A CYTOLOGICAL STUDY OF A TRIPLOID X DIPLOID CROSS OF SORGHUM VULGARE

by

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INTRODUCTION

An off-type sorghum plant having slightly less than normal vigor, early heading, excessive side branches, many tillers, and very low seed set was found in a row of White Collier sorgo at the Fort Hays Branch Experiment Station in 1953. It was assumed to be a haploid plant since the observed characteristics were similar to those reported in haploid sorghum by Brown (20).

Cytological examination of the microsporocytes showed that the plant was actually a triploid. It was recognized as a possible source of trisomics. It was assumed that Sorghum vulgare is not a sufficient polyploid to allow missing chromosomes necessary for the occurrence of monosomics and nullisomics.

Although seven linkage groups, four of them involving three or more genes, have been studied in Sorghum vulgare, the chromosome with which they are each associated has not been determined. Any trisomics isolated probably would be of value in locating particular factors on specific chromosomes and in determining linkage groups.

A cytological study of the triploid plant and its progeny was undertaken to determine the chromosome number and meiotic behavior of the various plants. This would indicate the probable frequency of occurrence of plants with the various chromosome numbers and especially the frequency of occurrence of the trisomics expected from a triploid x diploid cross. Plants occurring in the progeny of the triploid x diploid cross with more than one extra chromosome probably could be used as the source of additional trisomics.

REVIEW OF LITERATURE

Triploidy is widespread in plants; it has been found in grasses, forest trees, garden flowers, crop plants, and in many plants having only botanical

interest. The following is a partial list of plants in which triploids have been reported: Aconitum Stoerkianum, Afify (1); Asimina triloba, Bowden (18); aster, Avers (3); banana, Wilson (74); canna, Belling (6); Chrysanthemum carinatum, Bergman (8); dactylorchid hybrids, Heslop-Harrison (38); Datura, Belling and Blakeslee (7), Blakeslee (11,14), Blakeslee and Belling (15), Blakeslee and Cartledge (16), Satina and Blakeslee (64,65), and Satina, et al. (66); guayule, Bergner (10); Hieracium umbellatum, Bergman (9); Hemerocallis fulva, Chandler (23); lime, Krug and Bacchi (48); lucerne, Julen (44); maize, McClintock (56) and Punyasingh (61); oats, Nishiyama (59); Oenothera, Capinpin (21) and Catcheside (22); onion, Clarke and McKay (25) and Levan (54); pineapple, Collins (26); Polygonatum multiflorum, Eigsti (27); Populus tremula, Johnsson (42,43); rice, Beachell and Jones (4); rye, Lamm (49); perennial ryegrass, Myers (58); sorghum, Chin (24) and Kidd (45); sugar beets, Peto and Boyes (60); tomatoes, Lesley (51), Lesley and Lesley (53), and Rick and Barton (63); Tradescantia hybrids, Giles (31) and King (47); and wheat hybrids, Kihara and Nishiyama (46) and Thompson (73).

Triploids may arise in several ways. Lesley and Lesley (53), working with tomatoes, and McClintock (56), working with maize, suggested that the triploids they found probably arose through the fusion of a diploid gamete (unreduced gametes which occur occasionally in diploid organisms) and a haploid gamete. Wilson (74) suggested this possible origin for triploids he found in varieties of the banana. He also suggested that they might have arisen from a cross of a tetraploid plant by a diploid plant. This latter possibility was suggested for the origin of triploid plants of Chrysanthemum carinatum studied by Bergman (8). Both these possible origins were mentioned by Belling (6) for triploids occurring in the canna. That triploid plants can arise from the cross of a tetraploid plant by a diploid plant was demonstrated by Giles (31), who produced

triploid Tradescantia hybrids, and by Peto and Boyes (60), who produced triploid sugar beets. A new triploid apomictic form of Hieracium umbellatum was found by Bergman (9).

Among cultivated plants, triploids occupy a fairly important position. Since many plants can be reproduced vegetatively, for example by grafts or cuttings, the sterility of the triploids can be by-passed and advantage taken of their sometimes superior qualities. Investigations by Peto and Boyes (60) indicated that triploid sugar beets may be superior to the diploids in respect to the yield of sugar, weight of the root, and particularly in the maintenance of the percentage of sugar with an increase in size of the root. Collins (26) found that triploid pineapples have a sugar and acid content slightly less than diploid hybrids as well as larger size. The seedless condition of the bananas studied by Wilson (74) was derived from their triploid nature. A number of other fruits, such as the Gravenstein and Baldwin apples, are triploids. The Keizerskroon tulip, which has unusually large flowers, is a triploid (Srb and Owen, 71). Krug and Bacchi (48) reported that triploid limes, which are almost completely seedless, are highly productive, have larger fruits than the diploid limes, are very juicy, and have a thin rind. They recommended that the synthesis of new triploids be encouraged.

Plant characteristics of triploids have been found to vary with the species of plant. Julen (44) reported that triploid lucerne (alfalfa) seemed more vigorous than the diploid lucerne. The leaves were longer and broader than those of the parents (tetraploid and diploid strains). Johnsson (43) found that triploid Populus tremula had larger and thicker leaves than the diploid. The stomata were larger, the wood cells were longer, the cells were 20 percent wider than those of the diploid, but there was little difference in height and no difference in diameter due to the increase in chromosome number. Peto and Boyes (60)

summarized data for triploid sugar beets that suggested that organ size tended to be directly proportional to the increase in cell size. Larger stomata also were present. Collins (26) found that triploid pineapples were larger than the diploid hybrids and matured more slowly. Beachell and Jones (4) found that triploid rice plants were not as tall, tillered less, were less fertile, and had coarser leaves and larger florets and seeds than diploid plants of the varieties studied. Lesley (51), working with triploid tomatoes, found that the triploid plant was usually a replica of the corresponding diploid but was distinguished by the larger size of organs, cells, and nuclei. Polyploid sorghum found by Chin (24) was stouter and shorter than diploid sorghum and had a later flowering time.

Fertility of triploid plants has been found to vary with the species, ranging from very good to complete sterility. Julen (44) found that triploid lucerne had good fertility. Avers (3) attributed the high fertility that he found in triploid aster hybrids to two successive equational divisions of the univalents. In triploid maize Punyasingh (61) found 85 to 97 percent of mature pollen grains were normal in appearance and well-filled with starch. Lamm (49) noted in triploid rye that the pollen grains were slightly larger than those in diploid rye and that the percent of good pollen was 83 percent. The triploid plants were completely self-sterile and did not function as the pollen parent in crosses with diploid plants. As a female parent, in crosses with diploid plants, they gave diploid progeny. Xing (47) found the percent of good pollen, on six successive days, in triploid Tradescantia ranged from 28 to 65 percent with an average of 47 percent. He thought pollen sterility was due to a chromosome deficiency. Belling (6) found about one-half of the pollen grains of triploid cannas to be empty or nearly so. The high proportion (43 percent) of bad grains and wide diversity in size of good grains that Blakeslee and

Cartledge (16) found in the pollen of triploid Daturas was thought to be due to an unbalance brought about by more than a single chromosome.

