 11

Figure 12

Plate VII

Figure 13

Figure 14

Figure 15

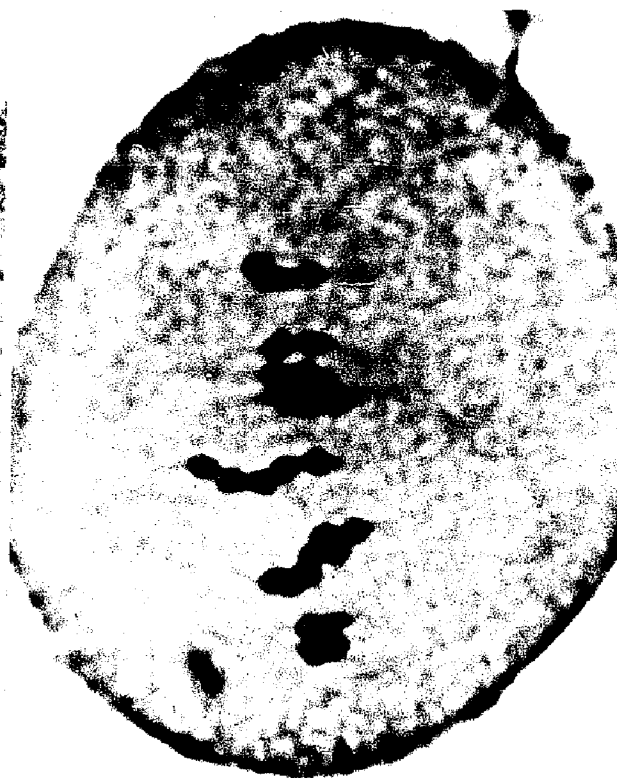


Figure 16

Plate VIII

Figure 17

Figure 18

Figure 19

Plate IX

Figure 20

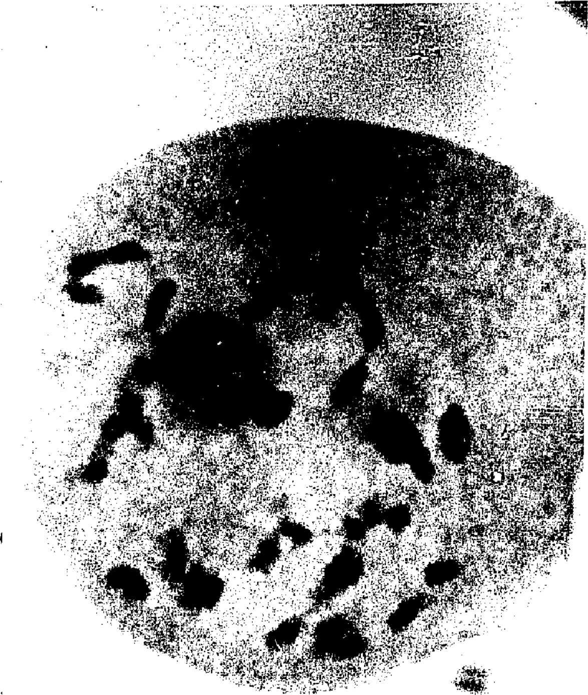


Figure 21

Figure 22

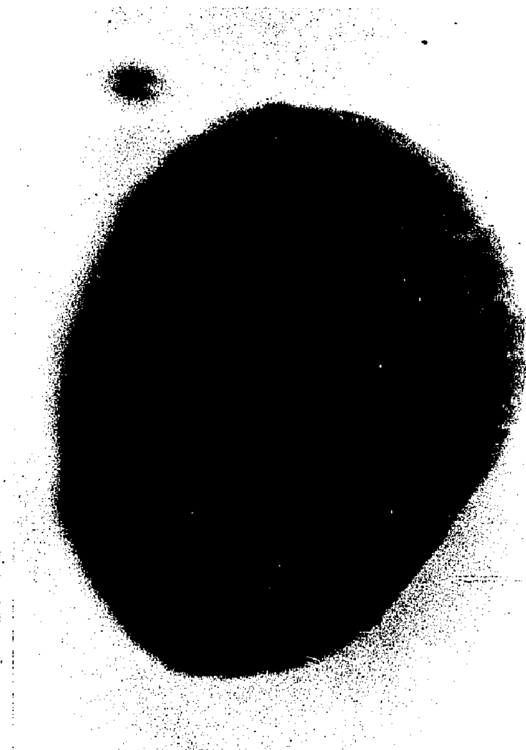


Figure 23

Plate X

Figure 24

Figure 25

Figure 26

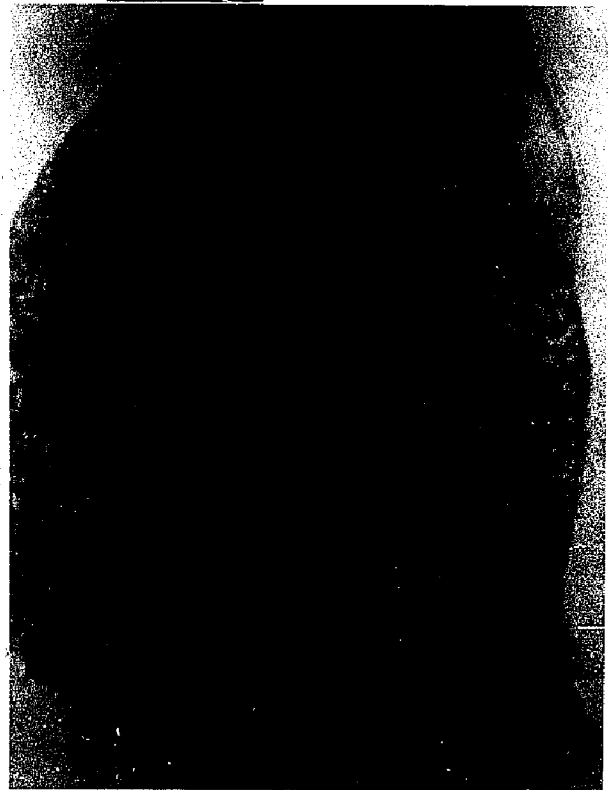


Figure 27

F_2 Generation

Normal F_1 diploid plants of the two crosses were allowed to self-pollinate during the spring of 1958. Each F_2 progeny came from the seeds of a single fruit. The F_2 generation of the woolly cross was obtained from a selfed woolly F_1 diploid plant. Aceto-carmine smears of PMC of all the plants of the F_2 progeny involving woolly (No.581603) and of selected plants of the F_2 progeny involving Walter-15 (No. 581604) were made and examined for asynapsis. Scoring of PMC for asynapsis was done primarily at metaphase I. Later experience, however, showed that mid or late diakinesis stages were equally informative and reliable. Asynapsis wherever detected in the smears was found to be present in both metaphase and diakinesis. So there could hardly be any mistake in distinguishing genuine asynapsis from early anaphasic separation of bivalents. It was therefore supposed that disjunction of bivalents was occurring sometime in early diakinesis or prior to that. The exact stage of occurrence of asynapsis was not determined. Presence of 12 bivalents in late diakinesis was considered normal synapsis. It is quite conceivable that breaking loose of bivalents at such a late stage of prophase I, when spindle formation is almost complete can hardly bring about any erratic distribution of the chromosomes in the ensuing anaphase.

The intensity of asynapsis was found to be variable in various PMC of the same preparation. The intensity ranged from one pair to as many as four pairs. In the same preparation, cells with the normal number of 12 bivalents were also seen.

No macroscopic morphological differences were discernible between normal and asynaptic plants, neither did unfruitfulness offer any clue to identification of the asynaptic plants. Many of the plants that were unfruitful did not necessarily have asynapsis in their PMC. On the contrary quite a few plants that did bear some fruit were found to be asynaptic. Generally asynapsis was of mild intensity in both crosses. In the woolly cross, asynapsis was noted only among the woolly plants.

