THE PRODUCTION AND IDENTIFICATION OF PRIMARY TRISOMIC TYPES OF SUGAR BEETS (BETA VULGARIS L.)

A Thesis

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ABSTRACT

Three distinct primary trisomic types, identified on the basis of plant morphology and designated as #1, #2 and #3, were obtained with a frequency of 35.48 per cent in the progeny of a triploid X diploid cross of an inbred line of sugar beets (Beta vulgaris L.). Trisomic type #1 was cytologically identified as the trisomic for the satellited chromosome.

Pollen fertility in the trisomics ranged from 4.81 to 84.49 per cent with type #1 exhibiting the lowest. Pollen grain diameter ranged from 17.80 $\pm$ 0.31 to 23.07 $\pm$ 0.41 microns; micropollen was observed in all types.

The mean transmission frequency of the extra chromosome was 22.07 per cent (17.33 - 30.88 per cent). No transmission of the extra chromosome through the pollen was detected, nor were there any unrelated trisomics detected in the progeny of the trisomics.

In M-I of PMC's of trisomics two configurations, i.e., $8^{II} + 1^{III}$ and $9^{II} + 1^{I}$ occurred in 14.28 per cent of the cases. The most common form of the trivalent was a chain and a ring (85.6 per cent). Partial synapsis was observed, there being 0.269, 0.282 and 0.597 univalents and 0.778, 0.795 and 0.724 trivalents per cell for types #1, #2 and #3 respectively, and 6.56 trivalents for the triploid.

The high rate (33.3 per cent) of elimination of the extra chromosome in type #3 was attributed to the high frequency of univalents in this type.

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INTRODUCTION

The inheritance of a number of characters has been investigated in sugar beets (Beta vulgaris L.), including root, leaf, petiole, vein and crown colour, albinism, mendelian male sterility, monogerm and multigerm seed characters, and annual habit.

These investigations have assigned most of the genes to three linkage groups: (1) the Y-R-B linkage group which contains most of the genes for the colour of different plant parts, the gene for annual habit, and the gene for resistance to curly top; (2) a linkage group with the gene for monogerm seed character and a gene for late bolting, and (3) the linkage group with the gene for the mendelian male sterility.

The inheritance of a number of other characters has been investigated but no linkage data are available although some of them are reported as being probably independent of the Y-R-B linkage group.

Trisomics have been successfully used in assigning genes to particular chromosomes, associating linkage groups with chromosomes and testing the independence of linkage groups.

Eight out of the possible nine different trisomic types have been produced in sugar beets but this material is not a homozygous line.

This fact, together with the establishment of only three linkage groups out of the nine possible ones, was the main reason for undertaking the present study, i.e., the production and identification of the trisomic series in an inbred line of sugar beets so that it

could be used for testing the independence of the reported linkage groups and the assigning of some of the known genes to their respective linkage groups.

LITERATURE REVIEW

The first trisomic series was produced in Datura by Blakeslee and his associates (4, 5, 6, 7, 8) who made an extensive study of the trisomics and used the trisomic method in assigning genes to different chromosomes (9, 10, 11).

These studies in Datura stimulated a series of similar studies in other species.

In barley, Katterman (39) and Smith (73) each described three primary trisomic types. McLennan (50) obtained trisomics in the progeny of an X-ray induced mutant. Tsuchiya (79) obtained six primary trisomic types in Hordeum sativum. The same worker obtained the complete series from progenies of autotriploid plants in wild barley, Hordeum spontaneum (80, 81). More recently, he produced the trisomic series in a cultivated variety (83). Ramage (56) obtained primary and tertiary trisomics from interchange heterozygotes in H. vulgare. Kerber (40) obtained trisomics from triploid plants. The barley trisomics were identified on their morphology and were used in assigning genes to different chromosomes and to associate chromosomes with their linkage groups.

In Lycopersicon, eleven trisomic types were reported by Lesley (41, 42) in the progeny of a triploid plant. The plants were thought to represent the primary trisomics. Later Rick and Barton (63) and Rick et al. (64) obtained all the primary trisomic types in a cultivated variety from the progeny of triploid X diploid crosses. The

trisomic types were distinct from each other and the diploids, and were identified on plant morphology and karyotype at the pachytene stage. The trisomics were used to study the inheritance of a number of characters and associate chromosomes with their linkage groups.

In Spinacia oleracea, Tabushi (77) obtained four of the six primary trisomic types by crossing diploids to triploids. Janick et al. (35) succeeded in producing all six trisomic types and identified them on the basis of plant morphology. The identification was verified by karyotype studies (21). They associated the sex determing factor with one of the chromosomes.

In rye, Secale cereale, Tagagi (78) reported his cytological studies on a trisomic plant which he obtained in the progeny of a fifteen chromosome plant. Kamanoi and Jenkins (38) obtained all primary trisomic types in the progeny of crosses between triploids and diploids. They identified the trisomic types by plant morphology and karyotype.

In Zea mays the trisomics were produced from the progeny of an individual triploid plant. The trisomics were similar to the diploids and to each other in morphology. The series was identified on the basis of the karyotype and linkage relationships (48, 49).

In wheat, Triticum aestivum, Sears (69, 70) has established the complete trisomic series in the variety Chinese Spring. The trisomic plants occurred in the progenies of haploids and triploids.

Trisomics have been produced in the genus Nicotiana in many ways i.e., spontaneously, from asynaptic trisomics, from irradiated plants and crosses of triploids to diploids. The complete series has been

produced in N. sylvestris (2n=24) and eight out of the twenty-four possible trisomics have also been produced in N. tabacum. The trisomics were identified on their karyotype (in five of the N. sylvestris) and on plant characteristics like growth habit, leaf, flower, and capsule characteristics (17, 30, 31, 72).

Trisomics have also been produced in numerous other species including the following:

Five types out of twelve in Oryze sativa (71), a number of trisomics plants in Sorghum vulgare (53, 54) and some in Lolium perenne (52). The complete trisomic series in Antirrhinum majus (65, 66, 75), five out of six in Crepis capillaris (3, 45) some in Crepis tectorum (29), Oenothera biennis and O. lamarckiana (14, 22, 32, 61, 62), Matthiola incana (24, 25, 26), Pisum, in the progeny of an interchange heterozygote (76), six out of seven in Petunia hybrida (19, 33, 43), some in Populus tremula (36, 37) and one male trisomic plant in Ricinus communis (34).

In the genus Collinsia, trisomics have been produced either through the action of colchicine on diploids or triploid X diploid crosses in the species C. heterophylla and C. tinctoria (16, 20, 27, 55, 74). Vasek (84, 85, 87) obtained a number of trisomic plants in Clarkia unguiculata in the progeny of triploid X diploid crosses.

Savitsky and Savitsky (cited by Butterfass 13) were the first to observe trisomic plants in Beta vulgaris L. Later in 1942, Levan (44) obtained sixty-two trisomic plants in the progeny of colchicine treated plants, which he classified in five different types, i.e.,

Glass, Lettuce, Mosaic, Horseradish and Bullate, and identified the Horseradish type as being trisomic for the satellited chromosome on the basis of the trivalent association with the nucleolus in meiotic prophase. He reported on the meiotic behaviour of the trisomic types and on some twenty chromosome plants.

Mochizuki (51) obtained trisomic plants in crosses of polyploid sugar beets, but did not study them.

Butterfass (13) reported on eight different trisomic types obtained by crossing triploid plants as females to diploids. He identified the trisomic types on the basis of their morphology and named them as 2x+I, 2x+II, and so on, and identified the trisomic type 2n+I as being trisomic for the satellited chromosome on the basis of cytological studies on resting nuclei (60).

Linde-Laursen (46) reported on the vigour and frequency of trisomics in the progeny of different crosses.

Schneider (68) obtained a number of trisomics which he did not study and claimed the existence of monosomic plants.

Thus, the only trisomic types available as of now in sugar beets are the ones produced by Butterfass (13). This material segregates for the colour of the petiole and possibly for other characters as well and is, therefore, not suitable for genetic studies.

MATERIALS AND METHODS

As experimental material an inbred (S_5) line of sugar beets, kindly supplied by Dr. J. S. McFarlane of ARS, USDA, Salinas, Cal., was used. The line designated as Co-539 is a white-rooted, bolting resistant, self fertile, multigerm variety.

Diploid and tetraploid plants of the above line were given photothermal induction as described by Gaskill (28) i.e., the plants were placed in a cold chamber for three and a half months at 40-45°F. under continuous illumination. The above process induces the plants to bolt early, thus assuring a generation in eight months. In order to ensure maximum seed production, the plants were grown to the twelve leaf stage before they were induced to bolt.

After the photothermal induction, the plants were taken to the greenhouse where hand crosses were made between the 4n and the 2n plants. The resulting progeny was analyzed cytologically, as described below, for the identification of the triploid plants. The triploids along with the diploids, at the twelve leaf stage, were given photothermal induction as described above. Hand crosses were made using the triploid as female and diploid and triploid plants were grown side by side and the seed was harvested from the triploids. It seems that all seed set on the triploids was the product of pollen from the diploids, as no seed was set on the branches of triploids placed under bags.

The progenies of the above crosses were analyzed cytologically as described below. Trisomic and disomic plants were grown under the same conditions throughout their life, so they could be validly compared.

Cytological techniques

(1) Mitotic analyses.

Plants to be analyzed were fertilized five to six days prior to the sampling. The night before the sampling, the plants were watered and kept warm. The next morning, between nine and ten o'clock, young heart leaves, still whitish in colour and about four to six millimeters in length, were collected into ice water; care being taken not to damage the apex during the sampling. The vials with the heart leaves were kept at 0°C. for twenty-four hours. They were then fixed in a solution of three parts ninety-five per cent ethanol and one part glacial acetic acid, where they remained for at least forty-eight hours before they were analyzed. The samples can be kept, at room temperature, in this solution for long periods of time with no apparent unfavorable effects as far as counting of the chromosomes is concerned. The heart leaves were hydrolyzed at 60°C. for eight minutes in 1N HCL. Feulgen reagent was used for the staining and 0.5 per cent acetocarmine for the counter staining. The slides were heated to facilitate spreading. When the cytoplasm had absorbed too much stain, a drop of forty-five per cent acetic acid was used to destain it. Shorter periods of cold pretreatment (six hours) were also used and found to cause less chromosome contraction and allow the observation of secondary constrictions and satellites.