The percent of pollen germination among triploid cultures of Polygonatum multiflorum was found by Eigsti (27) to be much lower than that of tetraploid and diploid species. No more than five percent of the mature pollen grains of a triploid clone of Hemerocallis fulva germinated on artificial media (Chandler, 23). These plants were self-sterile, and abortion in megasporogenesis reduced the number of crossed seeds. Thompson (73) found that triploid wheat hybrids were nearly sterile, as did Lesley (51) with tomatoes. Little viable seed was produced. Triploid Allium Schoenoprasum (Levan, 54) and triploid pineapples (Collins, 26) were found to be completely self-sterile. The former in free flowering gave rise to about 700 progeny, and pollen of the latter, applied to a diploid plant, produced a few viable seeds. The reciprocal cross of the latter was unsuccessful. Except for occasional seeds, triploid rice plants were found by Beachell and Jones (4) to be entirely sterile. Wilson (74) found that the triploid Canary banana was apparently completely sterile.

Triploid hybrids have been produced in a number of genera. Meiosis in such triploids differs somewhat from meiosis in autopolyploid triploid plants. Nishiyama (59) studied the triploid hybrids of Avena barbata (2n = 28) x A. strigosa (2n = 14) and A. wiestii (2n = 14), and their F_2 to F_6 progenies. The triploid hybrids had 21 somatic chromosomes, seven from the diploid parent and 14 from the tetraploid. At metaphase I of the pollen mother cells, seven bivalents and seven univalents usually were counted. Among the univalents, five were capable of mating with some of the bivalents to form trivalents. Two bivalents paired weakly with each other at their ends. Therefore, eight bivalents and five univalents were found in rare cases. One N-shaped tetrapartite complex occurred rarely, due to pairing of the eighth bivalent with one of the

seven bivalents. Components of the bivalents, trivalents, and tetrapartite complex disjoined at anaphase I and went to opposite poles in a normal manner. The univalents arranged themselves on the equator, and after the bivalents had gone to the poles, most of them split longitudinally. The halves wandered to opposite poles, some being included in the daughter nuclei and some not. Lagging was observed. At anaphase II or telophase II lagging chromosomes often were seen. Most were monads, and a few were dyads. These lagging chromosomes were eliminated in about 19 percent of the cases. Accordingly the gametes had any number of chromosomes from seven to 14.

Thompson (73) found that at the first division of a hybrid between Triticum monococcum and a variety of T. turgidum three to seven bivalent and 15, 13, 11, nine or seven univalent chromosomes appeared. After the bivalents divided, the univalents arranged themselves on the equatorial plate and divided equationally. At the second division some of the chromosomes lagged, failed to divide, and wandered at random to the poles. Their number corresponded to that of the univalents of the first division. Each usually contained several micronuclei. Kihara and Nishiyama (46) found that in the triploid wheat hybrids Triticum dicoccum used as a female x T. monococcum as a male and T. aegilopoides boeoticum as a female x T. dicoccum as a male, there were various modifications of the normal chromosome combination (seven bivalents and seven univalents), such as three trivalent chromosomes, which consisted of the union of three bivalents and three univalents. The number of trivalents varied from none to three. In some cases there was a tetrapartite (not tetravalent) chromosome.

The meiotic behavior of the presumed triploid F_1 hybrids of the parentages Orchis fuchsii x O. purpurella and O. fuchsii x O. praetermissa was found to be essentially the same by Heslop-Harrison (38). Multivalents were not formed

while 20 bivalents and 20 univalents formed regularly at metaphase I. The univalents divided in meiosis I but not in meiosis II, at the close of which they were incorporated at random in telophase nuclei or formed independent micronuclei.

Clarke and McKay (25) backcrossed the amphidiploid obtained from the cross Allium cepa L. var. Australian Brown x A. fistulosum L. type Nebuka with both parent species, giving rise to triploids. During meiosis the triploids regularly formed eight bivalents and eight univalents (two derived from one species formed a bivalent). The formation of bridges and fragments was frequent.

Giles (31) studied the chromosome behavior at meiosis in triploid Tradescantia hybrids which resulted from the cross diploid T. paludosa Anders. and Woods as a female x tetraploid T. canaliculata Raf. as a male. Meiosis in the triploid hybrids was much more irregular than in the parents. The average number of trivalents for five plants was 3.6 per cell. The triploid hybrids had more bridges per cell than the parents.

Triploid hybrids between Aster shortii Lindl. and A. cordifolius L. were found by Avers (3) to be highly fertile. Lagging chromosomes were rarely seen. As mentioned earlier, observations indicated that the univalents did not misdivide but rather underwent two successive equational divisions.

Meiosis in autopolyploid triploid plants has been studied in a large number of species. Belling (5) reported that trivalents of short chromosomes with medium constrictions, such as those in Datura and Canna, either form some of five configurations: boat-, frying pan-, Y-, V-, or J-shape, or one homologue shows separation from the other two which form a bivalent, usually a ring. These five were all the configurations which had been seen among several hundred trivalents of triploids and primary trisomics in Datura and Canna. The V-shape was the commonest type. The rod and ring and V-shape formed 70 percent of the

trivalents found. The univalents were always more or less straight.

In a triploid Canna Belling (6) found that all the chromosomes regularly formed triads in the prophase and metaphase of first division and passed, two and one at random, to either pole. In an examination of clones, he found five completely or nearly triploid and irregular in first division and one clone regularly triploid, showing nine trivalents at prophase and metaphase I. The latter had smaller flowers and was of smaller size.

Belling and Blakeslee (7) found 12 sets of trivalents at metaphase I in triploid Daturas. Sometimes two of three rod-shaped chromosomes were united together at both ends and the third was joined on at one end only, or the three formed a hook. Two chromosomes usually passed to one pole and one to the other from each trivalent. Thirteen percent of cases of detachment in metaphase II were seen. Therefore microcytes formed.

Satina and Blakeslee (65) found that most extra chromosomes in Datura were not transmitted through the pollen. The assortment of chromosomes at the first meiotic division in 1,000 pollen mother cells approached random distribution with increases toward the haploid and diploid classes of nuclei, which made these classes 16 times as frequent as the calculated values. Lagging chromosomes were responsible for about 4.5 percent elimination of chromosomes in the first meiotic division and about 2.5 percent elimination in the second division. The chromosome distribution was responsible for a slight increase in the frequency of classes with smaller chromosomes numbers. Counts in 500 dividing pollen grains showed that division occurred regardless of the chromosome number. The number of haploid grains recorded was over 100 times the number expected from random assortment. Abortion of 40 to 50 percent of the pollen began at various stages of growth after the nucleus in the pollen grains had divided. Hence, in the mature grains that remained the number with ln

chromosomes was further increased.

Satina and Blakeslee (64) found that in the female gametophyte of triploid Datura, as in the pollen, the assortment of chromosomes at the first meiotic division approached random distribution with increases toward the classes with lower and those with higher numbers of chromosomes and with corresponding decreases in the classes with the intermediate numbers. About 52 percent of the nuclei at the chalazal end showed elimination of lagging chromosomes at the first division and about the same percent at the second division. No elimination of chromosomes was observed in the three mitotic divisions in the embryo sac. Chromosome elimination in the meiotic division caused a distinct increase in the frequency of nuclei with the smaller chromosome numbers. As a result, 30 times as many female gametes with n+1 and 280 times as many with n chromosomes as expected from random assortment occurred.