A comparable F_2 progeny (No. 581607) was grown in the University Vegetable greenhouse during the 1958-59 winter. It yielded results similar to those of field-grown progeny. Frequency of asynaptic plants was of the same magnitude and again only the woolly plants had asynapsis. Of the 157 plants in the two progenies only 6 were asynaptic. Of these 6 only 3 were completely unfruitful.

The cross involving Walter-15 (No. 581604) was not so thoroughly checked for asynapsis. In this case the cytological examination of PMC for asynapsis was confined to the less fruitful plants. Only a few fully fruitful plants were examined. The entire progeny of 116 plants had only one completely unfruitful plant. Six plants including the one unfruitful plant were observed to have a mild type of asynapsis. The maximum number of affected chromosome pairs was three. In most cases asynapsis was confined to one pair only. The data are given in Table 4.

Segregation data from field grown F_2 plants relative to the marker genes were obtained. Since fruits did not ripen before frost, no data could be obtained for flesh color or skin color. The data are presented in Table 3.

TABLE 3

Monohybrid segregation data in F_2 from asynaptic Marglobe X Woolly (No. 581603)

Genotype	Exp seg. ratio	No. of plants Obs.	Exp.		X^2	df	P
$Wo\overset{+}{wo}$		49	47				
$\overset{+}{wo}\overset{+}{wo}$	2:1	22	24		0.25	1	0.63
Total		71	71				
$\overset{+}{c}$ -		50	53				
cc	3:1	21	18		0.67	1	0.43
Total		71	71				
$\overset{+}{j}$ -		71	53				
jj	3:1	0	18		24.11**	1	0.005
Total		71	71				
$\overset{+}{u}$ -		43	49				
uu	3:1	22	16		2.98	1	0.09
Total		65	65				
				or			
$\overset{+}{as}$ -	3:1	68	53	66.5			
asas	or	3	18	4.5	16.74**	1	0.01
Total	15:1 (for	71	71		or		or
	2 genes)				0.53		0.48

** Significant at 1% level.

The data show normal segregation for *Wo*, *c*, and *u* but very devious behavior in respect of *j*. There was total elimination of *jj* homozygotes in the progeny. In order to verify this unique segregation of *j* two more progenies No. 581606 and No. 581607 of the same cross were grown in the University Vegetable greenhouse during the 1958-59 winter. The consolidated data of all the progenies are given in Table 5.

TABLE 4

Monohybrid segregation data in F_2 from asynaptic Marglobe X Walter-15 Progeny No. 581604

Genotype	Expected ratio	Observed number	Expected number	X^2	df	P
as^+ -		110	87 109			
	3:1 or 15:1		or	24.32**		
as as	(for 2 genes)	6	29 7.2	or	1	.01 or
				0.24		0.65
Total		116	116			

**Significant at 1% level.

The monohybrid segregation data for asynapsis in Walter cross also show highly significant deficiency of asynaptic plants, but closely fit the two-gene segregation ratio.

TABLE 5

Pooled monohybrid segregation data in F_2 from asynaptic Marglobe X Woolly: Progenies No. 58-1603, -1606, -1607.

Genotype	Expected ratio	Observed number	Expected number	X	df	P	Heterogeneity	df	P
$Wo\,wo^{+}$	2:1	147	154						
$wo^{+}wo^{+}$		84	77	0.95	1	0.36	1.68	2	0.45
Total		231	231						
c^{+}-	3:1	172	173						
cc		59	58	0.02	1	0.90	1.83	2	0.42
Total		231	231						
j^{+}-	3:1	227	173						
jj		4	58	66.80**	1	0.01	0.27	2	0.88
Total		231	231						
u^{+}-		148	158						
uu	3:1	63	53	2.52	1	0.12	1.17	2	0.56
Total		211	211						
t^{+}-		123	120						
tt	3:1	37	40	0.25	1	0.64	0.26	1	0.64
Total		160	160						
bk^{+}--		103	106.5						
bkbk	3:1	39	35.5	0.45	1	0.50	0.01	1	0.99
Total		142	142						
y^{+}-		86	88.5						
yy	3:1	32	29.5	0.28	1	0.62	0.01	1	0.99
Total		118	118						
as^{+}--	3:1	151	117.8	37.63**		0.01	0.33		0.59
asas	or	6	39.2	or	1	or	or	1	or
Total	15:1 (for 2 genes)	157	157	1.56		0.23	0.10		0.75

**Significant at 1% level.

It is evident from the Table 5 that only 4 jj individuals were recovered in the latter grown two progenies No. 581606 and No. 581607 comprised of 160 plants. Thus an extremely low recovery of jj plants (4/231=1.7%) was indicative of some sort of genetic interference with j gene in this particular cross.

Like j gene a low recovery of asas individuals did not fit the hypothetical monohybrid ratio; instead gave a good fit to 15:1 dihybrid ratio.

All the other genes closely fitted the expected monogenic segregation ratio.

A low heterogenity chi square in each instance indicated that all progenies behaved alike in regard to segregation of the marker genes as well as the as gene.

In order to test for linkage between any of the two genes involved in the cross, dihybrid segregation data were computed and tested in all possible combinations. These data are presented in Tables 6, 7, 8, 9, 10, 11 and 12.

Linkage intensities (recombination values) for normal segregation ratios in respect of both coupling and repulsion phases were calculated according to the formulas and tables outlined by Immer (20). For aberrant ratio in case of Wo gene the recombination values were calculated according to Allard's (1) formula 18.

TABLE 6

Dihybrid segregation data of F_2 progenies in relation to Wo gene

Genes involved with Wo		F2 classes				Total	X^2	df	P	% recombination
		WoX*	Wox	$\overset{+}{wo}$X	$\overset{+}{wo}$x					
1. c	Obs.	103	43	69	16	231	4.39	3	0.23	41.7
	Exp. (6:2:3:1)	115	38.6	58	19.3					
2. i	Obs.	167	2	60	2	231				
	Exp. (6:2:3:1)	115	38.6	58	19.3		79.81**	3	0.01	60.0+
3. u	Obs.	93	38	55	25	211	4.92	3	0.19	51.5
	Exp. (6:2:3:1)	105.6	35.2	52.8	17.6					
4. t	Obs.	76	21	47	16	160	3.06	3	0.40	42.9
	Exp. (6:2:3:1)	79	26.6	40	13.3					
5. bk	Obs.	62	22	41	17	142	4.13	3	0.25	52.2
	Exp. (6:2:3:1)	70.4	23.8	35.7	11.9					
6. y	Obs.	56	21	30	11	118	0.40	3	0.95	49.7
	Exp. (6:2:3:1)	59	19.6	29.5	9.8					
7. as	Obs.	98	6	53	0	157	35.98**	3	0.01	-
	Exp. (6:2:3:1)	118	26	40	13					

*X represents dominant allele of the gene(s) in the left-hand column and x the recessive allele.

