

AN AUTOTRIPLOID IN THE PEARL MILLET (*Pennisetum typhoides* S. & H.!)

BY N. KRISHNASWAMY, B.Sc., Ph.D.

AND

G. N. RANGASWAMI AYYANGAR, F.N.I., I.A.S.

(*Millets Breeding Station, Agricultural Research Institute, Coimbatore*)

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1. Introduction

TRIPLOIDS have been recorded amongst the cereals in Wheat (Thompson, 1929; Mather, 1935), Maize (Randolph and McClintock, 1926; McClintock, 1929), Rice (Nakamori, 1932; Ramiah *et al.*, 1933; Ramanujam, 1937), Oats, Barley and Rye (Müntzing, 1938). So far the occurrence of a triploid has not been reported in any of the millets and the present observation thus forms the first record of a triploid in *Pennisetum typhoides*.

Origin of the Triploid.—The present triploid is the progeny of a sterile plant which was observed in the lot M.S. 4477—*Arupatham Cumbu*, Velur, a fresh arrival at the Millets Breeding Station, Coimbatore, and grown in the summer of 1939. This sterile plant was about 100 cm. high with a number of tillers. The stems were thin and leaves normal; earheads rather short (15.9 cm.). The plant though surrounded by normal diploids and itself produced enough, free pollen failed to set seed. On examination the pollen did not show any indication of high sterility. Since the plant is protogynous and there were no seeds set in spite of abundance of pollen, it was thought to be female-sterile. The plant was noted rather late in the season and therefore efforts were made only to secure some seeds from it and no materials gathered for cytological examination because of the paucity of earheads. The stigmas were repeatedly dusted with pollen from other heads from the same plant and nine seeds were obtained from about a dozen heads. These seeds therefore were in a manner, from selfed heads.

The seeds were sown in pots in summer 1940 and later transplanted into the field. Only seven seeds germinated. Out of these seven plants four proved to be normal diploid, about 250 cm. high with full setting of seeds. Of the remaining three one was a partially sterile dwarf 38 cm. high with thin stems and produced only one head. This plant gave the diploid number of $2n = 14$ in the root-tips. The second plant was also partially sterile but the plant was vigorous and the seeds set fairly well.

The third plant was vigorous and healthy; the leaves were normal. Vegetatively the plant showed no difference from the others. Towards flowering time, however, the sheath showed a swelling above the flag node.



FIG. 1 (a)

(a) Diploid plant. 1/20 natural size



FIG. 1 (b)

(b) Triploid plant. 1/12 natural size

but no panicles emerged. On opening this portion a short highly abnormal panicle was seen. The spikelets were short, malformed and often much thickened. The glumes had a membranous, ligulate outgrowth at the tip. The stigmas and anthers were found in various stages of suppression. Some of the flowers were seen to have yellowish green, normally developed anthers.

The later heads of this plant were freely emerging and normally developed (Fig. 1 *b*). This plant on examination proved to be a triploid. It, however, showed no difference in other respects from the diploid. The following gives a comparative idea of pollen size, etc., between the diploid and the triploid:

	Height of plant	Length of leaf	Length of anther	Stomata		Pollen diameter	Sterility
				Length μ	Breadth μ		
Diploid ..	cm. 250	cm. 50	mm. 2.6	33.6	27.1	μ 38.8	% 8
Triploid ..	cm. 100	cm. 38	mm. 2.5	34.4	30.7	μ 32.9	% 50

2. Cytology

Materials and Methods.—The root-tips of the diploid and the triploid were fixed in Levitsky's fluid. The flower buds were gathered in the triploid both from the malformed and the well-formed, freely emerging earheads and fixed in modified Karpechenko's fluid. The sections were stained according to Feulgen's technique and counterstained with Fast-green (Jacob). The drawings were done with a Spencer's Camera-Lucida and Zeiss microscope. Unless otherwise stated all figures are drawn to a magnification of about $\times 1500$.