Catcheside (22) found that in triploid Oenothera pycnocarpa the 21 chromosomes were associated in various ways, including free univalents, rod and ring bivalents, chain, Y-shaped and "ring-and-rod" trivalents, chain, branched chain and "ring-and-chain" quadrivalents, and other associations involving higher numbers of chromosomes, with or without triple chiasmata. Capinpin (21) frequently observed pollen mother cells in triploid Oenotheras to be in different phases of mitosis in the same bud or even in a single loculus. In diakinesis open or closed chains of chromosomes, trivalents in diverse triple associations, bivalent pairs and unpaired chromosomes were found. Disjunction of the 21 chromosomes was 10-11, 9-12, and 8-13. At anaphase I two members of a trivalent moved to one pole and the third to the other. As many as seven chromosomes were found lagging in the equatorial plate, while 14 chromosomes moved to the poles. The chromosomes which lagged often disintegrated. It seemed apparent that the high percentage of pollen sterility in Oenothera triploids was due

mainly to the irregular and unequal distribution of chromosomes in the final division of sporogenesis.

In an investigation of the chromosome behavior in a triploid Tradescantia King (47) found that the heterotypic division involved 18 chromosomes which showed a marked tendency to form six trivalents. Bivalents and univalents also were found. Types of trivalent configurations and their frequency were: ring-rod type, 2.5 per cell; U-chain type, 2.1 per cell; J-chain type, 0.3 per cell; straight chain type, 0.5 per cell; and the Y-type, 0.2 per cell. A large and variable amount of lagging was exhibited at anaphase I and telophase I. Both univalents and bivalents often failed to get into the daughter nuclei and formed no microcytes. There seemed to be a tendency for an equal number of chromosomes to pass to opposite poles.

McClintock (56) and Punyasingh (61) found that at diakinesis in triploid maize there were many cases in which the chromosomes were arranged in ten groups of three each. The latter author examined 216 microsporocytes at diakinesis and metaphase I and found that 106 had ten trivalents, 66 had nine trivalents, 35 had eight trivalents, eight had seven trivalents, and one had six trivalents, the mean number being 9.24 $\pm$ 0.89. The presence of one to four univalents in about 50 percent of the cells and random two-from-one assortment of the trivalents resulted in unequal disjunction and irregular distribution of the chromosomes. Fewer lagging chromosomes per cell were noted in anaphase II and telophase II. At the quartet stage, only 43 of 404 microspores examined had visible remnants of lagging chromosomes, which in some cases formed micronuclei.

Kidd (45) found a triploid sorghum plant which behaved quite similarly to triploids previously reported. From a total of 24 cells, eight had ten trivalents, five had nine trivalents, one bivalent, and one univalent, six had eight trivalents, two bivalents, and two univalents, three had seven trivalents, three

bivalents, and three univalents, and one cell demonstrated each of the configurations six trivalents, four bivalents, and four univalents and four trivalents, five bivalents, and eight univalents.

A preponderance of paired, and a deficiency of single strands, was found by Myers (58) in the mid-prophase of meiosis in a triploid perennial ryegrass. At metaphase I 41.5 percent had seven trivalents; 32.5 percent had six trivalents, one bivalent, and one univalent; 19.5 percent had five trivalents, two bivalents and two univalents; 4.9 percent had four trivalents, three bivalents, and three univalents; and 1.8 percent had three trivalents, four bivalents, and four univalents. No other configurations were observed. Of the univalent chromosomes observed, 71 percent were oriented on the equatorial plate prior to initiation of anaphase I. Twenty-four percent were lying near the equatorial plate but not on it. At anaphase I cells were examined for lagging and the equational division of univalents. Thirty-seven percent had no univalents, 26 percent had one, 17 percent had two, nine percent had three, nine percent had four, one percent had five, and one percent had six. It was possible to count chromosomes in both groups in 21 anaphase I cells with no laggards. The distribution was 10-11 in nine, 9-12 in five, and 8-13 in seven. Among 100 groups of chromosomes, including sporocytes in which laggards occurred, five had seven chromosomes, 11 had eight, 25 had nine, 32 had ten, 14 had 11, seven had 12 and six had 13. Among 198 quartets, 26.8 percent showed no micronuclei, one micronucleus was found in each of 8.1 percent, while the remainder had two or more, the maximum being eight.

The following pairing types were found in a triploid rye plant by Lamm (49); six trivalents, one bivalent, and one univalent; five trivalents, two bivalents, and two univalents; four trivalents, three bivalents, and three univalents; three trivalents, four bivalents, and four univalents; two

trivalents, five bivalents, and five univalents; and seven bivalents and seven univalents. Univalents, rod bivalents, ring bivalents, chain trivalents, and frying pan trivalents were found. Lagging univalents were frequently seen at anaphase I. Some divided and some did not. Laggards were also seen at anaphase II, and micronuclei sometimes formed.

Chandler (23) found the following irregularities during meiosis in triploid plants of Hemerocallis fulva: a) Associations of homologous chromosomes in early prophases were of four types. All three homologues were associated rather closely, and in such cases few chromomeres failed to become associated with other chromomeres. Close pairing of two with loose association of the third was frequent. The third chromosome occasionally remained unassociated. Sometimes all three homologues of any one chromosome type remained unassociated. These resulted in univalents, bivalents, and trivalents. b) The distribution of chromosomes in the two divisions proceeded with much irregularity and differing numbers of chromosomes were distributed to the daughter nuclei. Laggards were observed in the equatorial region at anaphase I and anaphase II. These disintegrated or formed microcytes. c) Irregular numbers of nuclei were formed at the first and second divisions as a result of the incomplete association of homologous chromosomes of the prophases, and of unequal distribution of chromosomes during anaphase I and anaphase II. d) Irregular numbers of microspores were formed from single pollen mother cells.

Collins (26) reported that in the triploid pineapple, chromosome conjugation during meiosis often was very irregular, giving rise to trivalent, bivalent, and univalent units in varying numbers in different cells. No cases of micronuclei or microcytes were found.

In triploid bananas Wilson (74) found the nucleolus to be associated closely with about six chromosomes. In addition the earlier stages of prophase (leptotene-pachytene) showed indeterminate numbers of smaller and fainter nucleolus-

like bodies. Varieties varied as to the number of trivalents and univalents present. Most anaphase I cells showed lagging. Not infrequently one or more chromosomes were lying entirely away from the spindle area. The second division was quite normal in most cases. Micronuclei separated as micro-cells. The typical tetrad consisted of four large cells and a varying number of small ones.

Bergner (10) saw trivalents or bivalents and univalents at metaphase I in microsporocytes of triploid guayule. A tendency toward equal distribution of chromosomes at anaphase I was suggested.

In triploid Aconitum Stoerkianum Afify (1) found that the number of trivalents varied from five to none. Cells with three or four trivalents were most frequent. The number of bivalents varied from two to six with the greater number of nuclei having three, four, or five. The number of univalents was also variable, cells with three to 11 being observed. Multiple associations of more than three chromosomes were observed in 20 percent of the nuclei examined. These formed rings of four and chains of four, five, six, and seven chromosomes. Rings and chains of four were the most frequent. Chain trivalents were most frequent, although the frying pan type also occurred.