** Significant at 1% level.

TABLE 7

Dihybrid segregation data of F_2 progenies in relation to *c* gene

Genes involved with c		F_2 classes				Total	X^2	df	P	% recombination
		$\overset{+}{c}X$	$\overset{+}{c}x$	cX	cx					
1. *j*	Obs.	161	3	66						
	Exp.	129.6	43.2	43.2	14.4	231	69.52**	3	0.01	47.1
	(9:3:3:1)									
2. *u*	Obs.	113	44	38	16					
	Exp.	118.8	39.6	39.6	13.2	211	1.42	3	0.50	51.1
	(9:3:3:1)									
3. *t*	Obs.	96	26	27	11					
	Exp.	90	30	30	10	160	1.33	3	0.50	55.7
	(9:3:3:1)									
4. *bk*	Obs.	81	28	22	11	142	1.36	3	0.50	55.2
	Exp.	80	26.6	26.6	8.9					
	(9:3:3:1)									
5. *y*	Obs.	65	24	21	8					
	Exp.	66.2	22.2	22.2	7.4	118	0.28	3	0.91	50.4
	(9:3:3:1)									
6. *as*	Obs.	108	5	43	1					
	Exp.	88.2	29.4	29.4	9.8	157	38.88**	3	0.01	40.5
	(9:3:3:1)									

** Significant at 1% level.

TABLE 8

Dihybrid segregation data of F_2 progenies in relation to u gene

Genes involved with u		F_2 classes $\overset{+}{u}X$	$\overset{+}{u}x$	uX	ux	Total	X^2	df	P	% re-combi-nation
1. j	Obs.	148	59	3	1	211	61.77**	3	0.01	47.5
	Exp. (9:3:3:1)	118.8	39.6	39.6	13.2					
2. t	Obs.	87	21	25	13	146	3.67	3	0.32	60.0+
	Exp. (9:3:3:1)	82	27.4	27.4	9.1					
3. bk	Obs.	74	28	29	11	142	1.24	3	0.75	50.0
	Exp. (9:3:3:1)	80	26.6	26.6	8.9					
4. y	Obs	63	29	23	13	118	5.45	3	0.16	52.9
	Exp. (9:3:3:1)	66.2	22.2	22.2	7.4					
5. as	Obs.	94	3	40	1	138	38.14**	3	0.01	46.6
	Exp. (9:3:3:1)	77.4	26	26	8.6					

**Significant at 1% level.

TABLE 9

Dihybrid segregation data of F_2 progenies in relation to <u>t</u> gene

Genes involved with <u>t</u>		F_2 classes				Total	X^2	df	P	% recombination
		$\overset{+}{t}X$	$\overset{+}{t}x$	tX	tx					
1. <u>j</u> (9:3:3:1)	Obs.	119	37	4	0	160	43.50**	3	0.01	--
	Exp.	90	30	30	10					
2. <u>bk</u> (9:3:3:1)	Obs.	79	29	24	10	142	0.62	3	0.89	51.8
	Exp.	80	26.6	26.6	8.9					
3. <u>y</u> (9:3:3:1)	Obs.	65	27	21	5	118	1.90	3	0.60	42.3
	Exp.	66.2	22.2	22.6	7.4					
4. <u>as</u> (9:3:3:1)	Obs.	62	3	21	0	86	21.14**	3	0.01	--
	Exp.	48.6	16	16	5.4					

** Significant at 1% level.

TABLE 10

Dihybrid segregation data of F_2 progenies in relation to bk gene

Genes involved with bk		F_2 classes bkX (+)	bkx (+)	bkX	bkx	Total	X^2	df	P	% recombination
1. j	Obs.	99	39	4	0	142	38.39**	3	0.01	--
	Exp. (9:3:3:1)	80	26.6	26.6	8.9					
2. y	Obs.	57	21	29	11	118	5.16	3	0.17	50.4
	Exp. (9:3:3:1)	66.2	22.2	22.2	7.4					
3. as	Obs.	52	0	18	1	71	21.16**	3	0.01	--
	Exp. (9:3:3:1)	40.5	13.5	13.5	4.5					

** Significant at 1% level.

TABLE 11

Dihybrid segregation data of F_2 progenies in relation to y gene

Genes involved with y		F_2 classes $\overset{+}{y}X$	$\overset{+}{y}x$	yX	yx	Total	X^2	df	P	% recombination
1. j	Obs.	83	31	3	1	118	39.10**	3	.01	51.6
	Exp. (9:3:3:1)	66.2	22.2	22.2	7.4					
2. as	Obs.	42	0	15	1	58	17.14**	3	.01	--
	Exp. (9:3:3:1)	32.4	10.8	10.8	3.6					

** Significant at 1% level.

TABLE 12

Dihybrid segregation data of F_2 progenies in relation to j gene

Genes involved with j		F_2 classes $\overset{+}{j}X$	$\overset{+}{j}x$	jX	jx	Total	X^2	df	P	% recombination
1. as	Obs.	145	6	6	0	157	83.82**	3	.01	--
	Exp. (9:3:3:1)	88.2	29.5	29.5	9.8					

** Significant at 1% level.

The dihybrid segregation data reported in the foregoing tables indicate that the marker genes involved in the cross segregated independently of one another despite reported linkage between some of them. For example, Wo and bk genes belong to linkage group I and are reported only 13 map units apart (46); similarly u and t have common linkage group VII located 59 map units apart (46).

Backcross Generation

An extremely low recovery of jj individuals in F_2 called for further investigation in respect to the discrepant behavior of the j gene. Reciprocal backcross progenies of the cross between Marglobe and woolly were therefore studied. Three of the backcross progenies hereafter referred to as No. 581608, 581609, and 581610 were derived from the cross of F_1 nonwoolly as maternal parent and the inbred woolly as the pollen parent. Three reciprocal backcross progenies, hereafter referred to as No. 581611, 581612, and 581613 originated from the cross between a nonwoolly member of the inbred woolly strain used as material parent and a woolly F_1 plant as pollen parent. These six backcross progenies were grown in the University Vegetable greenhouse, Columbus, during the winter of 1958-59. Tables 13 and 14 respectively contain the monohybrid segregation data.

TABLE 13

Pooled monohybrid segregation data of backcross progenies No. 58-1608, 58-1609 and 58-1610

♀ F_I x ♂ P

Genotype	Expected segregation ratio	Observed number	Expected number	X^2	df	P	Heterogeneity X^2	df	P
Wowo$^+$ wo$^+$wo$^+$	1:1	94 94 188	94 94 188	0	1	1.00	0.45	2	0.80
c$^+$- cc	1:1	106 82 188	94 94 188	3.06	1	0.08	1.49	2	0.48
j$^+$- jj	1:1	99 89 188	94 94 188	0.53	1	0.48	2.78	2	0.25
u$^+$- uu	1:1	84 85 169	84.5 84.5 169	0	1	70.99	0.47	2	0.79
bk$^+$-- bkbk	1:1	82 80 162	84.5 84.5 169	0.026	1	70.99	1.33	2	0.52
t$^+$- tt	1:1	89 87 176	88 88 176	0.02	1	0.90	5.44	2	0.07
y$^+$- yy	1:1	103 66 169	84.5 84.5 169	8.10**	1	0.01	0.78	2	0.69

** Significant at 1% level.

TABLE 14

Pooled monohybrid segregation data of backcross progenies
No. 58-1611, 58-1612, and 58-1613
♀ P X ♂ F_1

Genotype	Expected segregation ratio	Observed number	Expected number	X^2	df	P	Heterogeneity X^2	df	P
$Wo\,wb^{+}$ $wb^{+}wb^{+}$	1:1	87 109 196	98 98 196	2.47	1	0.13	1.22	2	0.56
c^{+}- cc	1:1	109 87 196	98 98 196	2.47	1	0.13	1.22	2	0.56
j^{+}- jj	1:1	181 14 195	97.5 97.5 195	143.02**	1	0.01	0.16	2	0.93
u^{+}- uu	1:1	83 95 178	89 89 178	0.81	1	0.40	0.71	2	0.80
bk^{+}-- bkbk	1:1	91 87 178	89 89 178	0.08	1	0.72	2.83	2	0.45
t^{+}- tt	1:1	92 92 184	92 92 184	0	1	1.00	2.03	2	0.38
y^{+}- yy	1:1	105 82 187	93.5 93.5 187	2.83	1	0.25	5.03	2	0.08

** Significant at 1% level.

Perusal of Tables 13 and 14 reveals that while there was normal segregation of all other marker genes in both categories of backcrosses, the _j_ behaved differently in each case. There was normal segregation of the _j_ in the backcross where the parent plant was used as pollen parent and F_1 plant as the maternal parent. In the reciprocal cross the data simulated the pattern of F_2 segregation in respect to this gene; that is, there was very low recovery of _jj_ individuals. This anomalous behavior of the _j_ is dealt with in the "Discussion."

The monohybrid segregation data pooled from all six backcross progenies with respect to the marker genes other than _j_ are presented in Table 15.