(a) Mitosis—

The counterstaining with Fast-green brought the nucleoli into prominence so that it was possible to distinguish in early telophase in the triploid three small nucleoli initiating themselves each on one chromosome (Fig. 2 *f*). In the resting nucleus three nucleoli could be counted and in no case were

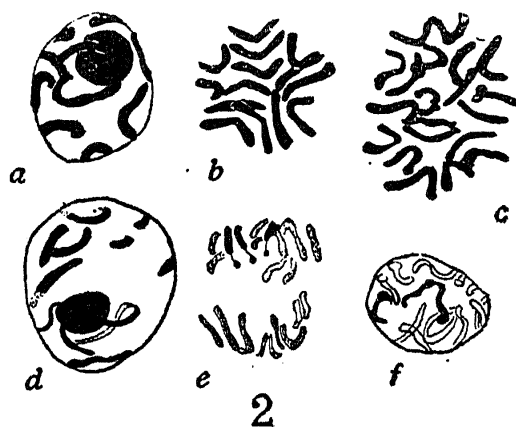


FIG. 2

(a) Diploid, prophase showing nucleus with 2 nucleolar chromosomes. (b) Metaphase plate of diploid with 14 chromosomes. (c) Triploid metaphase plate—21 chromosomes. (d) Triploid prophase with 3 nucleolar chromosomes. (e) Telophase of triploid showing 3 sat-chromosomes. (f) Early telophase of triploid showing the 3 nucleoli initiating on nucleolar chromosomes.

there more than three, while owing to fusion of the three nucleoli number less than three were met with, *i.e.*, two or one. In such cases one nucleolus was always seen to be smaller than the other, showing that the larger has arisen from the fusion of two nucleoli. Fig. 2 *d* shows the nucleolus at the prochromosome stage with three chromosomes attached to one large nucleolus. At the prophase it was not possible to definitely find out whether all the three nucleolar chromosomes had satellites. However, in the side-view of a telophase three sat-chromosomes were seen (Fig. 2 *e*).

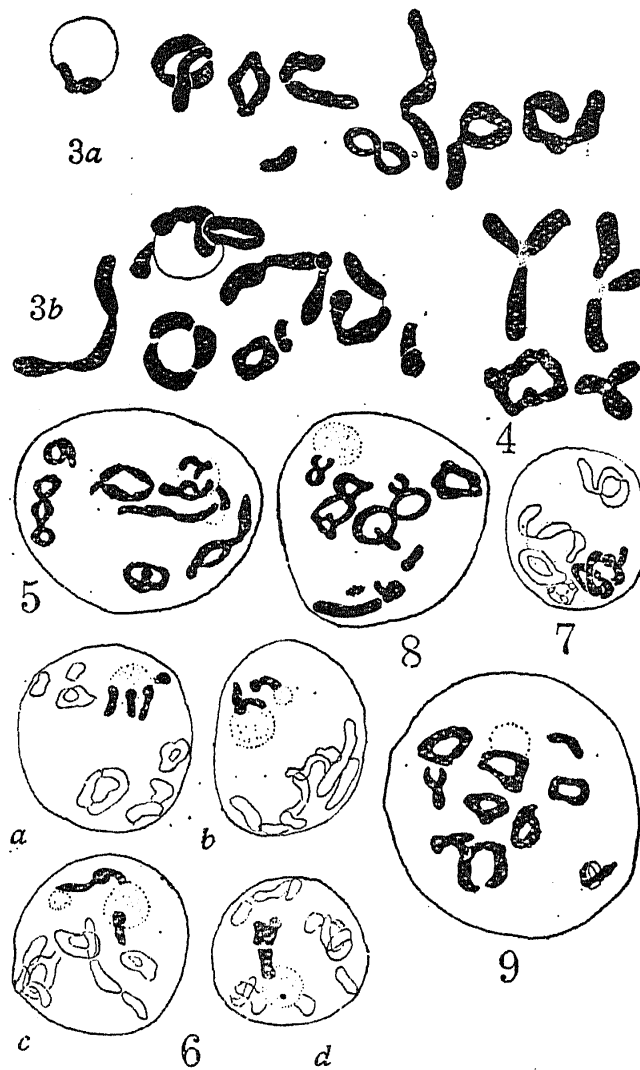
Metaphase.—At metaphase the chromosomes are rather long and hence not lying in one plane (Fig. 2 *c*). In some cases the three nucleoli persist at metaphase attached to their chromosomes. Sat-chromosomes are seen in metaphase but all three could not be seen in one and the same plate. The number of chromosomes as counted in the metaphase plate was found to be twenty-one. These metaphase chromosomes were not sufficiently distinctive to recognise homologues of each set.