In microsporogenesis of the apomictic triploid of Hieracium umbellatum Bergman (9) found that there was usually no pairing, but there was a semi-heterotypic division which gave restitution nuclei. There was a fragment which behaved like the other chromosomes. In exceptional cases there was some multivalent association. The hypothesis was presented that the asyndesis in the triploid was gene-conditioned and that the gene for asyndesis was identical with or closely linked to the gene for apomixis.

Bergman (8) found that in microsporogenesis in Chrysanthemum carinatum triploids, there were strong bivalent and trivalent associations. No asyndetic tendencies were observed. In the ovules of 26-chromosome plants there was total

asyndesis in 41.9 percent of the embryo mother cells and a 29-chromosome plant had 20 percent (i.e., about the same as in the diploids). Asyndesis was probably genetically conditioned.

Examples of triploidy in animals are rather uncommon although a few have been reported. Triploids have been found in salamanders and rabbits, and Bridges (19) has reported triploid intersexes in Drosophila melanogaster.

Since it was known that triploid x diploid crosses produced progeny constituting an aneuploid series, various investigators purposely made such crosses to obtain aneuploids. As Larson (50) stated, aneuploids can be of use in genetic analyses and theoretically, in breeding. Sears (67) has used nullisomics, monosomics, disomics, trisomics, and tetrasomics in such studies. McClintock and Hill (57) used a trisomic maize plant derived from a triploid cross in the cytological identification of the chromosome associated with the R-G linkage group.

In a triploid x diploid cross in maize Punyasingh (61) found that 66 percent of the progeny had no extra chromosome and 22 percent had but one extra chromosome. Male gametes of the triploid which had more than ten or 11 chromosomes rarely functioned in combination with the ten-chromosome gametes of the female. When the triploid was the female parent, 56 percent of the progeny had either 22 or 23 chromosomes, only 12 percent had 21 and less than two percent had 20 chromosomes. The tendency for most of the F_1 plants of the triploid x diploid cross to have either 20 or 21 chromosomes, with an indication that the number 28 was favored over the intermediate numbers from 22 to 27, was attributed to slower rate of growth of the pollen tubes with numbers of extra chromosomes intermediate between 10 and 20, since a much higher proportion of plants with extra chromosomes appeared in the progeny of a reciprocal cross in which pollen tube competition was lacking. Ears from the triploid x diploid

crosses were poorly filled and many seeds were only partly developed. There was very little evidence that zygotic elimination appreciably influenced the results of these crosses. Results of the reciprocal cross indicated that zygotic lethality was a significant factor in determining the frequency of the various chromosome numbers in this cross. Seedlings produced by the small seeds had a higher mean number of chromosomes than those obtained from the large seeds. There was a reduced germination of the smaller seeds.

McClintock (56) studied the progeny of a triploid x diploid cross in maize. Out of 50 F_1 plants eight were trisomic, six were double trisomics, and seven were triple trisomics.

Crosses of diploid and triploid races of Populus tremula (Johnsson, 42) were noteworthy in that individuals with aneuploid chromosome numbers were produced in a high frequency, in which respect P. tremula differed greatly from nearly all species in which such crosses have been investigated. Crosses in both directions gave the same results, thus showing that pollen grains were not more susceptible to numerically unbalanced chromosome numbers than the embryo-sacs. Usually progenies, both after selfing and after crosses with diploids, consisted of diploids and individuals having one or more supernumerary chromosomes. There was a distinct over-representation of individuals with the diploid chromosome number.

Of 90 F triploid x diploid plants of Nicotiana sylvestris (Goodspeed and Avery, 32) which reached maturity, 17 had one extra chromosome. The others were of higher chromosome numbers.

Satina, et al. (66) found that following triploid x diploid pollinations in Datura, fertilization could occur in ovules with female gametes which had chromosome numbers from 12 to 24. The majority of the female gametes remained unfertilized. Elimination of the female gametes and of zygotes at various

stages of development reduced the number of seeds in triploid x diploid capsules to an average of about 61 against an average of about ten times as many for comparable diploid x diploid capsules. The 2n seeds averaged larger than 2n+1 seeds and the latter averaged larger than 2n+1+1 seeds. Certain chromosomes when present as extras in 2n+1 embryos caused the seeds to be larger, and certain other chromosomes caused the seeds to be smaller. Seeds which were 2n germinated promptly within three to 12 days, while germination was delayed in some seeds with extra chromosomes. The number of 2n individuals in the offspring was 816 times the expected number on the basis of random assortment of chromosomes. This was attributed to zygote and gametophyte elimination.

Myers (58) found that in the offspring of a triploid x diploid cross in perennial ryegrass 25.2 percent were 2n, 43.7 percent were 2n+1, 22.7 percent were 2n+2, 5.0 percent were 2n+3, and 3.4 percent were 2n+4. These resulted from an 85.5 percent seed set on the triploid plant.

Lesley (51) found that in the F_1 progeny from a triploid x diploid cross in tomatoes, the chromosome numbers did not have a binomial distribution but ranged from 24, the diploid somatic number, to 27, with the mode at 25 chromosomes. The smaller seeds from the cross gave more 26- and 27-chromosome plants than did the larger seeds. From the reciprocal cross only two plants were obtained, both diploid.

Aneuploids are a common feature in species which behave cytologically like autopolyploids. Such a case in the aneuploidy found in Phalaris (canary grass) by Hanson and Hill (37).

Goodspeed and Avery (32) reported that trisomics were of frequent occurrence and were known in almost every genus employed in genetic work, but that usually not all of the theoretically possible types had been secured and only limited numbers of their features were investigated. Nicotiana sylvestris

trisomics were first recognized in 1928. Some had since occurred in the offspring of others (Goodspeed and Avery, 32). These authors listed several sources of trisomics: 1) diploids, including genic and 2n variants; 2) nonasynaptic trisomics; 3) X_1 and X_2 (successive generations derived from X-ray treatment of reproductive or somatic tissues); 4) asynaptic diploids and trisomics; and 5) triploid x diploid. Double and triple trisomics arose from asynaptic trisomics and triploid x diploid crosses. In Nicotiana sylvestris the F_1 triploid x diploid was the most prolific both in the number of trisomics and in the number of different types relative to the total plants grown. Of 90 plants which reached maturity, 17 had one extra chromosome, and 15 of these were primary trisomics.

Blakeslee (11,13), Blakeslee and Belling (15), and Blakeslee and Farnham (17) studied aberrant plants of Datura stramonium. Over a period of years, each of the 12 different chromosomes which make up a genome in Datura was observed one or more times in the trisomic condition.

The following is a partial list of the species of plants in which trisomics have been found: Allium Schoenoprasum, Levan (54); barley, Smith (70); maize, Einset (28), Hill (39), McClintock (56), and Rhoades (62); Oenothera, Anderson (2), Goodwin (33), and Håkansson (36); Pisum elatius, Håkansson (35); rye, Takagi (72); and tomatoes, Lesley (51,52), and Rick and Barton (63).

Hill (39) reported that in Zea mays L. it was practically impossible to recognize trisomic individuals other than by cytological examination. The presence of an extra chromosome was phenotypically recognizable only in a slight decrease in size and vigor.