The combined backcross data disclosed an unexpected deficiency of _cc_ and _yy_ plants. The F_2 data for these genes showed normal assortment. Perusal of individual progenies indicates that except in one or two cases the deviations are not significant. The deficiency of _cc_ plants has especially been striking in one progeny (No. 581608). If this single progeny is ignored as a chance deviation, the overall deficiency becomes statistically non-significant. The pooled data, thus, merely reflects the cumulative deficiency as a significant deficiency. Gametes carrying recessive genes are generally believed to be lacking in strength and power of survival in the face of competition with those carrying the dominant alleles. Such an explanation does not seem to be convincing when deficiency exists for some and not for other recessive genes unless, of course, further presumption is made that a "differential

TABLE 15

Monohybrid segregation data of all six backcross progenies (No. 581608-581613)

Genotype	Expected segregation ratio	Observed number	Expected number	X^2	df	P	Heterogeneity X^2	df	P
$Wowo^{+}$	1:1	181	192	1.26	1	0.27	2.88	5	0.72
$wo^{+}wo^{+}$		203	192						
		384	384						
c^{+}-	1:1	215	192	5.51*	1	0.02	2.73	5	0.74
cc		169	192						
		384	384						
u^{+}-	1:1	167	173.5	0.49	1	0.49	1.33	5	0.83
uu		180	173.5						
		347	347						
bk^{+}--	1:1	175	173.5	0.02	1	0.90	3.10	5	0.68
bkbk		172	173.5						
		347	347						
t^{+}-	1:1	181	180	0.01	1	0.90	7.98	5	0.18
tt		179	180						
		360	360						
Y^{+}-	1:1	208	178	10.11**	1	0.01	6.73	5	0.26
yy		148	178						
		356	356						

*Significant at 5% level.
**Significant at 1% level.

of strength and power" exists for the various recessive alleles. In order to authenicate such a postulation large size of the population becomes necessary.

Other genes, namely, Wo, u, t, and bk seem to assort normally as in the F_2 generation.

As with the F_2 data, backcross data have been subjected to tests for linkage between the various genes. In order to investigate such relationships with respect to j gene data from only those progenies in which j gave normal monohybrid segregation are used. These data are presented in Tables 16, 17, 18, 19, 20 and 21.

Except for deviation in respect to yy individuals and cc individuals which showed deficiency in the nonwoolly category of plants, the backcross segregation of other marker genes almost simulated the F_2 segregation pattern. The peculiar behavior of j gene is dealt with in detail in the Discussion.

TABLE 16

Dihybrid segregation data from backcrosses in relation to Wo gene

Genes involved with Wo	Backcross classes WoX	Wox	$\overset{+}{wo}X$	$\overset{+}{wo}x$	Total	X^2	df	P	% recombination
Obs.	92	89	121	81	383				
1. c Exp.	95.8	95.8	95.8	95.8		9.54*	3	0.02	44.8
(I:I:I:I)									
Obs.									
2. j Exp.	47	47	52	42	188				
(1:1:1:1)	47	47	47	47		1.06	3	0.79	48.2
obs.	77	75	77	87	316				
3. u Exp.	79	79	79	79		1.11	3	0.73	52.1
(1:1:1:1)									
Obs.	70	81	86	79	316	1.69	3	0.65	47.2
4. bkExp.	79	79	79	79					
(1:1:1:1)									
Obs.	75	80	88	82	325	1.06	3	0.79	48.1
5. t Exp.	81.3	81.3	81.3	81.3					
(1:1:1:1)									
Obs.	79	72	90	74	315				
6. y Exp.						2.47	3	0.49	48.6
(1:1:1:1)	78.8	78.8	78.8	78.8					

*Significant at 5% level.

TABLE 17

Dihybrid segregation data from backcrosses in relation to *c* gene.

Genes involved with *c*	Backcross classes				Total	X^2	df	P	% recombination
	$c^{+}X$	$c^{+}x$	cX	cx					
Obs.	58	49	41	40	188	4.46	3	0.23	48.0
1. *j* Exp.	47	47	47	47					
(1:1:1:1)									
Obs.	87	88	65	70	310	5.33	3	0.16	49.1
2. *u* Exp.	77.5	77.5	77.5	77.5					
(1:1:1:1)									
Obs.	89	86	67	74	316	4.02	3	0.26	48.1
3. *bk* Exp.	79	79	79	79					
(1:1:1:1)									
Obs.	97	79	68	81	325	5.27	3	0.17	44.7
4. *t* Exp.	81.3	81.3	81.3	81.3					
(1:1:1:1)									
Obs.	103	73	79	60	315	12.34**	3	0.01	49.0
5. *y* Exp.	78.8	78.8	78.8	78.8					
(1:1:1:1)									

** Significant at 1% level.

TABLE 18

Dihybrid segregation data from backcrosses in relation to *j* gene

Genes involved with *j*		Backcross Classes				Total	X^2	df	P	% recombination
		$\overset{+}{j}X$	$\overset{+}{j}x$	jX	jx					
1. *u*	Obs.	42	46	42	39	169	0.58	3	0.99	52.3
	Exp. (1:1:1:1)	42.3	42.3	42.3						
2. *bk*	Obs.	38	48	46	37	169	2.19	3	0.54	56.3
	Exp. (1:1:1:1)	42.3	42.3	42.3	42.3					
3. *t*	Obs.	41	51	48	36	176	3.13	3	0.39	57.3
	Exp. (1:1:1:1)	44	44	44	44					
4. *y*	Obs.	59	32	48	34	169	10.48*	3	0.04	45.1
	Exp. (1:1:1:1)	42.3	42.3	42.3	42.3					

*Significant at 5% level.

TABLE 19

Dihybrid segregation data from backcrosses in relation to u gene

Genes involved with u		Backcross classes $\overset{+}{u}X$	$\overset{+}{u}x$	uX	ux	Total	X^2	df	P	% recombina-
1. bk	Obs.	79	75	77	85	316	0.71	3	0.95	48.4
	Exp. (1:1:1:1)	79	79	79	79					
2. t	Obs.	92	62	75	82	311	6.12	3	0.11	43.3
	Exp. (1:1:1:1)	77.8	77.8	77.8	77.8					
3. y	Obs.	88	67	94	66	315	7.85*	3	0.05	51.1
	Exp. (1:1:1:1)	78.8	78.8	78.8	78.8					

* Significant at 5% level.

TABLE 20

Dihybrid segregation data from backcrosses in relation to bk gene

Genes involved with bk		Backcross classes				Total	X^2	df	P	% recombination
		$\overset{+}{b}\overset{+}{k}X$	$\overset{+}{b}\overset{+}{k}x$	bkX	bkx					
1. t	Obs.	87	75	69	85	316	2.73	3	0.45	45.0
	Exp. (1:1:1:1)	79	79	79	79					
2. y	Obs.	93	62	89	71	315	7.88*	3	0.05	47.5
	Exp. (1:1:1;1)	78.8	78.8	78.8	78.8					

*Significant at 5% level.

TABLE 21

Dihybrid segregation data from backcrosses in relation to t gene

Gene involved with t		Backcross classes				Total	X^2	df	P	% recombination
		$\overset{+}{t}X$	$\overset{+}{t}x$	tX	tx					
1. y	Obs.	89	73	93	60	315	8.79*	3	0.03	53.4
	Exp. (1:1:1:1)	78.8	78.8	78.8	78.8					

* Significant at 5% level.