The chromosomes of the diploid *Pennisetum* have been studied by Rau (1929), Audulow (1931), Rangaswami (1935) and Krishnaswamy (1939). The root-tip of a diploid, sister plant to the triploid, was examined for comparison. At prophase the maximum number of nucleoli produced were found to be two and only two chromosomes were seen attached to the nucleolus (Fig. 2 *a*). The number of chromosomes counted at the metaphase was fourteen (Fig. 2 *b*). The diploid to a certain extent showed somatic pairing and the homologues could be somewhat distinguished.

(b) *Meiosis*—

The prophase stages were difficult to study on account of the thinness of the threads. The stages were therefore followed from diakinesis onwards.

Diakinesis.—At diakinesis the chromosomes are much thickened and shortened. Trivalent associations are common. The most frequent configurations are chains of three Y's, and the 'Frying-pan' types. In three cases a ring of three chromosomes was observed. The trivalents usually occurred with a few bivalents and univalents. The most common associations are five and six trivalents with varying numbers of bivalents and univalents. Figs. 3 *a* and *b* represent two P.M.C.'s at diakinesis, with the chromosomes spaced apart. Fig. 3 *a* shows $4_{III} + 4_{II} + 1_I$, and Fig. 3 *b*— $4_{III} + 3_{II} + 3_I$. In Fig. 3 *b* is seen also a ring trivalent with terminalised chiasmata. Fig. 4 shows two Y-trivalents, one ring with non-terminalised chiasmata and one with triple chiasma. Fig. 5 is at late diplotene showing $2_{III} + 7_{II} + 1_I$. In only four cases seven trivalents, the maximum number possible, were observed.



FIGS. 3-9

Fig. 3.—Diakinesis. $\times 2250$. Fig. 4.—Diakinesis, figures Y-shaped, ring of three and triple chiasmata. $\times 2250$. Fig. 5.—Late diplotene. Fig. 6.—Pairing of nucleolar chromosomes. Fig. 7.—Interlocking. Fig. 8.—Late diplotene abnormal pairing. Fig. 9.—Diakinesis, showing no trivalents.

The nucleolar chromosomes usually form a bivalent and a univalent (Fig. 6 b). The univalent is always attached to a small nucleolus while the bivalent to a single large one. In Fig. 6 c two of the nucleolar chromosomes have paired at the free ends. At the other end they are attached one to a large nucleolus to which also a univalent is attached and the other of the pair to a smaller nucleolus. In these only the portions of the chromosomes free of the nucleolus are seen paired and never the region attached to the nucleolus. The only type of configuration these chromosomes form is the Y-type. The nucleoli interfere in the free association of the chromosomes and in one case all the three were seen side by side attached to one large nucleolus (Fig. 6 a). Owing to this mechanical interference the

nucleolar chromosomes almost always contribute to the number of the univalents. The following gives the frequency of the trivalent formations:

										Total
Trivalents per P.M.C.	0	1	2	3	4	5	6	7	
Number of P.M.C.'s observed	2	1	..	3	12	25	19	4	66

Mean number of trivalents per cell = 4.95. In the two cases in which a complete failure of trivalent formation was noted there were $8_{II} + 5_I$ and $10_{II} + 1_I$ (Fig. 9).

A few abnormalities in pairing were observed. Fig. 8 shows three ordinary bivalents, two figure of eight configurations and some univalent. One of the univalents is abnormally large while the other is normal. One P.M.C. showed two ring bivalents interlocked (Fig. 7). Associations of more than three chromosomes are drawn in Fig. 10 (*a*—shows a ring of three and a rod; *b*—shows a frying-pan type with two chromosomes attached