(2) Meiotic analyses.

Parts of the inflorescence were collected into a solution of 6:3:1 of ninety-five per cent ethanol, chloroform and glacial acetic acid and kept in this solution in a refrigerator until they were analyzed.

Acetocamine was used for staining. This technique was not satisfactory for prophase study and the following procedure was followed: After the flowers have been collected as above, they are placed in a solution of two per cent iron alum for thirty minutes. They are then transferred to 0.5 per cent solution of acetocarmine for forty-eight hours. Then they are analyzed as described, the difference being that a drop of forty-five per cent acetic acid is used to destain the cytoplasm.

Pollen studies

To determine the per cent viable pollen, ten fully developed flowers were collected at random from each plant. The five anthers from each flower were squashed in a drop of 0.5 per cent acetocarmine. The slides were then left at room temperature for fifteen minutes. Four counts were taken at random from each slide, the pollen grains being classified as stained or not stained. For the measurement of pollen diameter, two stained and two unstained pollen grains were measured from each slide. The measurements were taken with an ocular micrometer. The slides were gently heated to aid in the observation of the nuclei, but it was not easy to observe them in all cases.

Leaf measurements

Measurements were made on plants six to seven months old. Two representative leaves were selected from each plant under study. Equal numbers of trisomic and disomic sibs were used in comparisons. The width of the lamina and the total number of leaves were taken on living material. All other measurements were taken on leaves which were

pressed and kept at room temperature for ten days. The same measurements as those taken by Butterfass (13) were recorded, with the exception of the angle of the turning points of the lamina (Plate I illustrates the measurements taken). The values of the measurements of the two leaves were first averaged for each plant and then were used for the derivation of the average of the plants of a particular type.

The t-test was used to test the significance of the difference between the means.

Plate I. Diagram of leaf measurements

Figure 1. Diagram of leaf measurements

1. Total leaf length
2. Lamina length
3. Distance from turning points to top of lamina
4. Distance from widest point to top of lamina
5. Length of widest part of lamina
6. Distance of turning points of lamina
7. Petiole thickness

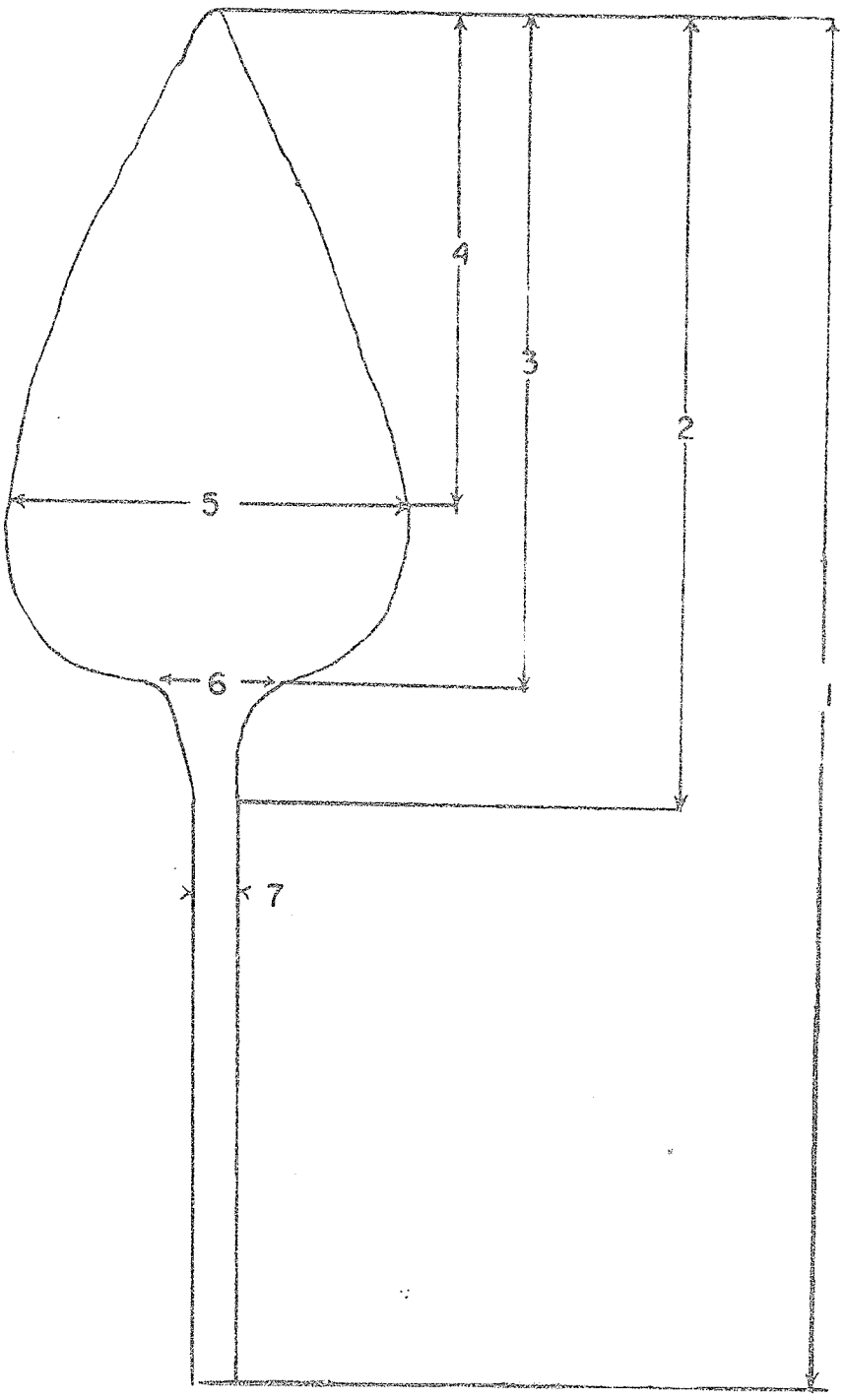

FIG. 1 DIAGRAM OF LEAF MEASUREMENTS

RESULTS

Progeny of triploids

The germination of the seed harvested from the triploid plants was low and varied with the plant from 5.8 per cent to 7.39 per cent.

A total of thirty-one plants were obtained which ranged in chromosome number from eighteen to thirty-six of which eleven or 35.48 per cent were trisomic (Table I and Plate 2, Figures 1, 2, and 3).

The first four trisomics obtained were selfed so as to obtain larger numbers of each type to aid in their classification. The remaining seven trisomics were obtained later and are not yet classified.

The classification and identification of the trisomic types

The trisomic plants obtained in the above four progenies were separated into three distinct groups on the basis of their morphology. Once they were separated the measurements reported in Table II were taken.

It was obvious from the descriptions given by Butterfass (13) and Levan (44) that one of the types was trisomic for the satellited chromosome and consequently attempts were made to verify it cytologically. It was impossible to make a definite identification on the basis of mitotic plates because the satellited chromosomes were difficult to identify.

Another attempt was made using the method described by Reitberger (60), which gave indications of the existence of three chromocenters in association with the nucleolus in the resting nuclei of leaf cells, but

TABLE I

CHROMOSOME NUMBERS OF 3n x 2n PROGENIES

Author	Total No. of Plants Examined	Chromosome number frequencies												
		18	19	20	21	22	23	24	25	26	27	29	34	36
Butterfass (13)	624	45	159	140	not reported									
Levan (44)	82	8	19	22	14	5	4	4	3	2	1			
Linde-Laursen (46)	127	26	35	23	14	4	6	8	8	2		1		
Mochizuki (51)	25	13	10	1										
Author	31	7	11	5					2	3	1		1	1

Plate 2. Mitotic metaphase cells of sugar beets

Figure 1 Tetraploid

Figure 2 Trisomic

Figure 3 Diploid

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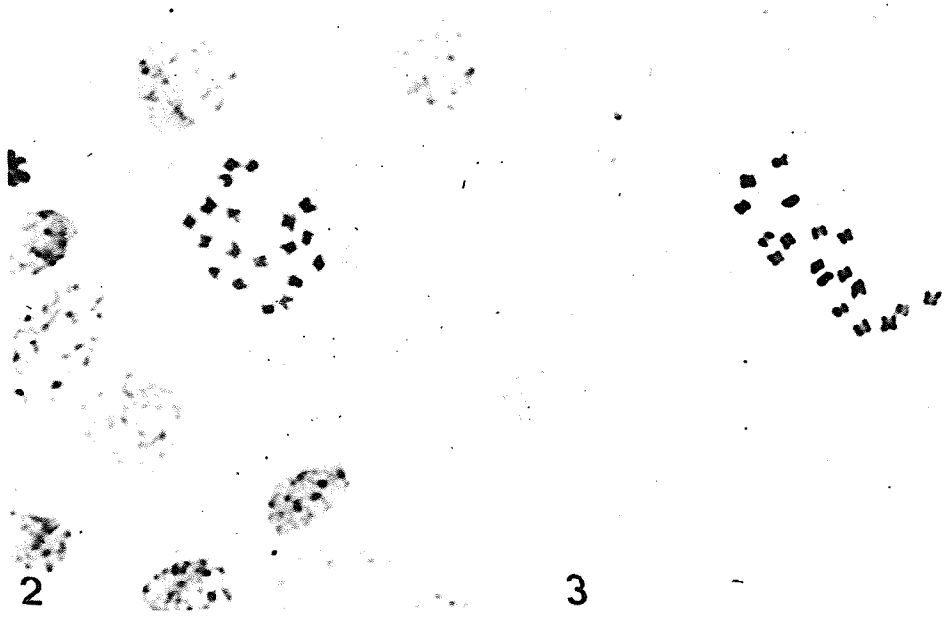

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TABLE II

LEAF MEASUREMENTS OF TRISOMIC SUGAR BEETS EXPRESSED IN PERCENT OF THE CORRESPONDING DIPLOID SIBS

Author	Trisomic type	No. of Plants	Leaf measurements									
			1	2	3	4	5	6	7	8	3/1	2/5
Butterfass (13)	2x + I	19	82*	82*	96	101	96	70*	100	105	116*	86*
Author	#1	10	77**	78	80	77**	67**	56**	62**	90	108	113
Butterfass	2x + IV	12	77*	89	81*	77*	103	100	118*	104	105	88*
Author	#2	5	55**	52**	70*	60**	72*	67**	80	122*	126**	87
Butterfass	2x + II	14	114*	114*	120*	117*	83*	72*	89*	122*	105	136*
Author	#3	5	82**	72**	78*	71	50**	97	79	132**	95	138**

* Significant at the 5% level

** Significant at the 1% level

positive identification could not be made.