TABLE 22

Recombination values of the genes involved in the present study, as calculated from F_2 data

	Wo	bk	c	j	u	t	as
Wo	-	-	-	-	-	-	-
bk	52.2	-					
c	41.7	55.2	-		-		-
j	60.0+	x	47.1	-			-
u	51.5	50.0	51.1	47.5	-		
t	52.9	51.8	55.7	x	60.0+	-	-
as	x	x	40.5	x	46.6	x	
y	49.7	50.4	50.4	45.1	52.9	42.3	x

[box] Known to be linked. (Boxed: Wo–bk; u–t)

TABLE 23

Recombination values of the marker genes involved in present study, as calculated from backcross data

	Wo	bk	c	j	u	t
Wo	-	-	-	-	-	-
bk	47.2	-	-	-	-	-
c	44.8	48.1	-	-	-	-
j	48.2	56.3	48.0	-	-	-
u	52.1	48.4	49.1	52.3	-	-
t	48.1	45.0	44.7	57.3	43.3	-
y	48.6	47.5	49.0	45.1	51.1	53.4

[box] known to be linked. (Boxed: Wo–bk; u–t)

F_3 Generation

Two fruits were set on one of the asynaptic plants of F_2 progeny No. 581603. This plant was woolly, potato leaf, jointed pedicel, nonuniform unripe fruit, red flesh color and colored skin of the ripe fruit. One of the fruits was set in the field and the other inside the greenhouse after the plant was moved into the greenhouse. Only 20 seeds were contained in the two fruits combined and produced 10 woolly and 4 nonwoolly seedlings.

Chi-square for this distribution of woolly and nonwoolly plants is only 0.3000 indicating a close fit to the expected 2:1 distribution.

All plants had potato leaf, jointed pedicel, yellow anther color (indicative of red flesh color), indicating that the progeny resulted from selfed F_2 homozygous for the characteristics enumerated above. Only 13 plants survived to give PMC for cytological examination. Of these only three were found to have asynapsis. Intensity of asynapsis in one case was very strong, measured by the low level of pairing in metaphase and diakinesis and the univalents scattered in an elongated spindle. In other cases asynapsis was of mild type, reminiscent of that observed in F_2, affecting one to six pairs of chromosomes. As before all the asynaptic plants were woolly.

F_2 Generation of Trisomics

Three progenies of three open-pollinated trisomics were raised in the Genetics Greenhouse during the winter and spring of 1959. The object of the study was to determine the transmissibility of the extra chromosome and also to identify the trisomics with respect to the linkage group(s) and/or the chromosome(s) with the help of altered genetic ratio of gene(s) in the segregating progeny. Two of the trisomics originated from asynaptic Marglobe crossed with woolly and the third one from the asynaptic Marglobe crossed with Walter-15. For this particular study one woolly and one nonwoolly trisomic of the former cross were selected. The data relative to the transmissibility of the extra chromosome are given in Table 24.

TABLE 24

Transmissibility of extra chromosome in open-pollinated trisomic progenies

Progeny number	Parentage	Number of plants			Total	% transmissibility
		2n	2n+1	Other		
591780	Asy. Marglobe X woolly (woolly)	48	0	0	48	0.00
591781	Asy. Marglobe X Woolly (Nonwoolly)	54	3	0	57	5.26
591782	Asy. Marglobe X Walter-15	39	3	0	42	7.12

As would naturally be expected the recovery of trisomics from an open-pollinated trisomic plant was less than that obtained by using normal pollen on the original Marglobe parent plant which was producing heterosomic megaspores as a result of asynapsis. A greater reduction in fertility usually results when the microspores are also heterosmic because of their poor viability. The transmissibility of the extra chromosome through megaspores also depends, to some extent, on the chromosome itself. This is known in tomato (24) and in Dutura (6). The three extra chromosomes involved in each of the three trisomics under discussion seem to be different since their transmissibility varies from nil to 7.12 per cent of total progeny.

The segregation data relative to the marker genes of the two relevant progenies are presented in Tables 25 and 26.

The trisomic ratios were computed assuming that heterosomic microspores did not survive and that one dose of a dominant gene was dominant over two of the recessive alleles and that the segregation unit was the chromosome rather than the chromatid. It may be noted that the data relative to the fruit characteristics were not complete because of unfruitfulness of several plants. According to the available data for progeny No. 591781, Table 25, three loci, namely, c, j and t fail to fit the disomic ratio. Wo is not being considered for the genetic ratio for the reason given earlier. Loci j and y do not fit the trisomic ratio. In view of the anomalous behavior of j as encountered in F_2 and some backcross progenies, its consideration

TABLE 25

Monohybrid segregation in F_2 progeny No. 591781 of Nonwoolly trisomic

	Number of genotypes													
	$Wowo^+$	wo^+wo^+	c^+-	cc	j^+-	jj	t^+-	tt	u^+-	uu	bk^+-	bkbk	y^+-	yy
1. Diploid														
Obs.	1*	53	48	6	54	0	51	3	22	2	19	5	9	7
Exp. (disomic for all genes, i.e., 2:1 for Wo and 3:1 for others)	36	18	40.5	13.5	40.5	13.5	40.5	13.5	18	6	18	6	12	4
X^2	102.07**		5.55**		18.00**		10.88**		3.56		0.22		3.0	
P_{1df}	.01		0.02		0.01		0.01		0.06		0.66		0.08	
Exp. (simplex trisomic for Wo, i.e., 1:1 and duplex trisomic for others, i.e., 8:1)	27	27	48	6	48	6	48	6	21.3	2.7	21.3	2.7	14.2	1.8
X^2	50.07**		0		6.75**		1.68		0.20		2.20		16.92**	
P_{1df}	.01		1.0		.01		0.21		0.66		0.15		.01	
2. Trisomic														
Obs.	0	3	3	0	3	0	3	0	-		-		-	

Exp. (7.2 for Wo and 9.0 for others)

P_{1df} - not calculated because sample too small to be meaningful.

*Suspected mixture at planting. **Significant at 1%.

TABLE 26

Monohybrid segregation in F_2 progeny No. 591780 of Woolly trisomic

	Number of genotypes													
	$Wo\overset{+}{wo}$	$\overset{+}{wo}\overset{+}{wo}$	$\overset{+}{c}$-	cc	$\overset{+}{i}$-	ii	$\overset{+}{t}$-	tt	$\overset{+}{u}$-	uu	$\overset{+}{bk}$-	bkbk	$\overset{+}{y}$-	yy
1. Diploid														
Obs.	32	16	38	10	46	2	29	11	20	5	20	5	0	14
Exp. (discomic for all genes, i.e., 2:1 for Wo and 3:1 for others)	32	16	36	12	36	12	30	10	18.8	6.2	18.8	6.2	10.5	3.5
X^2	0		0.44		11.08**		0.13		0.30		0.30		4.66**	
P_{1df}	1.0		0.50		0.01		0.73		0.61		0.61		0.03	
Exp. (Simplex trisomic for Wo, i.e., 1:1 and duplex trisomic for other genes, i.e., 8:1)	24	24	42.7	5.3	42.7	5.3	35.6	4.4	22.2	2.8	22.2	2.8	12.3	1.7
X^2	5.16*		4.67**		2.30		11.12**		1.94		1.94		1.93	
P_{1df}	0.03		0.03		0.14		.01		0.18		0.18		0.18	
2. Trisomic														
Obs.	0		0		0		0		0		0		0	
Exp. (Simplex trisomic for Wo, i.e., 7:2 and duplex trisomic for others, i.e., 9.0)														

**Significant at 1%.

is problematic the bk locus fits both disomic and trisomic ratios, but it being linked with Wo which neither fits disomic nor trisomic ratio; involvement of this locus in the trisome is not possible, especially when more complete data are available for Wo and only incomplete for bk. The other three loci fitting the trisomic ratio are c, t, and u. In view of the existing evidence of significant deficiency of cc individuals in backcross data, Table 15, it is difficult to say whether or not the recovery of cc individuals in this progeny is influenced by natural deficiency as experienced in backcross or is the result of trisomic segregation. On the other hand, t and u loci of linkage group VII show similar trisomic segregation. The chi square for disomic segregation of u is large enough to be regarded as similar to t. Since c is located on chromosome No. 6 (46) and t and u on chromosome No. 10, linkage between t and c is out of question. It seems, therefore, more likely that the trisomic under question is triplo for chromosome No. 10 carrying loci of linkage group VII.