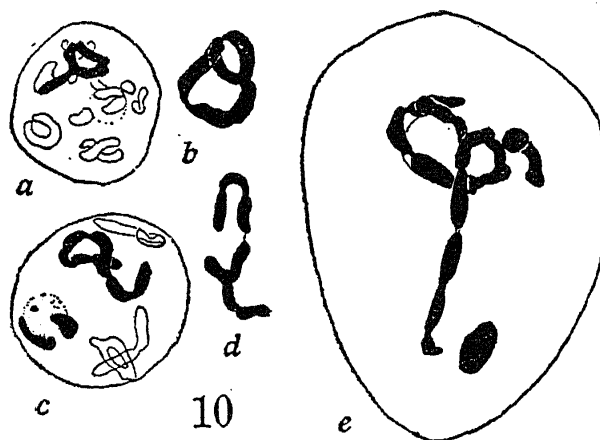


FIG. 10

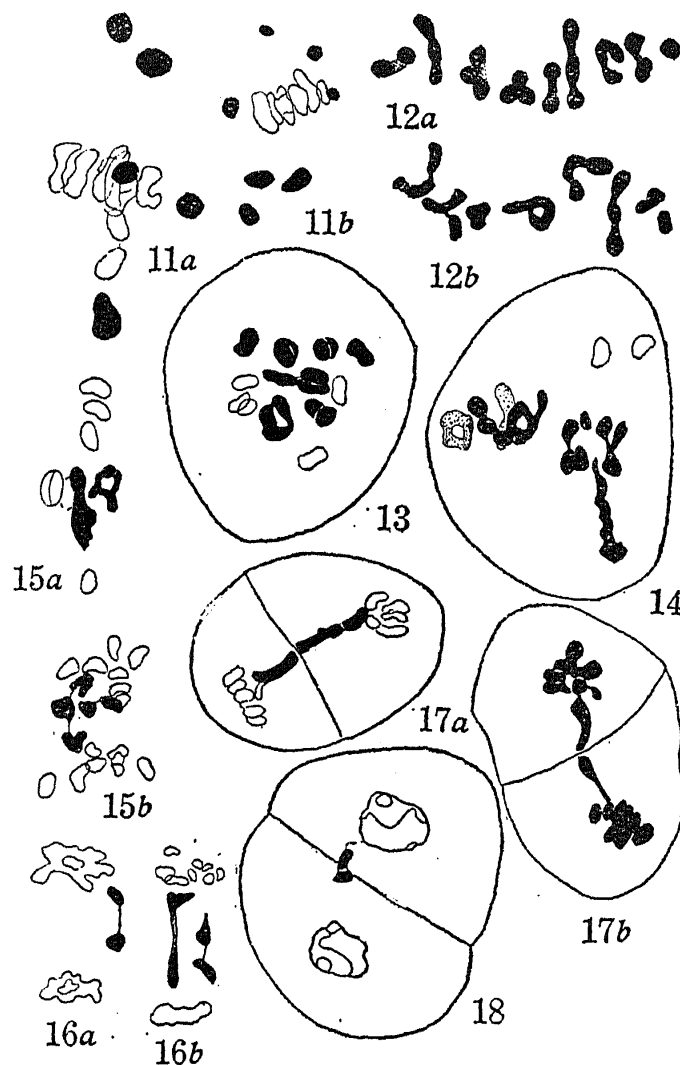
Multivalent associations at diakinesis: (*a*) A ring of three and a rod. (*b*) Chain of five. (*c*) and (*d*) Chain of seven. (*e*) Chain of ten.

tandem to the rod; *c*—is a chain of seven; *d*—consists of a normal chain of three associated to a Y-type, while one of the arms of the Y has another chromosome; *e*—is a chain of ten chromosomes *plus* one chain of three ($1_{II} + 1_I$).

Metaphase.—At metaphase the chromosomes form a more or less loose equatorial plate. The trivalents, bivalents and some univalents are arranged in a haphazard manner. The univalents are found mostly distributed in the spindle well outside the equatorial plate. Two metaphase plates are shown in Figs. 11 *a* and *b* with five and seven univalents. In Fig. 12 *a* and *b* are drawn two metaphase plates spaced out (*a*) $5_{III} + 2_{II} + 2_I$; (*b*) $6_{III} + 1_{II} + 1_I$. Fig. 13 is a polar view containing $2_{III} + 5_{II} + 5_I$. The number of univalents

occurring at the first metaphase plate varied from zero to seven, the most common number being one, two or three. A normal bipolar spindle is formed.