Positive identification was made, however, on the basis of chromosome associations with the nucleolus in meiotic prophase.

Once it was certain that the trisomic plants obtained belonged to three distinct groups, they were named as: (1) Trisomic type #1 (being trisomic for the satellited chromosome), trisomic type #2, and trisomic type #3.

The description of the trisomic types

1. Trisomic type #1.

This type is trisomic for the satellited chromosome and corresponds to the Horseradish type (44) and 2x + 1 (13).

Morphologically, plants of this type (Plate 3, Fig. 1) can be easily identified early because of their dark green, shiny thick leaves which are distinctly different from the leaves of the diploids and the other trisomics (Plate 4, Fig. 1). Their early growth is slower than that of the diploids. The leaves are erect, triangular in shape, rolled upwards at the edges and form a funnel-like structure.

The leaf lamina is wrinkled and sometimes twisted. The lamina is dark green, classified as Spinach green 0960, according to the colour charts of the British Colour Council (12). The lamina runs down the petioles which are thinner and shorter than the diploids; their surface is glossy and narrower than the diploids. The leaves, as a whole, are shorter than the diploids.

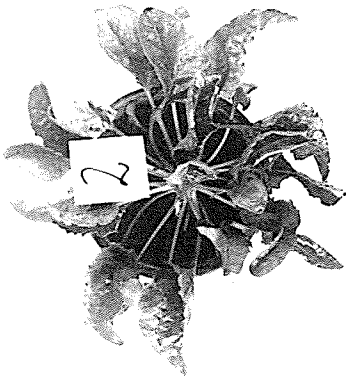
Plate 3. Typical plants of the trisomic types

Figure 1 Trisomic type #1

Figure 2 Trisomic type #2

Figure 3 Trisomic type #3

Figure 4 Diploid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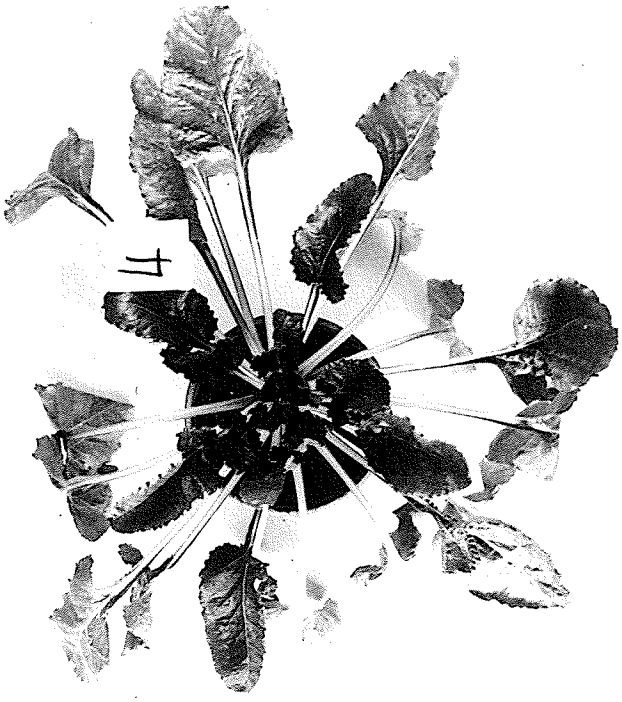
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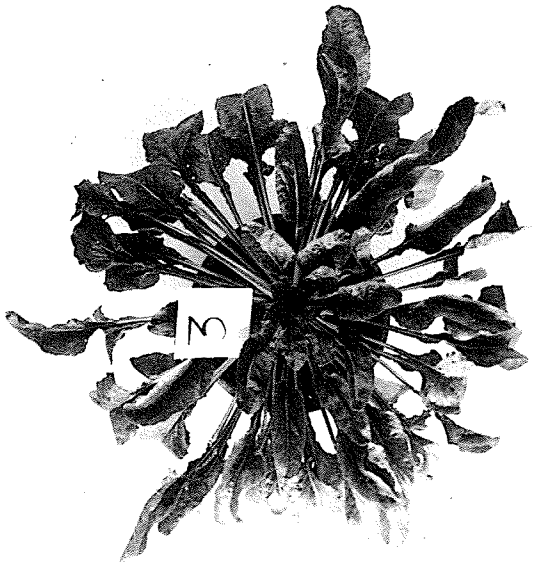
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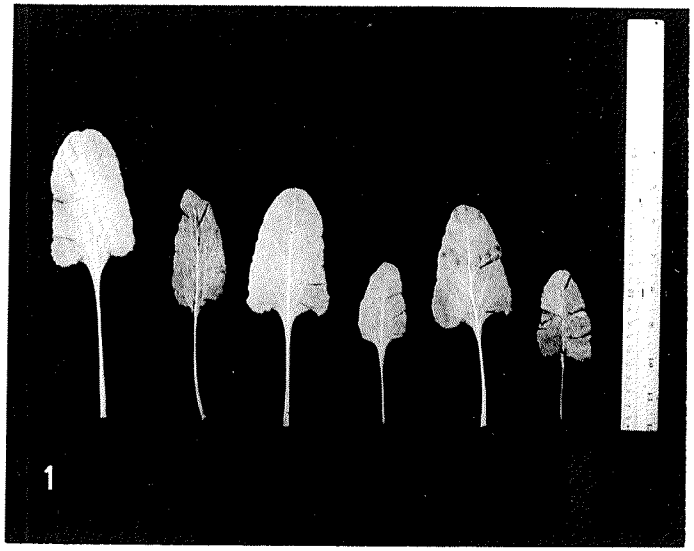

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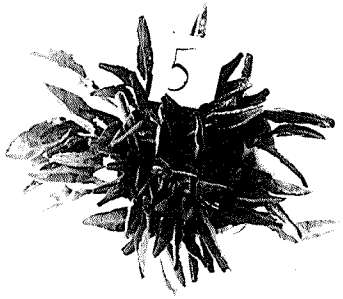

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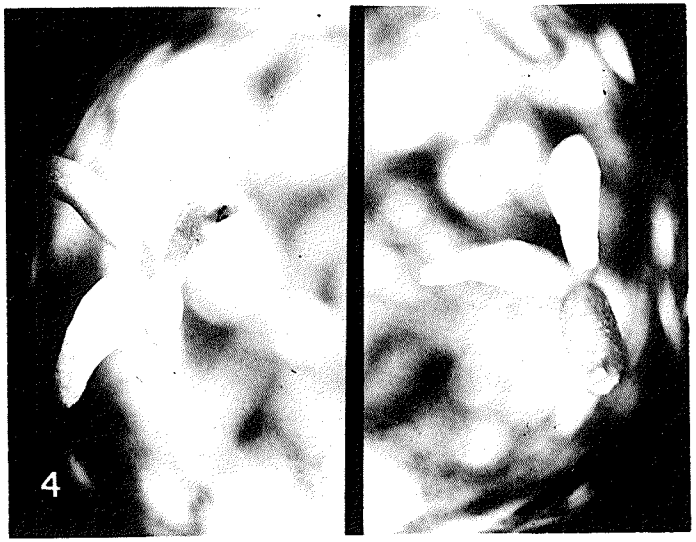

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Plants of this type were positively identified as being trisomic for the satellited chromosome by cytological examination at diakinesis. Three chromosomes were always associated with the nucleolus either in the form of a trivalent or a bivalent and a univalent, or rarely as three univalents (Plate 7, Figures 2 and 3).

In the prophase of second division, there were two chromosomes attached to the nucleolus in one cell and one in the other.

The satellited chromosome is the second largest of the chromosome complement of Beta vulgaris L. (1, 15, 88).

2. Trisomic type #2.

The plants of this type (Plates 3 and 4, Fig. 2) remain smaller than the diploids.

The leaves stand erect, are broad, spade-like and thicker than the diploids (Plate 4, Fig. 1). They are fleshy and have a rough appearance. The edge of the lamina is rolled upwards. The surface of the lamina is finely buckled and twisted. The colour of the leaves is classified as Spinach green 0960/1 (12), which is intermediate to the colours of trisomic types #1 and #3. The petioles are shorter and thicker than the diploids and leaf length, as a whole, is shorter. Plants of this line have twenty-five per cent more leaves than the diploids.

This type seems to correspond in some respects with the "Glass type" described by Levan (44) and the 2x +IV by Butterfass (13).

3. Trisomic type #3.

The plants of this type (Plate 3, Fig. 3/Plate 4, Fig. 2) have long leaves with a small lamina having a plain surface. The thickness of the leaf is normal. The colour is paler than the diploids and lighter than the other trisomic types. It is classified as pod green 061/1 (12). The petioles are shorter and thinner than the diploids, but wide at their base. The colour of the veins is lighter.

This type has about one-third more leaves than the diploids. Some side branches were observed at the time of bolting.

The shape and form of the leaves change with the age of the plants and the lamina becomes narrower and shorter, so that by the time of measurement it is almost half that of the diploid plants.

This type seems to correspond in some respects with the type 2x + II of Butterfass (13), although the comparison with plants kindly supplied by him does not reveal much similarity. Butterfass (13) also encountered difficulties in classifying this type.

Twenty chromosome plants

They were, as a rule, smaller than the trisomics with short narrow leaves (Plate 4, Figures 2 and 3) and almost as green as the diploids. No attempt was made to classify them.

Transmission frequencies

The transmission frequencies of the three trisomic types are shown in Table III, together with the seed germination.

TABLE III

GERMINATION AND EXTRA CHROMOSOME TRANSMISSION FREQUENCIES IN THE TRISOMICS

Type	No. of seeds	Germinated	Percentage	Trisomics	Trisomics in per cent Author	Trisomics in per cent Butterfass (13)
#1	211	150	71.09	26	17.33	30
#2	125	68	54.44	21	30.88	39
#3	125	81	64.80	19	23.45	18
Overall	461	299	64.85	66	22.07	20

As can be seen from the Table, the trisomic for the satellited chromosome exhibits the lowest transmission of the extra chromosome and trisomic type #2 the highest.

An attempt was made to determine whether there was higher transmission of the trisomics through seeds of smaller size, but no results were obtained since the germination of the small seeds was very low.