In the other progeny No. 591780, Table 26, the disomic ratio fits all other genes except y and j. As stated before the data for y represent only incomplete progeny, yet complete absence of homo- and/ or heterozygous individuals for the dominant allele y^+ is striking. In view of the peculiar segregation behavior of j discussed elsewhere it seems questionable to decide its linkage position on the basis of a trisomic segregation which fits nicely in this case. The two other loci bk and u also fit both disomic and trisomic ratios. These loci are, however, linked with Wo and t respectively for which more

complete data are available, that do not fit the trisomic ratio. Hence their consideration for being triplo for the respective chromosomes can be discounted. However, except for a possible association of y with earliness of ripening which fact has not been clearly established in other allied progenies, the odds seem to be more in favor of this trisomic being triplo for chromosome No. 1 which carries loci of linkage group III.

Consideration is now given to the theoretical effect of the unisexual gametophytic lethal gene x on the recovery of genes linked with it, when on a trisome.

A trisomic obtained from a cross involving the x gene could exist in eight possible ways with respect to the two linked genes. Barring any crossing over between x and the gene of interest, a hypothetical genotype frequency Table 27 has been computed on the bases of both chromosome and chromatid segregation. Other assumptions accompany the table. In order to identify the eight possible ways of the trisomicism, a new nomenclature is proposed. This is explained with the help of the following diagrams. In keeping with the common way of diagramatic representation, the a gene is substituted for x and the linked gene of interest is designated as b, symbolizing their recessive nature.

1. A simplex, B simplex single repulsion:

A____________________b
a____________________B
a____________________b

2. A simplex, B simplex double coupling:

A____________________B
a____________________b
a____________________b

3. A simplex, B duplex single coupling:

A____________________B
a____________________B
a____________________b

4. A simplex, B duplex double repulsion:

A____________________b
a____________________B
a____________________B

5. A duplex, B simplex single coupling:

A____________________B
A____________________b
a____________________b

6. A duplex, B simplex double repulsion:

A____________________b
A____________________b
a____________________B

7. A duplex, B duplex single repulsion:

A____________________B
A____________________b
a____________________B

8. A duplex, B duplex double coupling:

A____________________B
A____________________B
a____________________b

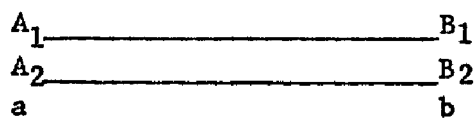
According to this nomenclature the type #8, i.e., A duplex, B duplex, double coupling phase, represents the trisomic, triplo for the chromosome carrying the two genes in the cross under discussion.

Assuming:

1. No crossing over
2. No lagging of chromosomes
3. No restitution of nuclei
4. No chromosomal aberrations
5. No survival of (n+1) microspores and hence no tetrasomic offspring
6. Complete survival of (n+1) megaspores and the resulting trisomic offspring
7. Dominance of single dominant gene over two recessive genes,

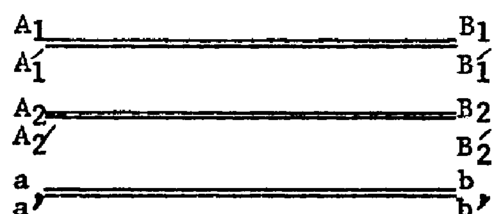
the following kinds and proportions of the gametes would be produced:

Chromosome segregation



(n) Gametes	(n+1) Gametes
(A_1-B_1)	$(A_2a - B_2b)$
$(A_2- B_2)$	$(A_1a - B_1b)$
$(a-b)$	$(A_1A_2- B_1B_2)$

Chromatid segregation



(n) Gametes	(n+1) Gametes
(A_1-B_1) $(A_1'-B_1')$	$(A_2A_2'-B_2B_2')$ $(aa' - bb')$
$(A_1- B_1)$	(A_2a-B_2b)
$(A_1'-B_1')$	$(A_2'a'-B_2'b')$
(A_1-B_1) $(B_1'-B_1')$	$(A_2'a-B_2'b)$ $(A_2a'-B_2b')$
(A_2-B_2) $(A_2'-B_2')$	$(A_1A_1'-B_1B_1')$ $(aa'-bb')$
(A_2-B_2) $(A_2'- B_2')$	(A_1a-B_1b) $(A_1'a' -B_1'b')$
$(A_2- B_2)$ $(A_2'- B_2')$	$(A_1'a -B_1'b)$ $(A_1a' -B_1b')$
$(a - b)$ $(a' - b')$	$(A_1A_1'-B_1B_1')$ $(A_2A_2'-B_2B_2')$
$(a - b)$ $(a' - b')$	$(A_1A_2-B_1B_2)$ $(A_1'A_2'- B_1'B_2')$
$(a - b)$ $(a' - b')$	$(A_1'A_2- B_1'B_2)$ $(A_1A_2'- B_1B_2')$

Upon collecting similar kinds of gametes, the proportion would be:

	Chromosome Segregation		Chromatid Segregation	
	(n) gametes	(n+1) gametes	(n) gametes	(n+1 gametes)
	2 (A - B)	1 (AA - BB)	12 (A - B)	8 (AA - BB)
	1 (a - b)	2 (Aa - Bb)	6 (a - b)	8 (Aa - Bb)
				2 (aa - bb)
Total	3	3	18	18

Since a is microsporic lethal the other gene linked with it would also disappear in the microspores. However, megaspores of all types would survive. Upon self fertilization the following progeny would be produced:

Chromosome Segregation

	♀ gametes	♂ gametes (A - B)
n	2 (A - B)	2 (Aa - BB)
	1 (a - b)	1 (Aa - Bb)
n+1	1 (AA -BB)	1 (AAA-BBB)
	2 (Aa - Bb)	2 (AAa-BBb)

Recovery of bb individuals among diploid offspring = 0

Recovery of bbb individuals among trisomic offspring = 0

Chromatid Segregation

	♀ gametes	♂ gametes (A - B)
n	6 (A - B)	6 (AA - BB)
	3 (a - b)	3 (Aa - Bb)
n+1	8 (AA-BB)	8 (AAA-BBB)
	8 (Aa-Bb)	8 (AAa-BBb)
	2 (aa-bb)	2 (Aaa-Bbb)

Recovery of bb individuals among diploid offspring = 0

Recovery of bbb individuals among trisomic offspring = 0

Similarly genotype frequencies have been computed for the remaining seven types which are given in the Table 27.

From the fraction of recombinant individuals one can calculate the fraction of recombinant gametes (crossover value) from which

TABLE 47

Hypothetical frequency of genotypes in a progeny from selfing of the eight possible types of trisomics, when both loci are on the trisome, and one locus, designated a, is microsporic lethal*