Punyasingh (61) found that maize plants with one or two chromosomes less than the diploid number were lacking in vigor and fertility, while plants with one or few chromosomes more than the diploid number were relatively much more

vigorous and fertile.

Einset (28) examined eight of the ten possible trisomic types of maize with regard to the effect of the extra chromosome on the morphology of the plant. In general, the trisomics were shorter and produced smaller ears than their disomic sister plants, but stocks of different trisomics showed different relative heights and ear lengths. On the average, the trisomic kernels were smaller than the disomic kernels on the same ear. In general, the effect of unbalance in chromosome number was deleterious.

Rhoades (62) reported a secondary trisome of chromosome five in maize which occurred among the progeny from a selfed plant trisomic for chromosome six. As a seedling, it resembled dwarf types of maize having an extremely stocky appearance with broad, blunt-pointed leaves. At maturity, the variant was of reduced stature and had thick, leathery leaves with broad, extremely blunt tips. The tassel was more compact and sturdier in appearance and was later in flowering.

In a study of the effects of single extra chromosomes on size in Nicotiana Smith (68) found that three of five different extra chromosomes each caused a reduction in size of all regions of the corolla. The other two caused an increase in one region and a decrease in the other. The length of the tubular part of the corolla increased with polyploidy, but limb measurement was affected adversely or unaffected.

Blakeslee (12) found that simple trisomic Globe Daturas were less vigorous than the normals. The 2n+2 Globe was still less vigorous than the trisomic Globe.

A trisomic plant of rye found by Takagi (72) was very delicate with slender stems and leaves.

Smith (70) found that trisomics in barley were about two-thirds of the

height of normals, vigorous, and produced several tillers. No obvious distinguishing morphological characters were noted.

Lesley (51) found that, in general, the simple trisomic types of tomatoes (compared with the diploids) were slower-growing and had a greater tendency to pollen sterility and unfruitfulness in the field. Lesley (52) thought that the small fruit size of triplo- and tetra-D trisomic types in the tomato might be due to an over-balance of genes for fruit size in the D chromosome, which does not contain the locus of any of the three gene pairs known to be linked with genes for fruit size.

In Populus tremula Johnsson (42) found that the great majority of all individuals with aneuploid chromosome numbers possessed poor growth and had the appearance of standing on the border-line of viability. Especially weak were plants having more than 57 chromosomes (the triploid number).

Pollen abortion has been found to be high in most trisomic plants. Blakeslee and Cartledge (16) attributed the excess of bad grains in trisomic Datura types to poor viability of the n+1 grains. Blakeslee and Farnham (17) found that the transmission of the Poinsettia trisomic in Datura was 30 percent through the egg cells. The transmission was slightly greater when the Poinsettia parent was pollinated from a normal or from another Poinsettia than when it was selfed. Blakeslee (13) found that the proportion of bad pollen grains varied in the different trisomic Daturas from eight percent in Globe to 21 percent in Spinach; all failed to transmit the trisomic complex to any considerable extent through the pollen, while one-fourth of the offspring received the complex through the egg cells.

Meiosis in aneuploids has been studied by various authors. McClintock (56) studied one strain of trisomic maize which always showed ten bivalents and one univalent. Variation in synaptic expression of the extra chromosome

was noted in eight other trisomic plants studied. Nine bivalents and one trivalent were found about twice as frequently as ten bivalents and one univalent. The univalent was sometimes lying in the spindle and sometimes not. It often split or lagged. Sometimes it was included in the reorganizing nuclei and sometimes not. When a trivalent was present, disjunction of the three homologues and passage of two to one pole and one toward the other seemed to be quite regular. Occasionally a dyad or monad lagged. Occasional secondary spindles were seen. The sporocytes seldom gave rise to more than four spores.

Einset (28,29) reported that more trivalents and fewer univalents were found at metaphase I of meiosis in trisomic maize stocks with long chromosomes in triplicate than in stocks with shorter ones. Transmission frequencies determined by somatic chromosome counts of 1916 plants ranged from about 50 percent for longer chromosomes to about 25 percent for shorter chromosomes and chromosomes of intermediate lengths exhibited intermediate transmission frequencies.

Hill (39) studied trisomic types in maize and obtained results similar to those of McClintock (56) mentioned above.

At metaphase I in a trisomic Oenothera, Goodwin (33) found a chain of 13 and ring bivalent, chains of seven and five chromosomes together with a ring bivalent and a univalent, a chain of ten chromosomes with a ring-and-rod bivalent together with a ring bivalent, and branched chains of four and five chromosomes.

Håkansson (36) made a study of chromosome arrangements in diakinesis and metaphase I of several trisomics from Oenothera lamarckiana. In lata, dependens, striata, and longepetiolata of Heribert-Nilssons' cultures and in lata, pallescens and liquida of DeVries, there was an open ring of 13

chromosomes and one free bivalent. A triple arrangement at the end of the chain was found in some cases. The trisomic curta had a chain of 11 and two bivalents. In nitens, which is also a constant trisomic, there was a chain of nine and three bivalents. In a secondary form from pulla the arrangement was a closed ring of six, three bivalents and one trivalent. A secondary form of cana of DeVries had 14 1/2 chromosomes, viz.: two bivalents and an open chain of 11, the half chromosome being at the end of the chain. Every degree of pairing had been found in lamarckiana mutants except no pair. In many trisomics, the chain in metaphase I was segmented into shorter chains. Chain and ring chromosomes were arranged in a zigzag; alternate chromosomes passed to the same pole in anaphase.

In limited meiosis material of trisomic Pisum elatius Håkansson (35) made the following observation: six bivalents and one trivalent were common, the shape of the trivalent being variable. In other cases seven bivalents and one univalent were seen. At anaphase I eight chromosomes usually went to one pole and seven to the other. But if a univalent was present at an earlier stage, the univalent divided and the halves sometimes were not included in the interkinesis nuclei.

In meiosis in the pollen mother cells of a simple trisomic in the tomato Lesley (51) found that the unpaired chromosome was not constant in behavior. At diakinesis it either formed a trisome or lay separate. It frequently lagged at anaphase I and anaphase II. The proportion of tetrads containing microcytes varied from 4.5 to 7.6 percent in the different simple trisomic types.

Smith (70) found that in some pollen mother cells of trisomic barley, the chromatids of the extra chromosome separated in the first division. Laggards occurred at anaphase II. Misdivision of the univalent and micronuclei were observed.

In a study of meiosis in a trisomic rye plant Takagi (72) found at diakinesis 50 percent of the cells showing six bivalents and one trivalent, and 50 percent showing seven bivalents and one univalent. The configurations at metaphase I were the same as those at diakinesis, but occasionally three univalents were observed. The trivalents were mostly V-shaped. At anaphase I the trivalent divided as usual, i.e., two chromosomes moved to one pole and one to the other. They were included in daughter nuclei. No laggards were seen in the equatorial region at interkinesis. At metaphase II seven and eight chromosomes were seen in the daughter cells. Sometimes the univalents lagged or divided and the halves moved to opposite poles but were not included in the reorganizing nuclei. The split univalents or single halves sometimes formed micronuclei at anaphase I.

Belling (5) reported the same types of trivalents in trisomic Datura and Canna as in the triploids of these genera mentioned above.