No transmission of the extra chromosome through the pollen was detected when the trisomic plants were grown side by side with cytoplasmically male sterile plants, but a twenty chromosome plant and a triploid were found in the progeny of trisomic type #1.

A plant with three cotyledons was found in the same progeny, as well as another one with four cotyledons which had twenty chromosomes (Plate 4, Fig. 4).

The twenty chromosome plants when forced to bolt produced short stalks and set some seed but no germination was detected in this seed.

In ascertaining the chromosome numbers of offspring of the trisomic types, chimeras were encountered, i.e., cells disomic or trisomic in the same plant. These plants were classified as diploids.

Pollen studies

The results of the pollen studies are summarized in Table IV.

The diameter of the pollen grains when stained varied from 17.80 ± 0.31 microns to 23.07 ± 0.41 microns and from 15.92 ± 0.25 to 18.42 ± 0.44 microns for those which did not stain.

Micropollen was observed in all three trisomic types. Pictures of the pollen grains from diploids and the three trisomic types are shown in Plate 5, Figures 1, 2, 3 and 4.

No difficulties were encountered in distinguishing the stained from the unstained pollen grains. Generally the unstained pollen grains had a smaller diameter (Table IV).

Pollen fertility in the different trisomic types ranged from almost complete sterility in some of the flowers of the trisomic type #1 to almost diploid-like behaviour in plants of trisomic type #3.

Plants of trisomic type #1 consistently gave lower pollen fertility both in the greenhouse and in the field (tetrazolium salts were used for the determination of the pollen fertility in the case of field-grown plants).

The mean pollen fertility for all three types combined is 53.7 per cent.

TABLE IV

POLLEN FERTILITY AND DIAMETER OF DIPLOIDS AND TRISOMICS

Description of Plant	Plant No.	Fertility per cent	Pollen Diameter in microns	
			Stained	Unstained
Diploid	3-30	84.59	21.16 ± .41	17.45 ± .34
Type #1	7-3	4.81	19.06 ± .55	16.09 ± .31
Trisomic	11-16	27.24	17.80 ± .31	15.92 ± .25
Type #2	2-34	66.83	23.07 ± .41	18.42 ± .44
Trisomic	2-46	65.73	22.39 ± .38	17.89 ± .42
Trisomic	3-9	84.49	22.12 ± .33	16.78 ± .25
Type #3	3-33	70.12	21.53 ± .36	17.01 ± .51
Mean for trisomics		53.7		

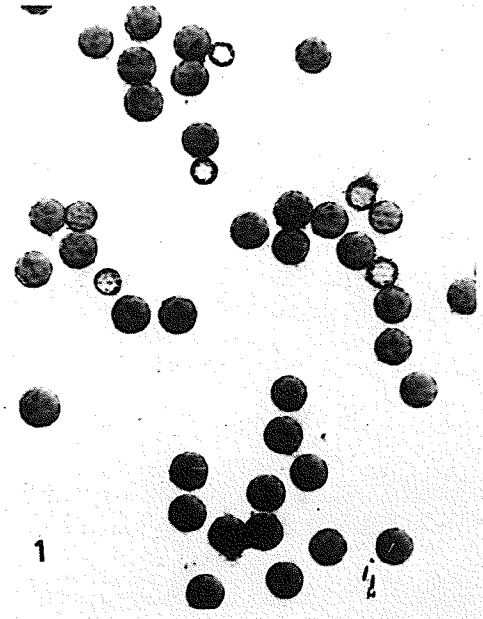
Plate 5. Pollen grains of diploid and trisomic sugar beets

Figure 1 Diploid.

Figure 2 Trisomic type #1.

Figure 3 Trisomic type #2.

Figure 4 Trisomic type #3.



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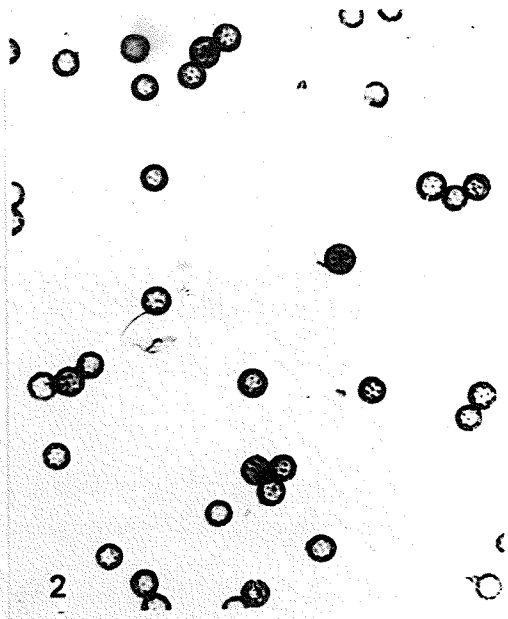

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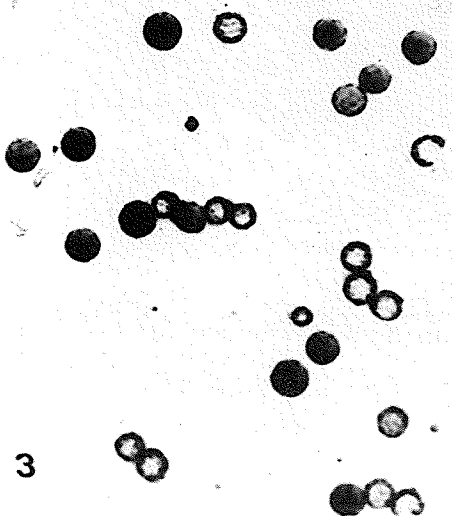

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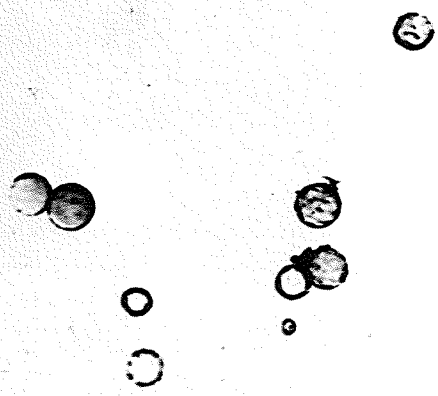

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At the stage when the pollen grains were examined, they were trinucleate, one of the nuclei being round and the other two sickle-shaped.

Meiotic studies

Diploids and triploids

Meiosis in the diploids was found to be very regular with nine bivalents.

In the triploids, a varying number of univalents, bivalents and trivalents was formed. The results obtained from the study of the first metaphase of pollen mother-cells are given in Table V.

The mean number of trivalents per cell is 6.66, the mode being seven trivalents per cell. The first three classes, namely nine, eight and seven trivalents per cell, constitute almost sixty per cent of the cases.

Trisomics

1. Trisomic type #1

a) Plant No. 7-3.

Study of the first metaphase of this plant showed a majority of cells with a trivalent (Table VI).

The form of the trivalent varied with the cell, being a chain in most of the cases (Table VII and Plate 6, Figures 1, 2, 3, and 4).

The same kind of configurations were observed in diakinesis. In first anaphase the division followed a regular pattern, the most common distribution being nine chromosomes to one pole and ten to the other. Sometimes the univalent divided late at the equator.

TABLE V

CHROMOSOME ASSOCIATION FREQUENCY IN M-I OF PMC'S FROM TRIPLOIDS

CHROMOSOME CONFIGURATIONS	Author				Linde-Laursen (46)		Levan* (44)		Mochizuki* (51)			
	No. cells		Per cent		No. cells	Per cent	No. cells	Per cent	No. cells		Per cent	
9^{III}	9		15.		21	44	15	21	7	17	14	34
$8^{III} + 1^{II} + 1^{I}$ $8^{III} + 3^{I}$	9 1	10	16.7		19	40	27	38	9	14	18	28
$7^{III} + 2^{II} + 2^{I}$ $7^{III} + 3^{II}$	8 8	16	26.7		7	15	20	28	13	9	26	18
$6^{III} + 3^{II} + 3^{I}$ $6^{III} + 4^{II} + 1^{I}$	6 5	11	18.4		1	2	6	8	7	5	16	10
$5^{III} + 4^{II} + 4^{I}$ $5^{III} + 5^{II} + 2^{I}$ $5^{III} + 6^{II}$	2 7 1	10	16.7		-	-	3	4	6	4	12	8
$4^{III} + 5^{II} + 5^{I}$ $4^{III} + 7^{II} + 1^{I}$	1 1	2	3.4		-	-	1	1	5	1	10	2
$3^{III} + 8^{II} + 2^{I}$	1		1.7		-	-	-	-	2	-	4	-
$2^{III} + 9^{II} + 3^{I}$	1		1.7		-	-	-	-	1	-	2	-
	60				48		72		50	50		

* Percentages calculated by author.

TABLE VI

CHROMOSOME ASSOCIATION FREQUENCY IN M-I OF PMC'S OF TRISOMICS

Type	Plant No.	Chromosome associations: $8^{II} + 1^{III}$ No. cells	$8^{II} + 1^{III}$ Per cent	$9^{II} + 1^{I}$ No. cells	$9^{II} + 1^{I}$ Per cent	$7^{II} + I^{III} 2 + ^{I}$ No. cells	$7^{II} + I^{III} 2 + ^{I}$ Per cent	Other No. cells	Other Per cent	Total No. of cells
#1	7-3	125	78.12	34	21.25	1	0.62	-	-	160
#1	11-16	59	58.41	34	33.66	4	3.96	4	3.96	101
#1	11-50	145	81.46	33	18.54	-	-	-	-	178
#2	2-34	79	84.04	13	13.83	-	-	2	2.22	94
#2	2-46	97	69.28	37	26.43	3	2.14	3	2.14	140
#3	3-9	94	54.02	52	29.88	9	5.17	19	10.9	174
Average		599	70.72	203	23.96	17	2.00	28	3.30	847

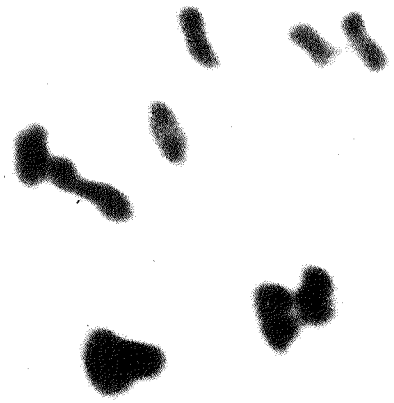
Plate 6. Trivalent configurations in trisomics.