Anaphase.—At anaphase the bivalents are seen to separate first. The trivalents disjoin in two and one each going to one pole. In Fig. 14 at early anaphase ($5_{III} + 2_{II} + 2_{I}$) three trivalents are seen disjoining into two and one. In Fig. 15 *a* is a ring trivalent with interstitial chiasma and a chain trivalent separating into one and two. Fig. 15 *b* shows a trivalent rather late in disjoining. Very often one to two trivalents were seen lagging owing to delay in disjunction (Figs. 16 *a* and *b*). Chromatin bridges were observed in a few cases. These bridges persist so long that they get cut in two by the



FIGS. 11-18

Fig. 11.—Side view of metaphase I: (a) $\times 2250$,—showing 5_{I} ; (b) showing 7_{I} . Fig. 12. metaphase I. Side view chromosomes spaced out: (a) $5_{III} + 2_{II} + 2_{I}$; (b) $6_{III} + 1_{II} + 1_{I}$. Fig. 13.—Polar view of metaphase I. Fig. 14.—Anaphase early. Fig. 15.—Anaphase: disjunction of the trivalents. Fig. 16.—Lagging of bivalents and trivalents. Fig. 17.—Chromatin bridge first division, cut by the interphase wall. Fig. 18.—Fragment caught in the interphase wall with remnant of bridge.

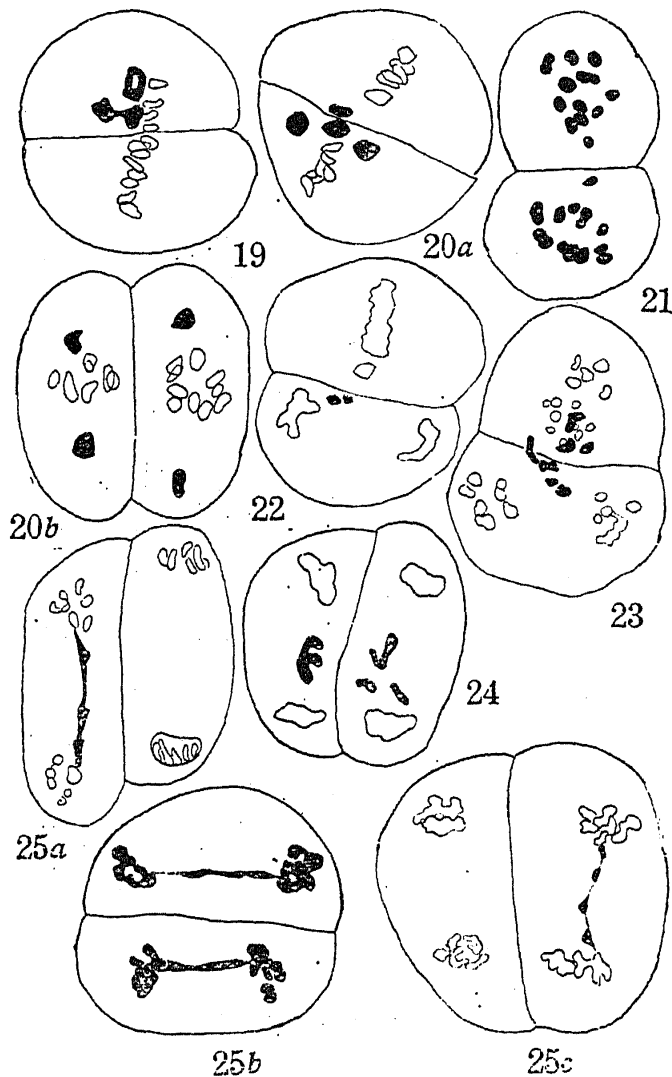
growing interphase wall (Figs. 17 *a* and *b*). In a few instances one to two univalents were found dividing at the equator towards late anaphase. It was frequently observed that the univalents after coming to the equator failed to divide and move to the poles, consequently they were also cut in two by the growth of the interphase wall. The fragmentation of the chromosomes thus resulted. The analysis of thirteen clear late anaphase stages gave the following distributions of the chromosomes. In a few of them it was seen that trivalents had moved to the poles without disjunction.