Studies of meiosis in aneuploids of higher chromosome numbers have been made. Hill (39) found that meiosis in a 2n+2 maize plant was regular. He observed nine bivalents and one quadrivalent, 11 bivalents, and ten bivalents and two univalents, the first being the most frequent. There was regular distribution of the 22 chromosomes.

McClintock (56) reported that meiosis in 2n+2 maize plants was similar to that in trisomics. The univalents acted similarly but independently. Eight bivalents and two trivalents were most frequent, nine bivalents, one trivalent, and one univalent were less frequent, and ten bivalents and two univalents were least frequent. The anaphases were more irregular than those of the trisomics. Frequently 11 chromosomes moved to each pole although 10-12 distributions were numerous. Lagging or splitting univalents were numerous. Anaphase II was less regular and there was often lagging. Sometimes an irregular spore quartet

formed. Multiple chromosome numbers were observed in some cells.

McClintock (56) also described meiosis in 2n+3 maize plants. Two plants had seven bivalents and three trivalents, three had six bivalents and four trivalents, one had five bivalents and five trivalents, and one had three bivalents and seven trivalents. The presence of extra chromosomes was suggested in the small size and decreased vigor of these plants. There was a general tendency on the part of the univalents to be associated with bivalents to form trivalents at diakinesis and metaphase I. There was more irregularity at anaphase I due to the extra chromosomes. Variation in spore formation increased accordingly.

A good review of trisomic inheritance was given in the Poinsettia mutant of Datura by Blakeslee and Farnham (17), and in maize by Emset (28,29), Hill (39), McClintock (56), and McClintock and Hill (57).

Various studies have been made of the cytology of the genus Sorghum. Huskins and Smith (40) studied seven of the diploid forms of Sorghum in the subsection Eu- sorghum. Ten bivalents were most commonly found, but quadrivalent associations were also common and sexivalents were found occasionally. Fewer than seven units of association were not found in this Sorghum material. These authors said that this fact, together with the frequency with which the chromosome number seven and its multiples occurs in the Gramineae, raised the possibility of it, rather than five, being the basic number.

Garber (30) reported that all the species placed in the subsection Para-sorghum had a haploid chromosome number of five. Excepting S. halepense (n= 20), all species in the subsection Eu-sorghum have a haploid chromosome number of ten. He said that it was probable that the basic chromosome number for the genus Sorghum was five, because it was more than coincidence that the subsection Para-sorghum had a haploid chromosome number of five, the maximum

number of tetravalents observed in S. halepense was five, and a species, while not closely related, in the tribe Andropogoneae, Hyparrhenia hirta, had a chromosome number (n = 15) which was a multiple of five and not ten or seven. On this basis it was suggested that S. vulgare was an allotetraploid.

Brown (20) observed bivalents in about ten percent of metaphase I cells of a haploid Sorghum vulgare plant. This was evidence to Hadley (34) that perhaps ten was not the basic number of chromosomes.

The relative lengths of the chromosomes in S. vulgare were reported by Longley (55). The chromosomes showed the centromere region as a clear area with a deeply staining thread on either side. The staining quality of the thread weakened very appreciably a short distance on either side of the centromere region, and the rest of the thread stained rather poorly. All ten chromosomes of this sorghum were unmarked by knobs. The longest chromosome was found to be attached to the nucleolus at a point near its middle and only a short distance from the centromere region. A second grain sorghum studied was found to be similar.

Chin (24) found that in diploid plants of S. vulgare, variety Hegari, the chromosomes usually paired as bivalents, although rings and chains of four were found occasionally. Most bivalents were associated as rings with two terminal chiasmata at metaphase I. In 18 percent of the bivalents, there were three chiasmata, while less than one percent were rod bivalents associated with a single chiasma.

MATERIALS AND METHODS

Materials

The triploid plant studied was found in 1953 at the Fort Hays Branch Experiment Station, Hays, Kansas, in a border row of a group of White Collier lines adjacent to a block of Waxy Atlas selections. From an infinitely large number of florets, about 100 seeds had been set from cross pollination.

The triploid plant was taken to the greenhouse during the winter of 1953-54. Upon selfing it was found to be completely sterile, verifying that the seed set in the field was from diploid White Collier or Waxy Atlas pollinations. One peculiarity noted was that the seed set on this plant was red, indicating it to be of hybrid origin rather than a polyploid of White Collier. This fact did not detract from the subsequent cytological studies, although it would have been advantageous to be dealing with known stock.

In early June, 1954, 50 seeds of those set on the triploid plant were planted in bands in the greenhouse and later set out in the field. Only 27 plants emerged and survived. In the field two of these were completely destroyed by rabbits. A chicken wire fence protected the remaining plants from further destruction.

Under the extremely adverse conditions of hail and high winds at Hays, 16 plants developed sufficiently for microsporocyte examination before frost. The remainder were brought to the greenhouse for examination during the winter. All the plants found to have extra chromosomes were also brought into the greenhouse.

Plant Characteristics of the Triploid Plant and Its Progeny

The triploid plant and its progeny were measured as to height in the field on July 23, 1954, and again in the greenhouse in June, 1955. Maturity was recorded whenever the various plants headed. Other plant characteristics were noted in the greenhouse in June, 1955.

The 64 remaining seeds of the triploid plant were planted in bands in the greenhouse in June, 1955. Only 24 emerged and survived. These were set out in a small plot and will be the source of further study.

Pollen Count of Aberrant F_1 Triploid Progeny and Normal Plants

Pollen was taken from blooming heads of the various aberrant and normal plants in the greenhouse on glass slides in the mornings of June 8 and 9, 1955. The slides were examined under the low power objective of a microscope. Counts of good and bad pollen were made from four randomly chosen objective fields for each plant.

Cytological Studies

The microsporocyte samples used in this study were collected when the head was still tightly held within the sorghum curl and before there was a very noticeable swelling. The heads were fixed in a solution of three parts of 95 percent ethyl alcohol and one part of propionic acid. They were stored in this same solution in a refrigerator.

Three days after fixing and at various times thereafter florets were dissected from the heads with dissecting needles. The three anthers were eased from the florets and smeared in Belling's iron acetocarmine (Johansen, 41) after the technique of Smith (69). It was found that acetocarmine stain two

years old stained the cytoplasm less darkly than freshly made stain so the former was used the most extensively. Cytological studies were made from both temporary smears and permanent slides made by the tertiary butyl alcohol method. Permanent slides made by this method were found to deteriorate rather rapidly.

In most cases so few cells at the desired stage were present on any one slide that a count and study was made of any desirable cells on the slides. Because of the lack of desirable material in some cases, only preliminary studies of meiosis were possible.

Fertility Studies

Several heads were bagged on the triploid and its progeny in the field and in the greenhouse shortly before blooming time to determine their fertility. Heavy kraft paper bags were used and were secured at the bottom with paper clips. The bags were removed from the heads after the flowers were senescent.

Methods

Photomicrographs were made with the aid of a Leitz research microscope which had a 90X oil immersion lens (N. A. 1.32), an oil condenser lens, and a 15X ocular eyepiece, and a Bausch and Lomb research microscope with a 98X oil immersion lens (N. A. 1.30) and 10X ocular eyepiece.

An Exacta camera with extension tubes equalling three inches or a plate type camera was fastened on the tube of the microscope whenever a photomicrograph was taken. Microfile film was used with the Exacta camera and Panchromatic Press, Type B sheet film was used with the plate type camera.