Figure 1 Frying pan.

Figure 2 Chain of three.

Figure 3 Open trivalent.

Figure 4 Arc.



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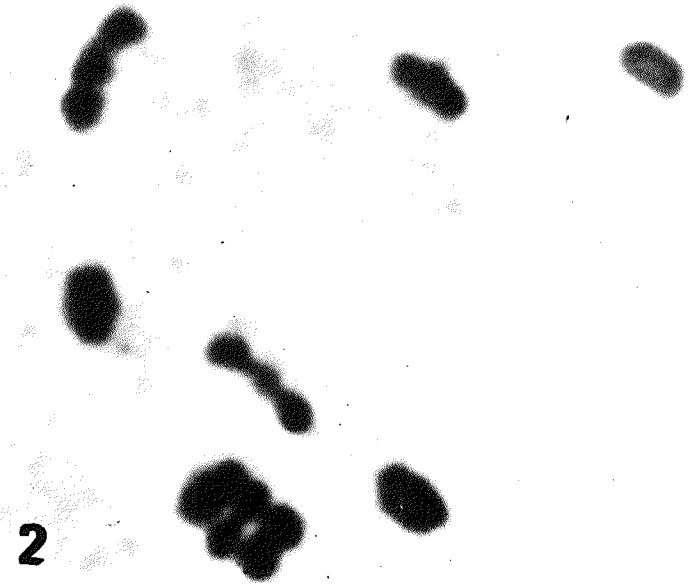

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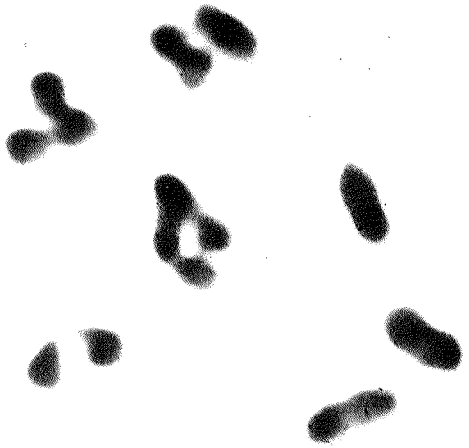

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In second prophase, in cells where the distribution in the preceding division was nine to one pole and ten to the other, there were two chromosomes attached to the nucleolus of one of the cells and one to the nucleolus of the other. Secondary pairing was also observed in a few cases.

The chromosome number was counted at the second telophase in a number of cells. In half of the cases, three nuclei had nine chromosomes each and the other ten; the next most frequent class being two nuclei with ten and two with nine chromosomes.

This plant was a primary trisomic. Pollen fertility was 4.81 per cent.

b) Plant No. 11-16

This plant showed a lower trivalent association than the rest of the plants belonging to this trisomic type (Table VI).

The same kind of configurations were observed in diakinesis where three chromosomes were associated with the nucleolus. Chromosomes dividing late at the equator were also observed.

The trivalent disjoined two to one at first metaphase in most of the cases (Plate 7, Fig. 5), and the univalent was included in one of the nuclei at the end of the first meiotic division in the majority of the cases.

The most common form of the trivalent was the chain (Table VII).

No micronuclei were observed in the tetrad stage in the few cells which were examined at this stage. In about half of the cases there was a nucleus with ten chromosomes in the final products of meiosis.

Plate 7. Meiotic configurations in trisomic type #1.

Figure 1 Pachytene.

Figure 2 Diakinesis.

Figure 3 Diakinesis.

Figure 4 First metaphase

Figure 5 Early A-I.

Figure 6 A-1 with lagging chromosomes

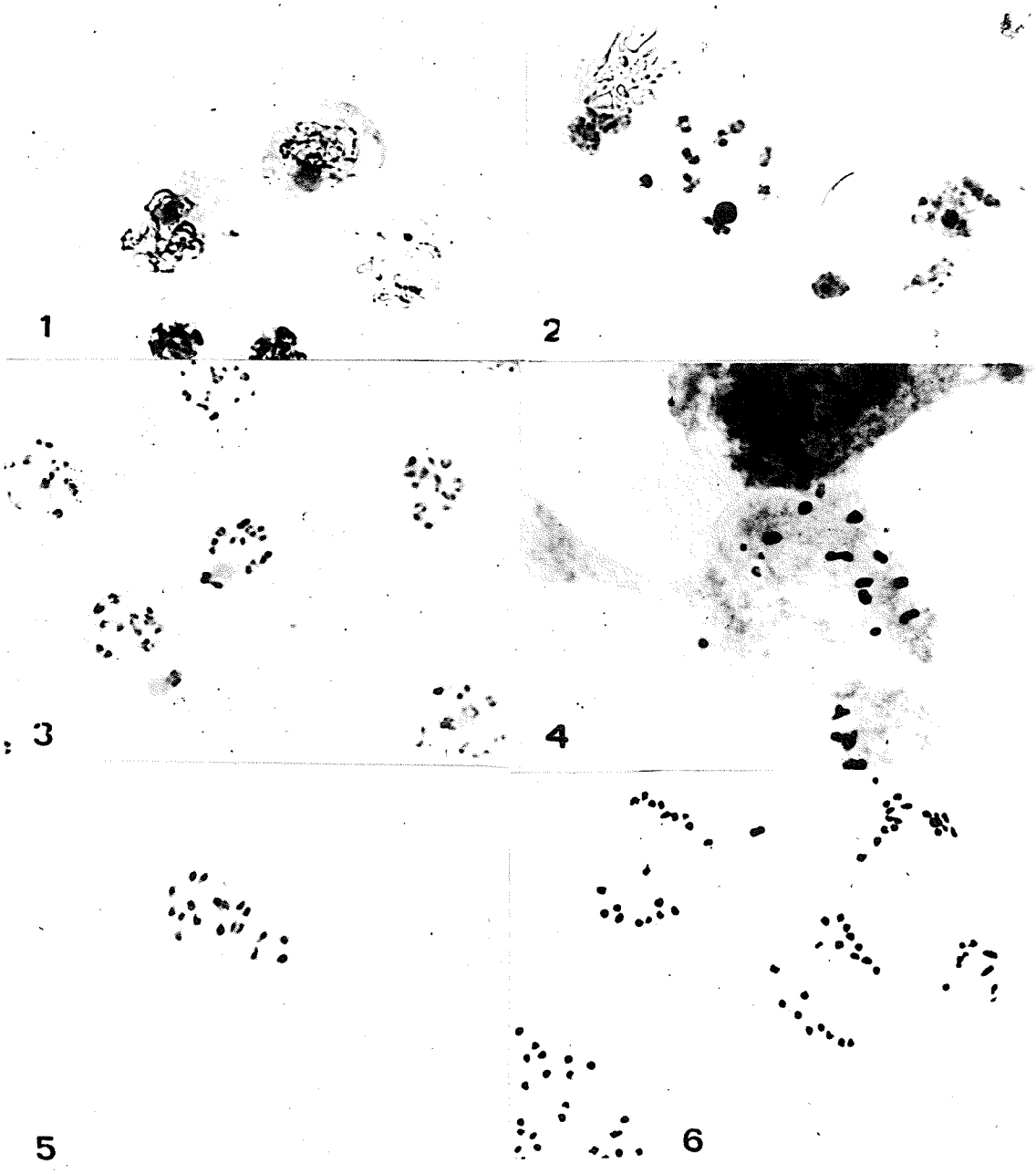
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Plate 7. (continued)

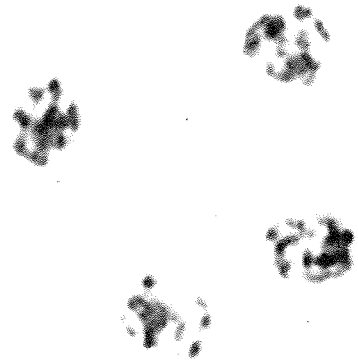
Figure 7 A-2.

Figure 8 T-II.

Figure 9 Tetrad with micronuclei.

Figure 10 Normal tetrad.

7



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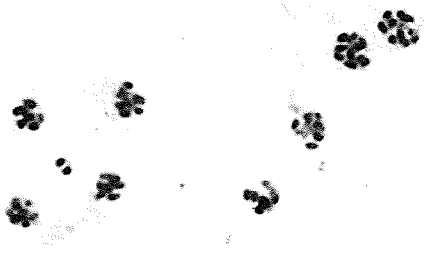

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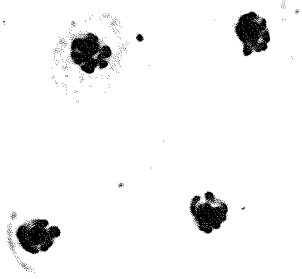

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The plant was a primary trisomic with 27.24 per cent pollen fertility.

TABLE VII

TRIVALENT FORM IN M-I OF PMC's FROM TRISOMICS

Type	Form of trivalents								No.
	CHAIN		RING		FRYING PAN		Y		
	No. cells	Per cent	No. cells	Per cent	No. cells	Per cent	No. cells	Per cent	Tri-valents
#1	161	87.0	13	7.0	4	2.2	7	3.78	185
#2	52	50.0	19	18.3	23	22.0	10	9.6	104
#3	18	75.0	5	20.8	1	4.2	-	-	24
Total	231	73.8	37	11.8	28	8.9	17	5.4	313

c) Plant No. 11-50

The chromosomes associated in this plant mostly in trivalents (Table VI). In diakinesis there were three chromosomes associated with the nucleolus mostly in the form of a trivalent and less frequently in the form of a bivalent plus a univalent, or three univalents. The univalent often divided late at the equator and long bridges of chromatin were observed (Plate 7, Figures 6 and 7).

The form of the trivalent varied (Table VII). The trivalent disjoined two to one in first metaphase. In some cases there was a bivalent dividing late at the equator the two chromosomes being connected by a long chromatin bridge.

The distribution of the chromosomes to the poles at the end of the first division was mostly nine to one pole and ten to the other (Table VIII). Secondary pairing between members of different bivalents

was observed and in one case two bivalents were associated with the trivalent.

TABLE VIII

CHROMOSOME NUMBERS AND THEIR FREQUENCY

IN MEIOTIC FIRST TELOPHASE NUCLEI (n= 9)

Trisomic type	Chromosome number of telophase nuclei		Extra chromosomes eliminated		Number of cells
			No.	%	
#1	118	82	18	18	100
#3	108	54	27	33.3	81

The number of tetrads with micronuclei was very small. There were some tetrads with two micronuclei, one case in which two large nuclei were observed with many chromosomes and chromosome fragments forming micronuclei and one case in which a chromosome pair seemed to be included in the micronucleus (Plate 7, Figures 8, 9, and 10).