Distribution of the chromosomes at first early telophase

12	1	8	1	
11	0	10	2	
11	1	9	1	
11	2	8	4	(Two trivalents without disjunction)
10	1	10	1	
10	2	9	1	
10	3	8	1	
10	1III	8	1	(One trivalent lagging)
9	4	8	1	

Telophase.—A regular interphase nucleus with nucleoli is formed. A few cells show the persistent first division bridge attached to a fragment (Fig. 18). Sometimes the fragment is cut in two by the cell wall. This particular fragment showed a subterminal achromatic portion. Univalents are sometimes seen lying near the poles without moving. These get included in the first division daughter nuclei.

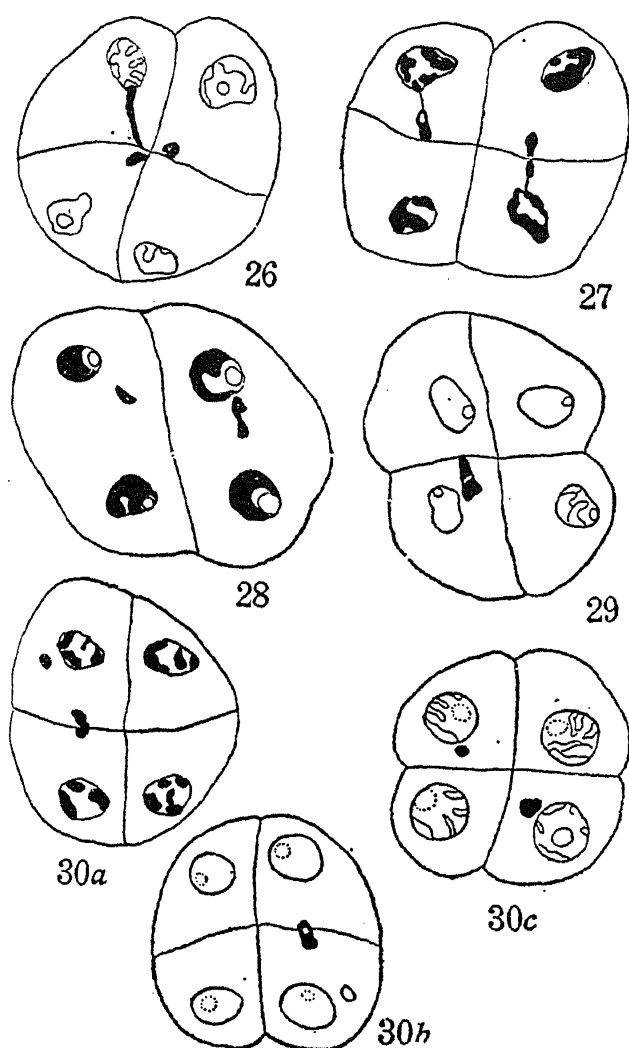
Second Division.—The second division plates are normal, but very often they are loosely formed (Fig. 19). Univalents of varying numbers are found distributed on the spindle. Some of them are at the poles while the others are still at the equatorial plate (Figs. 20 *a* and *b*). Polar view of second metaphase often shows chromosomes in excess of the expected numbers. This is probably due to univalents dividing and getting inclosed in the same nucleus (Fig. 21) (Randolph and McClintock, 1926; Kostoff and Kendall, 1931), the most common distribution being 9–11 with a univalent lagging. The exact numbers could not be determined in many second metaphase plates, especially where the numbers were high, owing to secondary associations and also due to the divided chromosomes sticking close together. Usually both cells divide together but in some cases one daughter cell ma



FIGS. 19-25

Fig. 19.—Metaphase II showing 2II in one plate. Fig. 20.—Univalents at metaphase II. Fig. 21.—Polar view of metaphase II. Fig. 22.—Disparity in the division time of the daughter cells. Fig. 23.—Univalents left on plate in division II. Fig. 24.—Trivalents disjoining at second division. Fig. 25.—Second division bridges.

be in telophase while its sister cell is still at metaphase (Fig. 22). In such cases usually the nuclei with smaller chromosome numbers divide earlier. In one P.M.C. a bivalent and a trivalent were found lagging each in one daughter nucleus (Fig. 24). Chromatin bridges are more frequent in the second division than in the first division. Either one daughter cell (Fig. 25 *a-e*) or both (Fig. 2 *b*) show the bridges. Tetrads are regularly formed and no restitution nuclei are formed. However, in many tetrads (Figs. 28-30) fragments and univalents occur in the cytoplasm. Fig. 23 shows univalents remaining at the equatorial plate at telophase. Figs. 26 and 27 show fragments in tetrads with chromatin bridge still persisting.