Magnification of the photomicrographs was determined with the aid of a stage micrometer.

EXPERIMENTAL RESULTS

Plant Characteristics of the Triploid Plant and Its Progeny

Height. As shown in Table 1 the triploid plant and all the surviving progeny of the triploid x diploid cross were measured while they were growing in the field. The heights were variable and did not give any indication of the later-determined chromosome numbers. On July 23, 1954, there was a range of heights from six to 24 inches.

The aberrant plants (with the exception of plant 25 which was left in the field due to the preliminary cytological examination of its microsporocytes seeming to indicate it was normal), the triploid, and one normal plant from the F_1 progeny of the triploid x diploid cross were measured for height in the greenhouse in June, 1955. As shown in Table 1 the heights ranged from 35 to 77 inches. Although the data were not analyzed, there seemed to be no relation between chromosome number and height. The tallest plant had six extra chromosomes and the shortest plant had two extra chromosomes which seemed to pair quite regularly during the early meiotic phases.

Plate I is a photograph of, from left to right, the triploid plant, the 2n+2+1+1+1+1 plant, the 2n+1+1+1 plant, the 2n+2 plant, trisomic plant 3, normal plant 6, and a plant of Sudan grass. The variation in height can readily be seen.

Plate II is a photograph of the eight remaining trisomics from the F_1 progeny of the triploid x diploid cross. The height can be seen to be variable.

Table 1. Plant characteristics of F_1 progeny of triploid x diploid Sorghum vulgare.

Plant no.	Chromosome no.	Maturity	Height[1] field	Height[1] greenhouse	Plant color	Seed color	Glume color	Stigma color	Head type	Head length[2] (av.)
1	2n+1	L	6	57	P	R	B	Y	C	2 1/2
2	2n+2	M	8	35	P	R	B	Y	C	1 1/2
3	2n+1	M	10	61	T	W	Br	W	O	3 1/2
4	2n+1	M	6	44	P	T	B	Y	C	2
6	2n	L	10	72	P	T	B	Y	O	4
7	2n	M	15	--	P	R	B	Y	-	-
8	2n+1	M	12	66	P	R	B	Y	O	4
9	2n+1+1	L	10	63	P	T	B	Y	O	4 1/2
10	2n+2+1 +1+1+1	M	15	77	P	R	B	Y	C	3 1/2
11	2n	M	18	--	P	R	B	Y	-	-
12	2n+1+1	L	12	61	T	R	Br	Y	O	5
13	2n+1+1 +1	L	12	72	P	R	S	Y	O	4
14	2n+1	M	14	53	P	R	B	Y	O	4
15	2n	M	16	--	P	R	B	Y	-	-
16	2n+1	L	12	72	P	T	B	Y	O	4 1/2
17	†[3]	E	12	44	T	T	T	Y	O	3
18	2n	L	24	--	P	R	B	Y	-	-
19	2n	M	24	--	P	R	B	Y	-	-
20	2n	M	15	--	P	R	B	Y	-	-
21	2n+1+1	L	8	51	P	T	B	Y	O	5 1/2
22	2n+1	L	12	70	P	W	B	W	C	3
23	2n	M	8	--	P	R	B	Y	-	-
24	2n	M	15	--	P	R	B	Y	-	-
25	2n+1	M	15	--	P	R	B	Y	-	-
26	2n+1	M	18	49	P	W	S	W	O	2 1/2
Triploid	3n	E	60	60	P	R	S	Y	O	5

[1] Height (in inches) of tallest tiller. Field--July 23, 1954. Greenhouse--June 10, 1955.

[2] In inches.

[3] Microsporocytes at proper stage unavailable.

L--late, M--medium, E--early, P--purple, T--tan, C--close, O--open, R--red, W--white, B--black, Br--brown, S--straw, Y--yellow.

EXPLANATION OF PLATE I

Comparison of heights of triploid plant, some of its progeny and Sudan grass. 1. Triploid plant. 2. Plant 10 (2n+6). 3. Plant 13 (2n+3). 4. Plant 9 (2n+1+1). 5. Plant 2 (2n+2). 6. Plant 3 (2n+1). 7. Plant 6 (2n). 8. Sudan grass.

PLATE I

EXPLANATION OF PLATE II

Comparison of heights of the various trisomics from the triploid x diploid cross.

1. Plant 26. 2. Plant 22. 3. Plant 16. 4. Plant 14. 5. Plant 8. 6. Plant 4. 7. Plant 3. 8. Plant 1.

PLATE II

Maturity. As shown in Table 1 the triploid and plant 17 were of early maturity, 15 of the plants were of medium maturity, and nine plants were of late maturity.

Fertility. All of the aberrant plants of the F_1 generation of the triploid x diploid cross and the triploid plant were highly sterile under bagging. The plants later determined to be normal with respect to chromosome number set seed under bagging. Under the conditions of open-pollination most of the aberrant plants from the triploid x diploid cross set a reasonably large amount of seeds. However, even under the conditions of open-pollination the amount of seeds set was very low for the triploid, plant 2, plant 10, and plant 13.

Seed Germination of Triploid. In June, 1954, 50 seeds of those set on the triploid plant were planted in bands in the greenhouse. Only 27 emerged and survived, giving a germination percent of 54 percent.

In June, 1955, the remaining 64 seeds from the triploid plant were planted in bands in the greenhouse. Only 24 emerged and survived, giving a germination percent of 38 percent.

Head Type. As shown in Table 1 the head type was determined only on the the triploid plant and its aberrant progeny. The triploid and 11 of its aberrant progeny had the open type of head. The remaining five aberrant plants had a very dense type of head.

Head Length. The head length of the triploid and its aberrant progeny were measured in the greenhouse (Table 1). The average head length of the triploid was five inches, while the head lengths of the progeny ranged from one and one-half inches for plant 2 to five and one-half inches for plant 21.

Plant Color. The triploid plant and its progeny with the exception of plant 3, plant 12, and plant 17 had purple plant color. Plant 3, plant 12,

and plant 17 had tan plant color (Table 1).

Glume Color. As shown in Table 1 the triploid plant and two of its progeny, plant 13 and plant 26, had straw-colored glumes. Plant 17 had tan-colored glumes. With the exception of plant 3 and plant 12 which had what may be termed brown glumes, the rest of the progeny of the triploid x diploid cross had black glumes.

Seed Color. The triploid plant and 16 of its progeny produced red seeds (Table 1). Plant 4, plant 6, plant 9, plant 16, plant 17, and plant 21 produced seeds which were essentially white during early development but which became tan-colored at maturity. Plants 3, 22, and 26 produced white seeds.

Stigma Color. It was found that without exception the plants which produced red- and tan-colored seeds possessed yellow stigmas and the plants which produced white seeds possessed white stigmas (Table 1). This is in agreement with the linkage reported in these characters.

Other Characteristics. It was found that plants 1, 6, 9, and 10 had awns on the glumes. None were noticed on the triploid plant.

Plant 2 was different from the other aberrant plants of the triploid x diploid progeny in some respects other than those previously mentioned. It had numerous tillers, about twice as many as the other aberrant plants, and many heads (approximately 100).