This plant was a primary trisomic with 9.59 per cent pollen fertility.

2. Trisomic type #2

a) Plant No. 2-34.

This plant showed a very high frequency of trivalent formation (Table VI). The form of the trivalent varied with the cell (Table VII).

In diakinesis of thirty-one cells examined, twenty-one showed a bivalent associated with the nucleolus; eight showed two univalents and in the rest of the cases there were more than two chromosomes

attached to the nucleolus. The chromosome associations at diakinesis were the same as in first metaphase. Thus, in 79.03 per cent of the cases examined, the association was $8^{II} + I^{III}$, in 17.23 per cent $9^{II} + I^{I}$.

In first metaphase, in one case there was a univalent in association with the trivalent.

In first anaphase, the chromosomes moved to the poles usually nine to one and ten to the other, the trivalent disjoining two to one in most of the cases.

An examination of the tetrads revealed that in 80.83 per cent of the cases no micronuclei were present. One micronucleus per tetrad was seen in 18.75 per cent of the cases.

This plant was a primary trisomic with 66.83 per cent pollen fertility.

b) Plant No. 2-46.

The most frequent chromosome association in this plant was $8^{II} + I^{III}$ (Table VI).

In diakinesis, only a bivalent or two univalents were attached to the nucleolus. The form of the trivalent varied with the cell (Table VII). The movement of the chromosomes to the poles was normal aside from the fact that a chromatin bridge was observed occasionally. The trivalent usually disjoined, two to one.

This plant was a primary trisomic with a pollen fertility of 65.73 per cent.

3. Trisomic type #3

a) Plant No. 3-9.

This plant exhibited the lowest percentage of trivalent formation (Table VI). The form of the trivalent varied with the cell (Table VII).

A high frequency of chromatin bridges was observed in this type both in first and second anaphase, and one of the bivalents was frequently stretched across the entire length of the cell. In diakinesis two chromosomes were associated with the nucleolus (Plate 8, Figure 1, 2, 3, and 4).

In A-I, the extra chromosome divided late at the equator and a very long chromatin bridge was observed in many cases connecting the products of division. The distribution of the chromosomes to the poles at the end of the first division can be seen in Table VIII.

In second telophase, the distribution of the chromosomes to the four poles was as follows: three nuclei with nine and one with ten chromosomes, two with nine and two with ten, or all four with ten chromosomes. In cases where there were two nuclei with ten chromosones, there was a chromatin bridge connecting two chromosomes. Up to two micronuclei were observed in some of the tetrads. This plant was a primary trisomic with 84.49 per cent pollen fertility.

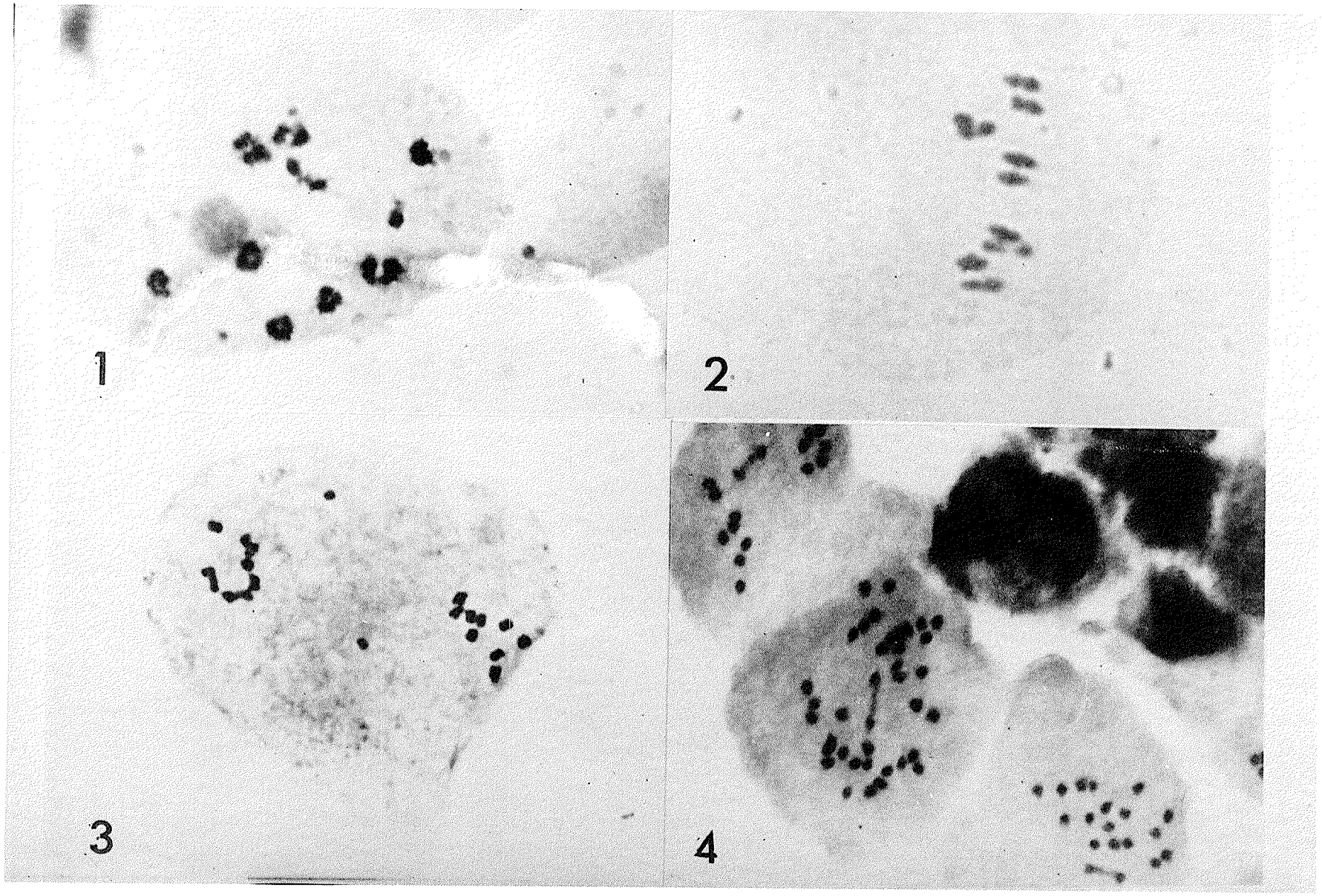
Plate 8. Meiotic configurations in trisomic type #3.

Figure 1. Diakinesis.

Figure 2. M-I.

Figure 3. A-1 and two lagging chromosomes.

Figure 4. Tetraploid sporocyte.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Synapsis in trisomics

The number of univalents, bivalents and trivalents per cell was determined and analyzed. The totals for each type are grouped in Table IX.

TABLE IX

SYNAPSIS IN TRISOMICS OF BETA VULGARIS (2n=18)

Trisomic type	No. of Cells	Number of I	Number of II	Number of III	I / Cell	II / Cell	III / Cell
#1	438	118	3600	341	0.269	8.219	0.778
#2	234	66	1917	186	0.288	8.192	0.795
#3	174	104	1418	126	0.597	8.114	0.724

As can be seen from the table, trisomic type #3 exhibits a very high frequency of univalent formation.

DISCUSSION

Progeny of triploids.

The per cent germination of the seed harvested from the triploid plants agrees with the results reported by Linde-Laursen (46), but it is different from the one reported by Levan (44) and by Mochizuki (51), who attributed the low germination of the seed to the presence of empty seeds. The empty seeds are mainly due to the abortion of embryos, since the seed coats seem to develop normally even if the embryos abort (51).

The plants with chromosome numbers over twenty-seven (Table I) in the progeny of the triploids are apparently a result of self-fertilization. There is a lack of plants having chromosome numbers between twenty and twenty-four. This is in agreement with the results reported by Mochizuki (51) but not with the results reported by Levan (44) and Linde-Laursen (46), who obtained plants having all intermediate chromosome numbers (Table I). This could be attributed to the different strains involved which might have different ability to tolerate increased numbers of extra chromosomes.

The percentage of the trisomics obtained is similar to the results obtained by Mochizuki (51) who reported forty per cent trisomics in the progeny of similar crosses, but it is higher than the percentages obtained by Butterfass (13), Levan (44) and Linde-Laursen (46), who reported 25.48 per cent 23.17 and 28.00 per cent respectively (Table I). The trisomics occur more often in the progeny of triploids crossed to diploids than in the offspring of the trisomics when crossed to diploids (Tables I and III). The same has been found by Tsuchiya (82) in barley.

Identification and classification of trisomics

While taking the leaf measurements some difficulties were encountered in determining the turning point of the lamina (Measurement 6) and in ascertaining the length of the lamina and the petiole (Measurement 2) especially in the cases where the lamina runs down the petiole. Nevertheless these measurements are included in Table II for the sake of comparison with the results obtained by Butterfass (13). As can be seen from the measurements in Table II, there are many differences, even in the cytologically identified trisomic type for the satellited chromosome, pointing to the fact that the differences should be attributed to the different strains of sugar beets involved, along with the possible influence of some environmental factors in favoring the expression of some characters and suppressing the expression of others. Apart from the definite identification of the trisomic type #1 as being the trisomic for the satellited chromosome, the association of the trisomic types #2 and #3 with the types 2x+IV and 2x+II of the trisomics produced by Butterfass (13) is provisional. The final and complete association is deferred until the whole trisomic series is produced in this line. Differences in certain characters of trisomics of the same species obtained from different material have been reported in other species (barley: 56, 82, and snapdragon: 66, 75).

Transmission frequencies

The twenty chromosome plant which was found in the progeny of the trisomic type #1 might have arisen through the occasional functioning

of an x + 1 pollen grain. The triploid plant obtained in this progeny apparently is a result of the fertilization of an unreduced egg by a normal pollen grain. Multiploid sporocytes were seen very rarely (Plate 8, Fig. 4).