FIGS. 26-30

Fig. 26.—Remnant of bridge and fragment cut by the intersecting wall. Fig. 27.—Two fragments one in each cell. Fig. 28.—A univalent and a fragment in the cytoplasm. Fig. 29.—A large fragment with achromatic portion. Fig. 30.—Fragments in tetrads.

3. Discussion

The frequency of the formation of the trivalents in this plant is high (5 per P.M.C.) and the maximum number of trivalents that can be formed in a P.M.C., *i.e.*, seven, was observed in 6 per cent. of the cells counted. The trivalents are usually found along with bivalents and univalents. Müntzing (1936) remarks that in experimental autopolyploids having more than two homologous chromosomes of each kind the formation of multiple associations is very characteristic. The maximum number of chromosomes in these associations correspond to the number of genomes present. He concludes: "In short the presence of multivalents indicates autopolyploidy and the absence of allopolyploidy." The occurrence of bivalents and univalents has been noted in other autotriploids also (Bleier, 1934). In fact, the maximal theoretically possible chromosome association never occurs

in reality. The chromosome association is almost always incomplete and this incompleteness varies considerably in different species (Müntzing, *loc. cit.*). The causes for failure of pairing are several. Kostoff and Kendall (*loc. cit.*) refer the varying number of trivalent formation to the degree of affinity among the homologous chromosomes. Sapehin (1933) is of the opinion that the conjugation of chromosomes is conditioned by genes and that the external conditions also exert a great influence on the conjugation of chromosomes. Federly (1932) is of a similar opinion. Dark (1932) considers the competition in pairing between the three homologous chromosomes of the triploid as the real reason for the failure of pairing. Darlington and Mather (1932) point out that if association between two members of a set of three homologous chromosomes were very extensive the chances of a chiasma forming between the free portion of one and the third chromosome would be correspondingly reduced and a bivalent and a univalent would result. Darlington (1929), however, says that failure in a polyploid to form trivalents, quadrivalents and so forth at the metaphase can in some measure be attributed to inability of a chromosome to maintain a connection with more than one other at a time and not necessarily to lack of affinity for more than one of its homologues. Further according to Müntzing (*loc. cit.*) non-conjugation does not necessarily mean non-homology, but conjugation is a strong indication of homology. Sansome and Philp (1939) distinguish triploids resulting from crossing two plants of different phylogeny and those arising through crossing of plants of similar origin. The first having three sets of chromosomes of which at least one is distinct from the other two is called allotriploid. The second class with all three sets of chromosomes homologous is called autotriploid. These evidences support the view that the plant described is an autotriploid. Its constitution may be represented as

A B C D E F G
A B C D E F G
A B C D E F G

The trivalent configurations are of the types expected in an autotriploid (Darlington,¹ 1937). The ring of three chromosomes, however, is an exception. This type of trivalent formation has been observed by other authors also (Affify, 1933; Philp and Huskins, 1931). Affify derives the ring of three chromosomes by assuming two homologous ends in one of the chromosomes (owing to segmental interchange). Thus the three chromosomes would be A-B, A-B and A-A, which would form a ring in diakinesis.

Multiple associations of more than three chromosomes have been met with in other triploids,—in *Aconitum* (Affify, *loc. cit.*), Rice (Ramanujam,

loc. cit.), *Mathiola incana* (Philp and Huskins, *loc. cit.*). These configurations are considered to be due to segmental interchange in some of the chromosomes. The complete failure of the trivalent leads to the formation of bivalents as in the case of the 9 and 10 bivalents. Yarnell (1929) in *Fragaria* ascribes these to pairing in non-homologous chromosomes. Darlington¹ (*loc. cit.*) however is of the opinion that these are all owing to interchange in the chromosomes.