Types of Trisomic Phase	A Simplex								A Duplex							
	B Simplex				B Duplex				B Simplex				B Duplex			
	Single Repulsion (1)		Double Coupling (2)		Single Repulsion (3)		Double Repulsion (4)		Single Coupling (5)		Double Repulsion (6)		Single Repulsion (7)		Double Coupling (8)**	
Genotypes	Chr'some Segre.	Chr'tid Segre.	Chr'some Segre.	Chr'tid Segre.	Chr'some Segre.	Chr'tid Segre	Chr'some Segre.	Chr'tid Segre.	Chr'some Segre.	Chr'tid Segre.	Chr'some Segre.	Chr'tid Segre.	Chr'some Segre.	Chr'tid Segre.	Chr'some Segre.	Chr'tid Segre.
Diploid AABB	0	0	2	6	2	6	0	0	1	3	0	0	1	3	4	12
AABb	0	0	0	0	0	0	0	0	2	6	0	0	2	6	0	0
AAbb	2	6	0	0	0	0	2	6	1	3	4	12	1	3	0	0
AaBB	0	0	0	0	2	6	0	0	0	0	0	0	1	3	0	0
AaBb	2	6	4	12	2	6	4	12	1	3	2	6	1	3	2	6
Aabb	2	6	0	0	0	0	0	0	1	3	0	0	0	0	0	0
aaBB	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
aaBb	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
aabb	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Recovery of bb	4	12	0	0	0	0	2	6	2	6	4	12	1	3	0	0
Trisomic																
AAABBB	0	0	0	2	0	2	0	0	0	1	0	0	0	1	2	8
AAABBb	0	0	0	0	0	0	0	0	1	3	0	0	1	3	0	0
AAABbb	0	0	0	0	0	0	0	0	1	3	0	0	1	3	0	0
AAAbbb	0	2	0	0	0	0	0	2	0	1	2	8	0	1	0	0
AAaBBB	0	0	0	0	2	4	0	0	0	0	0	0	1	2	0	0
AAaBBb	0	0	4	8	2	4	0	0	1	2	0	0	2	4	4	8
AAaBbb	2	4	0	0	0	0	4	8	2	4	4	8	1	2	0	0
AAabbb	2	4	0	0	0	0	0	0	1	2	0	0	0	0	0	0
AaaBBB	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0
AaaBBb	0	2	0	0	2	4	2	8	0	0	0	2	0	1	0	0
AaaBbb	2	4	2	8	0	2	0	0	0	1	0	0	0	0	0	2
Aaabbb	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0
aaaBBB	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
aaaBBb	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
aaaBbb	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
aaabbb	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Recovery of bbb	2	8	0	0	0	0	0	2	1	4	2	8	0	1	0	0
Total Progeny	12	36	12	36	12	36	12	36	12	36	12	36	12	36	12	36

*Assumptions: 1. No crossing over between loci of interest. 2. No lagging of chromosomes. 3. No restitution of nuclei. 4. No chromosomal aberrations. 5. All (n+1) megaspores and the resulting trisomic offspring survive. 6. No (n+1) microspores survive and hence tetrasomic offspring do not occur. 7. Dominance of single dominant allele over two recessive alleles.

**Represents the trisomic type of the present study.

those individuals originated. For example, if any of the present trisomics in this particular cross were triplo for the chromosome of the linkage group V there would be no _jj_ or _jjj_ individuals in the progeny and the recombinants would only result from crossing over in the microsporocytes:

producing viable (X-j) microspores. From the fraction of recombinants crossover value can be roughly calculated as for the backcross = $\frac{\text{Recombinants}}{\text{Total progeny}}$ X 100.

POLLEN STUDY

Pollen stainability data were obtained from greenhouse plants of both woolly and nonwoolly types with and without asynapsis. Among the synaptic plants three classes were recognized with respect to fruitfulness. Plants which bore fruits on all the clusters were classified as "fruitful"; those with one or two fruits as "partially fruitful" and those with no fruit as "unfruitful." The pollen was taken from anthers of comparable age, approximately one day after anthesis, on the same day. The anthers were macerated in aceto-carmine stain on the slide the same day. Counts were made at random from different fields. The relative data are presented in Tables 28 and 29.

TABLE 28

Pollen stainability data on three woolly and three nonwoolly plants at five months of age

Phenotype	Fruitful plant		Partially fruitful plant		Unfruitful plant	
	Pollen grains examined	% stain-able pollen	Pollen grains examined	% stain-able pollen	Pollen grains examined	% stain-able pollen
Nonwoolly	619	97.5	428	56.1	883	32.4
Woolly	655	85.1	998	38.5	515	2.9

The data indicate that there is a lesser proportion of stainable pollen in woolly plants of all the three classes of fruitfulness than in the nonwoolly plants of the corresponding classes.

TABLE 29

Pollen stainability data on asynaptic plants, one woolly and one nonwoolly, at ten months of age

Phenotype	Pollen grains examined	% stainable pollen
Nonwoolly	955	89.5
Woolly	1456	93.1

It may be pointed out that the nonwoolly asynaptic plant was unfruitful but two fruits were set on the asynaptic woolly plant. The amount of stainable pollen in both cases almost approached that of the fruitful plants of Table 28.

DISCUSSION

Since all F_1 diploid plants were normal vegetatively as well as reproductively and no asynapsis was observed in PMC of the diploid plants, it is concluded that the asynapsis in the Marglobe plant, if due to mutation, is governed by a recessive gene or genes. Soost (44) and Clayberg (12) came to similar conclusion regarding asynapsis in tomato.

Segregation of the Wo marker gene in F_1 was in close agreement with expectation as seen in Table 1.

All diploid plants had cut leaves, jointed pedicel with indeterminate inflorescence in some plants, nonuniform unripe fruit, red flesh color of the ripe fruit, non-beaked fruits, and pigmented skin of ripe fruits wherever examined. All these observations are in accord with the recessive nature of the marker genes.

The monohybrid and dihybrid segregation of various genes in F_2 suggested that all the marker genes except j (jointless pedicel) segregated normally and independent of one another.

Although the Wo and bk belong to linkage group I, and similarly the u and t also belong to the common linkage group VII, this relationship was not confirmed in the present study. In view of the comparatively large map distance between u and t, 59 map units (46), the lack of evidence of linkage in a small population as this is not surprising. The Wo and bk genes are, however, reported only 13 map units apart (46). Absence of linkage evidence in these two genes is rather perplexing and unaccountable by this writer. The backcross data

also support the independence of these two loci. The expression of the bk has been reported variable (38) in populations of different genetic backgroumd. This variability could possibly account for the discrepant situation observed; yet the relationship of the bk with other genes as well as its own good fit to 3:1 and 1:1 ratios in F_2 and backcross populations respectively (Tables 5 and 15) tends to invalidate the possible influence of a variable genetic background.

An extremely low frequency of jointless plants (jj) presented an intricate proposition. The backcross data, however, unraveled the intricacy.

In one of the backcrosses where an F_1 plant was used as the mother parent, a normal proportion of the jointless individuals appeared as seen in Table 13. In the other backcross in which the F_1 plant was used as pollen parent as in Table 14 the segregation behavior of the gene was similar to that in F_2. This indicates that the discrepancy of the j gene was brought about by pollen and not by the megaspores. This discrepancy is similar to a situation which Bohn and Tucker (7) encountered in their study of the I gene responsible for immunity to Fusarium oxysporium f. lycopersici, on one of their wilt immune accessions. They had observed that in the backcross where the F_1 (L. esculentum X L. pimpinellifolium) was used as mother plant the expected 1:1 ratio of immune and susceptible plants was obtained, but in the F_2 and in the backcross where L. esculentum was used as the mother plant and F_1 as pollen parent, immune plants were in excess. This anomalous behavior of the I gene was attributed

by the authors to a linked gene *x* influencing the effectiveness of the pollen. According to this postulation the potency of the male gametophyte carrying *x* is reduced when competing with gametophytes carrying $\overset{+}{x}$ allele. However, the *xx* genotype has normal fertility. Paddock (30) observed similar deviations in the F_2 segregation of *I* and *j* and therefore tentatively assigned both *I* and *x* to linkage group V. Since *j* belongs to linkage group V, location of *x* in the linkage group V is confirmed.

The genotype of the two parents involved in the cross with respect to *j* would be represented as follows:

Marglobe = $\dfrac{\overset{+}{j}---\overset{+}{x}}{\overset{+}{j}---\overset{+}{x}}$ and

Woolly = $\dfrac{j---x}{j---x}$

The F_1 plants of this cross would have this genotype:

F_1 = $\dfrac{\overset{+}{j}---\overset{+}{x}}{j---x}$

The F_1 plants would therefore produce the following four types of microspores:

Non cross-over type = i. $\overset{+}{j}---\overset{+}{x}$
ii. $j---x$

Cross-over type = iii. $\overset{+}{j}---x$
iv. $j---\overset{+}{x}$

Microspores of ii and iii types become eliminated in competition and only type i and iv are potent. The recovery of *jj* individuals in F_2 is computed by Paddock (31) to be one half of the crossing over percentage. This, in turn, provides a measure of intensity of linkage

between *j* and *x*. According to the F_2 data the linkage distance between the two loci comes to:

$(4/231 \times 100) \times 2 =$ App. 3.5 units

According to the backcross data, however, this distance is found to be:

$14/195 \times 100 = 7.2$ units

This latter distance agrees closely with what Paddock (31) has found.