The transmission frequencies of the different trisomic types reported herein (Table III) differ from those reported by Butterfass (13) who obtained 30 per cent transmission for trisomic type #1 as compared to 17.33 per cent obtained in this study 39 per cent for trisomic type #2 as compared to 30.88 per cent, and 18 per cent for trisomic type #3 as compared to 23.45 per cent. The overall transmission is not much different, being 20.84 per cent for the trisomic types involved in his case and 22.07 per cent in the present study. The reason for the difference remains obscure although the material used in this study is an inbred line and Beta vulgaris is otherwise strongly allogamous. Differences would be expected in different strains and perhaps a more valid comparison could be made if the progeny of more trisomic plants is studied, since the transmission frequencies reported here are derived from the analysis of the progeny of a single trisomic plant for each trisomic type, except for #1, where two plants were involved.

The chimeras observed in the progeny of the trisomic types were classified as diploids because it is possible that the primordia which initiate the heart leaves could come from a different area of the corpus from that which initiates the flowers (58).

Tricotyledonous plants occur spontaneously in populations of sugar beets. The character is not under hereditary control.

Pollen studies

The diameter of the pollen grains of the diploids as reported here agrees with the results reported by other workers (46, 58). Linde-Laursen (46) also reported smaller diameters for the unstained pollen grains and observed micropollen.

In connection with the low pollen fertility of trisomic type #1 it is of interest to note that Levan (44), too, reported this type to have the lowest pollen fertility.

The mean pollen fertility of the different trisomic types is 53.7 per cent which is slightly higher than that reported by Butterfass (13) for five of the eight trisomic types.

Savitsky and Gaskill (67) also found three nuclei in the pollen grains of mature buds and flowers meaning that the generative nucleus divides while the pollen grain is still in the anther and before germination takes place.

Meiotic studies

Diploids and triploids

Artschwager (2), Rasmusson and Levan (59), and Feltz (23) have reported complete bivalent formation in the diploid sugar beet.

The results obtained from the study of meiosis in triploid sugar beets are compared with the results reported by other authorities in Table V. A great variation in the number of trivalents per cell observed by different workers is apparent from the comparison. Differences in technique can be ruled out as a possible reason for the discrepancies since Mochizuki (51) who used the same technique reports different

frequencies of trivalent formation for the two strains he examined. Possibly the different strains examined so far have different properties as far as trivalent formation is concerned. The results obtained in the present study approximate the results for one of the strains examined by Mochizuki (51) and the results reported by Levan (44). It has been established that the chromosomes of the triploid move to the poles at random during the meiotic division (46, 51), and that there is a deficit of plates with chromosome numbers from fourteen toeighteen, which might account for the non-recovery of plants with chromosome numbers between twenty-one and twenty-four, and the clustering of the chromosome numbers around eighteen to twenty.

Trisomics

It was difficult to secure good plates for analysis at the pachytene stage. The lack of any complex configurations suggests that the plants examined were all primary trisomics. No pattern could be established as to any particular form of trivalent occurring more often in one of the trisomic types. By far the most common configurations were a straight chain or ring. There was a tendency for the number of trivalents to increase from diakinesis to first metaphase in plant No. 2-34, contrary to what has been established in barley (82) and rye (38), where the number of trivalents decreases from diakinesis to first metaphase. No explanation can be given for this discrepancy aside from the fact that the amount of data presently available is still limited, and the possibility that some of the trivalents escaped detection in diakinesis.

Although there were not many good plates at the tetrad stage, the number of micronuclei observed does not correlate with the number of the extra chromosomes which were eliminated (Table VIII).

Synapsis in trisomics

Theoretically the number of bivalents plus the number of trivalents should equal nine, and the number of trivalents plus the number of univalents should equal the number of extra chromosomes.

In this case, the former is less than nine and the latter more than the number of the extra chromosomes, meaning that full synapsis does not always occur. Certain chromosomes may have a lesser effect in promoting trivalent formation (63) and this might explain the lower trivalent formation in type #3.

The high frequency of elimination of the extra chromosome in trisomic type #3 (Table VIII) may be associated with the high frequency of univalent formation in this type, since the rate of elimination increases with the increase in univalent formation, from eighteen per cent for type #1 which has 0.269 univalents per cell to 33.3 per cent for type #3 having 0.597 univalents per cell. The frequency with which the trisomics form trivalents ranges from 0.72 per cell to 0.78 (Table IX). Approximately the same range has been found in Zea mays where it was 0.71 (48). It was lower in Nicotiana sylvestris, i.e., 0.37 (39) for four single trisomics, and 0.48 in eleven of the twelve primary trisomics of tomato (63). In Clarkia unguiculata (86), it was 0.43, increasing with the number of extra chromosomes per cell. This does not seem to be

the case in the material of the present study, since in the triploids examined the mean number of trivalents per cell per extra chromosome is 0.73, almost identical to the values observed for the trisomics.

Thus, although no chiasma frequencies were secured, the hypothesis that extra chromosomes increase the frequency of chiasmata and hence the frequency of trivalent formation (18, 47) does not seem to hold true for the material under study.

SUMMARY

1. Trisomic plants belonging to three primary trisomic types were obtained with a frequency of 35.48 per cent (Table I) in the progeny of triploid X diploid crosses of Beta vulgaris L.

2. The trisomics were classified according to their morphology into three types which were distinct from one another and from the diploids, and were named trisomic type #1, #2, and #3 (Plate 3).

3. Trisomic type #1 was identified cytologically as being the trisomic for the satellited chromosome (Plate 7, Figs. 2 and 3).

4. The pollen fertility of the trisomics ranged from 4.81 to 84.49 per cent, trisomic type #1 exhibiting the lowest pollen fertility (Table IV). Micropollen was observed in all three trisomic types. Unstained pollen grains had a smaller diameter. The diameter of the stained pollen grains varied from 17.80 ± 0.31 to 23.07 ± 0.41 microns (Table IV).

5. The transmission frequencies were 17.33, 30.88 and 23.45 per cent for the trisomic types #1, #2, and #3 respectively; the mean for the three combined being 22.07 per cent. No unrelated trisomics or transmission of the extra chromosome through the pollen was detected. (Table III)

6. Chromosome configurations in M-1 of PMC's were (Table VI): $8^{II} + 1^{III}$ (70.72 per cent), $9^{II} + 1^{I}$ (23.96 per cent) and others

(5.30 per cent). The form of the trivalents was a chain (73.8 per cent), a ring (11.8 per cent), a frying pan (8.94 per cent) and a Y (5.40 per cent), (Table VII).

7. There were 0.269, 0.282 and 0.597 univalents per cell and 0.778, 0.795, 0.724 trivalents per cell in trisomic types #1, #2, and #3 respectively (Table IX) and 6.56 trivalents per cell in the triploids (Table V), indicating that complete synapsis does not always occur.

8. The extra chromosome was eliminated in 18 per cent of the cases in meiotic first telophase in type #1 and 33.3 per cent in type #3. The high rate of elimination in type #3 is attributed to the greater frequency of univalents in this type (Table VIII).

BIBLIOGRAPHY

1. ADATI, S., and MITSUISHI, S. Karyotype analysis in the Beta species. Bull. Fac. Agr. Mis. Univ. 25, pp. 25-32. 1962.

2. ARTSCHWAGER, E. Development of flowers in the sugar beet. J. Agr. Research 34: 1-25. 1927.

3. BABCOCK, E. B., and NAVASCHIN, M. The genus Crepis. Bibliographia Genetica 6: 1-90. 1930.

4. BLAKESLEE, A. F. The Globe, a simple trisomic mutant in Datura. Proc. Nat. Acad. Sci. U. S. 7: 148-152. 1921a.

5. _____. The Globe mutant in Jimson weed (Datura stramonium). Genetics 6: 241-264. 1921b.

6. _____. Variations in Datura due to changes in chromosome number. Amer. Naturalist 56: 16-31. 1922.

7. _____. Extra chromosomes; a source of variations in the Jimson weed. Smithsonian Rep. 1930 Publ. 3096: 431-450. 1931.

8. _____. New Jimson weeds from old chromosomes. J. Heredity 25: 80-108. 1934.

9. _____, and AVERY, A. G. Three genes located in the 21.22 chromosome of the Jimson weed. J. Heredity 25: 393-404. 1934.

10. _____, and _____. Fifteen years of breeding records of 2n + 1 types in Datura stramonium. Coop. Res., Carnegie Inst. Wash. Publ. 501: 315-351. 1938.

11. _____, and FARNHAM, M. E. Trisomic inheritance in the Poinsettia mutant of Datura. Amer. Naturalist 57: 481-495. 1923.

12. BRITISH COLOUR COUNCIL. Horticultural colour chart. Vols. I, II. Banbery and London: Henry Stone & Son Ltd. "1939-1942".

13. BUTTERFASS, Th. Die Chloroplastenzahlen in verschienartigen Zellen trisomer Zuckerrüben (Beta vulgaris L.). Z. Bot. 52(1): 46-77. 1964.

14. CATHESIDE, D. G. The genetics of brevistylis in Oenothera. Heredity 8: 125-157. 1954.

15. CHARECKO-SAVICKAJA, E. I. (Today Savitsky, H.). The karyology of the genus Beta L. Sveklovodstvo (beet culture) Vol. 1. Biologija, Genetika i Selekcja Sacharnoj Svekly (Biology, genetics and breeding of sugar beets.). pp. 516-528. 1940.

16. CHOMCHALOW, N., and GARBER, E. D. The genus Collinsia. XXVI. Polyploidy and trisomy in C. tinctoria. Can. J. Genet. Cytol. 6(4): 488-499. 1964.

17. CLAUSEN, R. E., and GOODSPEED, T. H. Inheritance in Nicotiana tabacum. IV. The trisomic character "Enlarged". Genetics 9: 181-197. 1924.

18. DARLINGTON, C. D., and MATHER, K. The origin and behaviour of chiasmata. III. Triploid Tulipa. Cytologia 4: 1-15. 1932.

19. DERMEN, H. Polyploidy in Petunia. Amer. J. Botany 18: 250-261. 1931.

20. DHILON, T. S., and GARBER, E. D. The genus Collinsia. X. Aneuploidy in C. heteroplylla. Bot. Gaz. 121 (3): 125-133. 1960.

21. ELLIS, J. R., and JANICK, J. The chromosomes of Spinacia oleracea. Amer. J. Botany 47 (3): 210-214. 1960.

22. EMERSON, S. H. The trisomic derivatives of Oenothera lamarckiana. Genetics 21: 200-224. 1936.

23. FELTZ, H. Untersuchungen an diploiden und polyploiden Zuckerrüben. Cytologische Untersuchungen der Mikrosporogenese und Betrachtungen über ihre Bedeutung für die Zuckerrübenzüchtung. Z. Pflanzenzüch. 32: 275-300. 1953.