Lagging and bridge-formation have been observed in the first and with a greater frequency in the second division. In some of the P.M.C.'s both daughter nuclei showed each one bridge. One fragment in particular, with an achromatic portion, has been observed both at the interkinesis and also at the second division. The behaviour of this fragment indicates that it is acentric. Bridge-formation is the result of inversion. The presence of bridges at the first anaphase as also in the second indicates that crossing over has occurred between two dislocated chromatids giving a dicentric chromatid forming a bridge at the first division. The pairing of dislocated segments within one chromosome (inverted duplication) may occur as part of a trivalent combination. The two centromeres in such cases may pass to the same pole but a reciprocal bridge will form at the second division at anaphase (Darlington,¹ *loc. cit.*). Westfall (1940) has shown that inversion in one of the homologues of a set of three may lead to bridge formation either in the first or the second anaphase or no bridge formation at all depending on the random assortment of the dicentric chromosomes, but almost always an acentric fragment would result. Emsweller and Jones (1937) also showed fragmentation without bridge formation and put forward the probability of bridge formation without inversion. This they show is possible "when two chromosomes pair in such a manner that their insertion regions are not opposite each other and a single cross-over occurs in the interval between the insertions, a bridge will ordinarily result". They have found this type of pairing common in *A. cepa* × *fistulosum* hybrids. The present case is considered to be like those described by Westfall (*loc. cit.*) where inversion has occurred in one of the three homologous chromosomes of a trivalent and the bridge formation in the first or the second division being dependent on the random assortment of the dicentric chromosome.

The triploid may arise in hybrids between a tetraploid mother and a diploid father or as a mutation in a diploid population. Muntzing¹ (*loc. cit.*) has described a number of cases in which the triploid has arisen as one of the twin plants. The triploid can arise in a diploid population either (1) by dispermy, *i.e.*, two sperms fertilising the same egg (Rhoades, 1936; Ramanujam, *loc. cit.*), or (2) a diploid gamete may unite with a haploid

gamete. The diploid gamete may be the sperm (Rhoades, *loc. cit.*) or the egg. The latter is more common since a diploid egg is more functionable than a diploid sperm. Watkins (1932) has shown that lowering in the normal ($2n$ mother tissue and n pollen) ratio of the pollen tube to the female parent tissue in respect of their chromosome numbers results in the retardation of the growth of the pollen tube and fertilisation fails. Huskins (1934) records the possibilities of the triploid arising somatically. The present triploid has obviously arisen by the fusion of diploid and haploid gametes. It could not be said which of the gametes was diploid.

The plant produces some free pollen but yet it is highly sterile. A few seeds have been obtained by pollinating with the pollen from other heads of the same plant. A number of ears are being dusted with pollen from diploid plants. Levan (1936) found in the somatic counts of the progeny reciprocal crosses between diploid and triploid *A. schænoprasum* considerable differences in number according to whether the $2n$ or the $3n$ was the female parent. With $2n$ as the mother mostly diploids were obtained, while with $3n$ as mother all numbers from $2n$ to $3n$ were obtained. Huskins (*loc. cit.*) curiously enough obtained only $4n$ plants in the progeny of the triploid tomato. $4n$ Plants have also been reported in the progeny of other triploid plants (Sansome and Philp, *loc. cit.*).

4. Summary

- (1) An autotriploid plant was noted in the progeny of a sterile plant in *Pennisetum typhoides*, S and H.
- (2) Vegetative characteristics of this plant did not differ in any way from the diploid.
- (3) The $2n$ number of the plant is 21. The diploid shows $2n = 14$.
- (4) The meiosis showed a high frequency of trivalent formation. The most common configurations were chains of three, frying-pan and Y-types. Rings of three chromosomes were noted in a few cases.
- (5) Higher associations than three were met with. These are considered to be due to segmental interchange.
- (6) Fragmentation and bridge formation were frequent at the first and second anaphases. Inversion has taken place in one of the homologues of a trivalent. This plant therefore belongs to the structural hybrids class.
- (7) Tetrads were normally formed and some free pollen is obtained.
- (8) The plant is highly sterile. It is being crossed with diploid plants and also self-pollinated with a view to study the progeny.

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