A very low recovery of asynaptic plants in the same cross as seen in Table 5 would tempt one to associate asynapsis with *j* and *x* loci. But a similar low recovery of asynaptic plants in the other cross with Walter-15 in which *j* and *x* are not involved as given in Table 4, and also in the F_3 generation raised from a self-pollinated asynaptic F_2 plant would certainly not substantiate any such conclusion. Assuming that asynapsis is controlled by a single recessive gene or by two recessive genes as the F_2 data for both the crosses seem to suggest, the asynaptic F_2 plant should breed true for asynapsis in F_3. The F_3 data, however, do not verify this hypothesis.

In light of the fact that asynapsis was mild and affected only a few plants in the F_2 generation, one is led to suppose that the asynapsis might be an environmentally-induced physiological disturbance of meiosis as Johnsson (21) was inclined to believe. But persistence of asynapsis in F_2 and F_3 generations rule out the possibility of such a supposition.

On the contrary the fact that asynapsis did appear in successive generations suggests that the asynapsis is genetically transmissible. However, the failure of the F_2 asynaptic plant, presumably homozygous for asynapsis, to breed true for asynapsis runs counter to the assumption that asynapsis is controlled by one or two fully penetrant recessive genes.

The data indicate that the asynapsis gene(s) lack full penetrance and are, therefore, liable to fluctuate in expressivity. Variable expression of asynapsis in asynaptic plants under more or less like external conditions of growth is suggestive of interplay of some internal conditions with the action of the asynapsis gene(s). The internal conditions, aside from the modifying genes, may also include conditions directly or indirectly brought about by the external conditions. Manifestation of asynapsis only on woolly plants indicates that woolly plants furnish better conditions for the expression of asynapsis than do the nonwoolly.

These different conditions in the two categories of plants may exist due to the difference in the contents of certain metabolite(s) needed for the asynaptic association of the chromosomes during meiosis. The asynapsis gene(s) may show only when the amount of the required metabolite(s) falls below a threshold amount. Due to the obvious phenotypic differences in woolly and nonwoolly plants, the former plants probably have a lower photosynthetic activity. On this basis alone further differences in various metabolites are easy to imagine.

Further evidence of the differences between woolly and nonwoolly plants is furnished by pollen stainability data, Table 28. In all three fertility levels of plants of the two classes, woolly plant anthers had a lesser amount of stainable pollen. Variability in intensity of asynapsis within the same kind of plants may be due to the effect of modifying genes. Thus the expression of asynapsis may be possible in woolly plants and not in the nonwoolly plants under like external conditions.

The pollen stainability data given in Table 29 for asynaptic plants of the two classes indicate as high a proportion of stainable pollen as in the synaptic and fully fruitful plants of Table 28, although one of the asynaptic plants, namely, the nonwoolly was completely unfruitful. This casts considerable doubt on reliability of pollen stainability as a criterion of germinable or functional pollen.

From the point of view of the transmissibility behavior of the extra chromosome and the genetic ratio of the two progenies of trisomics originating from the cross between the asynaptic Marglobe and the woolly, the two trisomics were found to be different. Although the data relative to the fruit characteristics were not complete, the available evidence strongly favored the identification of the woolly trisomic as triplo-1 and of the nonwoolly trisomic as triplo-10.

Presence of asynapsis gene(s) in the F_2 and F_3 progenies did not apparently affect the segregation of other marker genes wherever such

computation was feasible. Seemingly there is no association between asynapsis gene(s) on one hand and the marker genes on the other, Table 22.

However, in dealing with the gene(s) of incomplete penetrance with the consequent variable expressivity, an extreme caution needs to be exercised in arriving at conclusions in regard to inheritance. In fact, such situations do not easily lend themselves to inheritance studies.

Anther Color and Flesh Color

The F_2 and backcross progenies were found to have been segregating for anther color. One group of plants had deep orange color anthers and the other pale yellow. This distinction was least confusing about two days after anthesis. To verify the suggestion in literature (38) that flesh color gene has pleiotropic effect on anther color, plants bearing orange anthers were tagged as the distinction became possible. On ripening of fruits a perfect correlation was found between orange anther color and tangerine (orange) fruit flesh color. The yellow anthers, on the other hand, were associated with ref flesh color.

Although there is not much in commón in histological development of these two tissues (15) of androecium and gynaeceum, on the basis of functional and possibly ontogenic analogy, they seem to be comparable. Pigmentation of the two tissues seems to be controlled by the same gene which also shows a time correlation. The gene action becomes

manifest in both tissues at their maturity, although the maturity of one occurs about two months ahead of the other. Several such genes are designated by a common symbol; asynapsis genes affecting both megasporocytes and microsporocytes at two different sites being the case in point. The gene action controlling pigmentation in the two tissues should be considered primary rather than pleiotropic. Since most studies concerned fruit and little or no attention had been paid to anthers such an oversight is conceivable. In the light of Grunberg's (17) concept of "Tiddue-specific gene action" it is suggested that a common symbol be used for the gene(s) controlling pigmentation of anthers and fruit flesh of the tomato. In view of this it becomes appropriate to assign a symbol descriptive of anther color on which tissue (organ) the expression of the gene first becomes manifest. Because of the comparatively short life of anther and variability of pigmentation dee to environments, differentiation of color may present difficulty especially where the color of the pigments is not distinctly different.However, in those cases where parents of contrasting anther and fruit flesh color are used, scoring of gene segregation in the progeny is possible on the basis of anther color. This becomes all the more advantageous in cases where failure of fruit set due to gene sterility or other hazards prevents study of the genes affecting fruit characteristics.

SUMMARY

1. Data from F_1, F_2, and F_3 generations indicate that the asynapsis seen in PMC in a Marglobe plant of tomato contributed to its unfruitfulness.

2. The segregation for asynapsis in F_2 was not monogenic. Asynapsis in an F_3 generation obtained from selfing an asynaptic F_2 plant was variable and did not affect all the plants. Therefore the asynapsis gene(s) had incomplete penetrance and/or modifiers.

3. Recombination values provide no evidence of linkage between the asynapsis gene(s) and any of the marker genes used in the study.

4. The presence of aneuploids, primarily trisomics, in F_1 indicates that asynapsis was operative in megasporocytes as well.

5. Diversity in morphology and fertility of the various trisomics suggest that asynapsis was affecting various pairs of chromosomes in a general way instead of being specific to any particular pair or pairs of chromosomes. Two of the trisomics were tentatively identified to be triplo-1 and triplo-10.

6. The map distance between the microsporic lethal gene *x* and the marker gene *j* of linkage group V was estimated from backcross data to be 7.2.

7. A hypothetical frequency table giving recovery of different genotypes in the selfed progeny of trisomic for a situation when a microsporic lethal gene is linked with the gene of interest is computed for both chromosome and modified chromatid bases of segregation. The necessary new terminology is proposed.

8. One aneuploid plant contained as many as 9-10 extra chromosomes in PMC. This observation extends the known upper limit of the chromosomes in the aneuploid tomato.

9. A perfect association of orange anther color with tangerine flesh color and yellow anther color with red flesh color was found in this study.

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I, Het Ram Kalia, was born in Bhalwani, District Kangra, Punjab, India, August 26, 1922. I passed the Matriculation Examination of the Punjab University from Government High School Hamirpur in 1940. I received a Bachelor of Science degree in Agriculture from the Punjab University in 1944. I held the position of Vegetable Research Assistant in the Punjab Department of Agriculture until 1955 when I was granted leave of absence for graduate study in this country.

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