24. FROST, H. B. Mutation in Matthiola. Univ. Cal. Publ. Agr. Sci. 2: 81-190. 1919.

25. _____. Chromosome mutant types in stocks. 1. Characters due to extra chromosomes. J. Heredity 18: 475-486. 1927.

26. _____. Trisomic inheritance of doubleness, complicated by lethals in Matthiola incana. Proc. Nat. Acad. Sci. U.S. 17: 499-509. 1931.

27. GARBER, E. D. The genus Collinsia. XXII. Trisomy in C. heterophylla. Bot. Gaz. 125 (1): 46-50. 1964.

28. GASKILL, J. O. Induction of reproductive development in sugar beets by photothermal treatment of young seedlings. Proc. Amer. Soc. Sugar Beet Technol. pp. 112-120. 1952.

29. GERASSIMOVA, H. A translocation between the B- and D-chromosomes and the trisomic effect of the B-chromosome in Crepis tinctorum L. Akademia Nauk, USSR Izvestia. Ser. Biolog. 1: 31-44. (English summary). 1940.

30. GOODSPEED, T. H. and AVERY, P. Trisomic and other types in Nicotiana sylvestris. J. Genet. 38: 381-458. 1939.

31. _____, and _____. The twelfth primary trisomic type in Nicotiana sylvestris. Proc. Nat. Acad. Sci. U.S. 27: 13-14. 1941.

32. HERZOG, C. Genetische und cytologische Untersuchungen über 15-chromosomige Mutanten von Oenothera biennis und Oenothera lamarckiana. Flora 134: 377-432. 1940.

33. HESEMAN, C. U. Cytogenetische Untersuchungen an Trisomen von Petunia hybrida. Z. Pflanzenzüch. 51 (1): 1-11. 1964.

34. JAKOB, K. M. A trisomic male castor bean plant. J. Heredity 54: 292-296. 1963.

35. JANICK, J., MAHONEY, D. L., and PFAHLER, P. L. The trisomics of Spinacea oleracea. J. Heredity 50: 46-50. 1959.

36. JOHNSSON, H. Cytological studies of diploid and triploid Populus tremula L. and of crosses between them. Hereditas XXVI. 1940.

37. _____. Cytological studies of triploid progenies of Populus tremula L. Hereditas 28: 306-312. 1942.

38. KAMANOI, M., and JENKINS, B. C. Trisomics in common rye, Secale cereale L. Seiken Ziho 13: 118-123. 1962.

39. KATTERMAN, G. Sterilitäs Studien bei Hordeum distichum. Z. indukt. Abstamm- u. Vererblehre 77: 63-103. 1939.

40. KERBER, E. R. Trisomics in barley. Science 120: 808-809. 1954.

41. LESLEY, J. W. A cytological and genetical study of progenies of triploid tomatoes. Genetics 13: 1-43. 1928.

42. _____. Trisomic types of the tomato and their relation to the genes. Genetics 17: 545-559. 1932.

43. LEVAN, A. Chromosome numbers in Petunia. Hereditas (Lund) 23: 99-112. 1937.

44. _____. The effect of chromosomal variation in sugar beets. Hereditas (Lund) 28: 345-399. 1942.

45. LEWITSKY, G. A. A cytological study of the progeny of X-rayed Crepis capillaris Wallr. Cytologia II: 1-29. 1940.

46. LINDE-LAURSEN, I. Studies in cytology and fertility of polyploid and aneuploid beet. Royal Vet. and Agr. Coll., Copenhagen, Yearbook 1964, pp. 92-120.

47. MATHER, K. Competition for chiasmata in triploid and trisomic maize. Z. Zellforsch, u. Mikrosk. Anat. Abt. b: chromosome: Z. Zellkern u. Chromosomenforsch. 1 (1): 119-129. 1939.

48. McCLINTOCK, B. A cytological and genetical study of triploid maize. Genetics 14: 180-222. 1929.

49. _____, and HILL, H. E. The cytological identification of the chromosome associated with the r-g linkage group in Zea mays. Genetics 16: 175-190. 1931.

50. McLENNAN, H. A. "Cytogenetic studies of a strain of barley with long chromosomes." Unpublished Master's Thesis, The University of Minnesota, 1947.

51. MOCHIZUKI, A. Genetic and cytological studies on the genus Beta. In "Improvement of sugar beets by means of triploidy" edited by S. Matsumura, (Tokyo: Science-Sha, 1953), pp. 14-39.

52. MYERS, W. M. Cytological studies of a triploid perennial ryegrass and its progeny. J. Heredity 35: 17-23. 1944.

53. PRICE, E. M., and ROSS, W. M. The occurrence of trisomics and other aneuploids in a cross of triploid X diploid Sorghum vulgare. Agron. J. 47: 591-592. 1955.

54. _____, and _____. Cytological study of a triploid X diploid cross of Sorghum vulgare Pers. Agron. J. 49: 237-240. 1957.

55. RAI, K. S., and GARBER, E. D. The genus Collinsia. XI. Trisomic inheritance in C. heterophylla. Bot. Gaz. 122 (2): 109-117. 1960.

56. RAMAGE, R. T. "The trisomics of barley." Unpublished Ph.D. Thesis, The University of Minnesota, 1955.

57. _____, and DAY, A. D. Separation of trisomic and diploid barley seeds produced by interchange heterozygotes. Agron. J. 52: 590-591. 1960.

58. RANK, G. H. "The occurrence and nature of polyploidy in a colchicine treated population of sugar beets." Unpublished Master's Thesis, The University of Manitoba, 1964.

59. RASMUSSON, J., and LEVAN, A. Tetraploid sugar beets from colchicine treatments. Hereditas 25: 97-102. 1939.

60. REITBERGER, A. Ruhenkernuntersuchungen bei gesunden und viruskranken Diploiden und Polyploiden von Beta vulgaris L. Züchter 26 (4/5): 106-117. 1956.

61. RENNER, O. Zur kenntnis der 15-chromosomigen Mutanten von Oenothera lamarckiana. Flora 134: 257-310. 1940.

62. _____. Kurze Mitteilungen über Oenothera VI. Über die 15-chromosomigen Mutanten dependens, incana, scintilans, glossa, tripus. Flora 137: 216-229. 1943.

63. RICK, C. M., and BARTON, D. W. Cytological and genetical identification of the primary trisomics of tomato. Genetics 39 (5): 640-666. 1954.

64. _____, et al. Further studies on the primary trisomics of tomato. Can. J. Genet. Cytol. 6: 93-108. 1964.

65. RUDORF-LAURITZEN, M. The trisomics of Antirrhinum majus L. Proc. Intern. Congr. Genet. 10th Congr. Montreal 2: 243-244. 1958.

66. SAMPSON, D. R., et al. Triploid X diploid progenies and the primary trisomics of Antirrhinum majus. Can. J. Genet. Cytol. 3 (2): 184-194. 1961.

67. SAVITSKY, H., and GASKILL, J. O. A cytological study of F_1 hybrids between Swiss chard and Beta webbiana. J. Amer. Soc. Sugar Beet Technol. IX (5): 433-449. 1957.

68. SCHNEIDER, H. Methods zur Erzeugung tetraploider Beta - Rüben auf blütenbiologischem Wege. Züchter 35 (1/2): 37-40. 1965.

69. SEARS, E. R. Monosomes, trisomes and segmental interchanges from a haploid of Triticum vulgare. Genetics 24: 509-523. 1939.

70. _____. The aneuploids of common wheat. Univ. Mo., Coll. Agr., Agr. Exptl. Sta. Research Bull. 572. 1954.

71. SEN, S. K. Cytogenetics of trisomics in rice. Cytologia 30 (2): 229-238. 1965.

72. SMITH, H. H. Effects of genomic balance, polyploidy and single extra chromosomes on size in Nicotiana. Genetics 28: 227-236. 1943.

73. SMITH, L. An inversion, a reciprocal translocation, trisomics and tetraploids in barley. J. Agr. Research 63: 741-750. 1941.

74. SORIANO, J. D. The genus Collinsia. IV. The cytogenetics of colchicine-induced reciprocal translocations in C. heterophylla. Bot. Gaz. 118: 139-145. 1957.

75. STUBBE, H. Studien über heteroploide Formen von Antirrhinum majus L. I. Mitteilung: Zur Morphologie und Genetik der Trisomen Anaemica, Fusca, Purpurea, Rotunda. Planta 22: 153-170. 1934.

76. SUTTON, E. Trisomics in Pisum sativum derived from an interchange heterozygote. J. Genet. 38: 459-476. 1939.

77. TABUSHI, J. Trisomics of spinach. Seiken Ziho 9: 49-57. 1958.

78. TAGAGI, F. Karyological studies on rye. 1. A trisomic plant. Cytologia 6: 496-501. 1935.

79. TSUCHIYA, T. Cytogenetics of a hypo-triploid barley and its progeny. Mem. Beppu (Women's) Univ. 2: 19-42. 1952.

80. _____. Trisomics in barley. Japan. J. Genet. 29: 179. 1954.

81. _____. Studies on the trisomics in barley. L. Origin and the characteristics of primary simple trisomics in Hordeum spontaneum C. Koch. Seiken Ziho 9: 68-86. 1958.

82. _____. Cytogenetic studies of trisomics in barley. Japan. J. Botany 17: 177-213. 1960.

83. _____. Personal communication. 1966.

84. VASEK, F. C. Induced aneuploidy in Clarkia unguiculata. (Onagraceae). Amer. J. Botany 43 (5): 366-371. 1956.

85. _____. Trisomic transmission in Clarkia unguiculata. Amer. J. Botany 48 (9): 829-833. 1961.

86. _____. Trivalent formation in multiple trisomics of Clarkia unguiculata. Amer. J. Botany 50 (3): 244-247. 1963a.

87. _____. Phenotypic variation in trisomics of Clarkia unguiculata. Amer. J. Botany 50 (4): 308-314. 1963b.

88. ZAJKOVSKAJA, N. E. (Morphologie der chromosomen der Zuckerrübe). Veroffentlichungen des wiss. Forschungsinstituts der Zuckerindustrie der Ud SSR 23 (4): 43-67. 1935.