Plant 17 seemed to be a healthy plant but produced only a few tillers and only a few heads.

All the aberrant plants except plant 2 had such tall, weak, and spindly tillers that they had to be supported in the greenhouse with stakes.

Pollen Count of Aberrant F_1 Triploid Progeny and Normal Plants

Table 2 shows the results of a pollen count of the aberrant F_1 triploid progeny and of normal plants. The average percent of full pollen grains for the various aberrant plants ranged from 2.9 percent for trisomic plant 16 to 52.4 percent for trisomic plant 8. It was noted that the average percent of full pollen grains for the aberrant plants was less than the average percent of full pollen grains for the normal plants. No striking relation between chromosome number of the aberrant plants and percent of full pollen grains was noticed. The average percent of full pollen grains for the trisomic plants ranged from 2.9 percent for plant 16 to 52.4 percent for plant 8. Plant 10 with six extra chromosomes had 19.4 percent of full pollen grains. Plant 13 with three extra chromosomes had 4.0 percent of full pollen grains. The average percent of full pollen grains for the plants with two extra chromosomes ranged from 34.2 percent for plant 21 to 15.8 percent for plant 12.

The average percent of full pollen grains for normal plants on the same day as the count for the aberrant plants was found to be 66.9 percent. The following day the percent of full pollen grains for the normal plants was found to be 8646 percent and 87.9 percent, the average of the two percents being 86.3 percent.

The corrected average of full pollen grains for the aberrant plants, based on an average of 80 percent full pollen in normal plants, is given in Table 2.

Cytological Studies of Meiosis

Meiosis in Diploid Plants. In the meiotic prophase stages occurring before diakinesis it was difficult to determine much about pairing and

Table 2. Pollen count of aberrant and normal plants from F_1 progeny of triploid x diploid Sorghum vulgare.

Plant no.	First trial			Second trial			Third trial			Fourth trial			Average of four trials	Corrected average percent full[1]
	No. full	No. empty	Per-cent full	No. full	No. empty	Per-cent full	No. full	No. empty	Per-cent full	No. full	No. empty	Per-cent full		
1	16	32	33.3	22	32	40.7	16	15	51.6	12	25	32.4	39.5	49.4
2	11	34	24.4	18	68	20.9	19	36	34.6	24	110	17.9	24.5	30.6
3	1	37	2.6	2	24	7.7	0	39	0.0	1	36	2.7	3.3	4.1
4	25	23	52.1	42	39	51.9	21	27	43.8	32	35	47.8	48.9	61.1
6	20	54	27.0	9	48	15.8	11	52	17.5	23	60	27.7	22.0	27.5
8	48	44	52.2	41	48	46.1	59	26	69.4	38	53	41.8	52.4	65.4
9	15	71	17.4	23	55	29.5	17	29	37.0	32	54	37.2	30.3	37.8
10	20	67	23.0	12	71	14.5	19	45	29.7	10	87	10.3	19.4	24.2
12	53	108	32.9	33	122	21.3	14	144	8.9	0	106	0.0	15.8	19.7
13	4	93	4.1	3	114	2.6	4	107	3.7	5	89	5.6	4.0	5.0
14	0	58	0.0	0	70	0.0	3	55	5.2	10	91	9.9	3.8	4.7
16	0	87	0.0	1	85	1.2	5	65	7.1	3	87	3.3	2.9	3.6
17[2]	--	--	---	--	--	---	--	--	---	--	--	---	---	---
21	36	33	52.2	29	47	38.2	40	98	29.0	14	66	17.5	34.2	42.8
22	60	66	47.6	25	69	26.6	33	69	32.4	52	67	43.7	37.6	47.0
26	4	48	7.7	1	89	1.1	7	47	13.0	0	35	0.0	5.4	6.8
Check[3]	79	26	75.2	58	37	61.1	66	34	66.7	58	32	64.4	66.9	---
Check[4]	144	15	90.6	159	33	82.8	163	32	83.6	132	30	81.5	84.6	---
Check[4]	84	9	90.3	84	10	89.4	118	16	88.1	83	16	83.8	87.9	---

[1] Based on an average of 80% good pollen in normal plants.

[2] No pollen available.

[3] Same day as pollen count on aberrants.

[4] Day after pollen count on aberrants.

relationships of the chromosomes. At diakinesis ten pairs of chromosomes were easily distinguished, one pair being regularly attached to the nucleolus. It was impossible to determine the manner of attachment of the one pair. At metaphase I the ten pairs of chromosomes were regularly arranged on the equatorial plate. At anaphase I the bivalents disjoined reductionally with ten univalents moving to each pole.

Very little could be determined about the mitotic prophase stage. The mitotic divisions were normal with ten univalents moving to each of the four daughter cells. No micronuclei were observed in the quartet cells.

In general, chromosomes of diploid sorghum seemed much less attenuated than those of corn at comparable stages, especially at anaphase I, prophase II, metaphase II, and telophase II. The anaphase I and anaphase II stages were observed to be quite rare in the diploid smears. It was found that as a rule in the quartet cells in the diploid sorghum plant one-half of the quartet goes through the stages at a faster rate than the other half.

Plant 6 (found to be normal by cytological methods) of the F_1 generation of the triploid x diploid cross showed five instances of nine bivalents at metaphase I lying on the equatorial plate and one bivalent lying off the plate. One instance was found in which one quadrivalent occurred and one bivalent was lying off the equatorial plate at metaphase I. Figures 1 and 2, Plate III, show, respectively, photomicrographs of a microsporocyte at diakinesis in diploid Sorghum vulgare with ten pairs of chromosomes clearly visible and metaphase I with nine bivalents and one bivalent which has divided early.

In the three anthers from a floret, it was often possible to find both first and second division meiotic figures.

EXPLANATION OF PLATE III

Fig. 1. A pollen mother cell from a diploid plant of Sorghum vulgare showing 10_{II} at diakinesis. 3325X

Fig. 2. A pollen mother cell from a diploid plant of Sorghum vulgare showing 9_{II} and 2_{I} at metaphase I. 3325X

PLATE III

Fig. 1

Fig. 2

Meiosis in the Triploid Plant. As shown in Table 3 a few cells were found in the microsporocytes of the triploid plant which contained the diploid number of chromosomes rather than the expected number of 30. Two cells at diakinesis showed 30 chromosomes and 24 at metaphase I showed the same number. In all observed cases the chromosomes were arranged regularly on the equatorial plate at metaphase I. Laggards were observed in nine cells at anaphase I, in 17 cells at telophase I, in 22 cells at metaphase II, in two cells at anaphase II, and in seven cells at telophase II (Table 3).

Various types of chromosome orientation were observed at diakinesis, metaphase I, and metaphase II as shown in Table 4. At metaphase I two cells were seen which showed ten trivalents. The most frequently occurring type of trivalent was the rod type. Thirteen of the rod type were seen as compared with three of the V-shape and one of the frying pan type. Nine trivalents, one bivalent, and one univalent were observed in two cells at diakinesis and in eight cells at metaphase I. Eight trivalents, two bivalents, and two univalents were observed in eight cells at metaphase I. Seven trivalents, three bivalents, and three univalents were observed in five cells at metaphase I and in one cell at the same stage six trivalents, four bivalents, and four univalents were observed.

At metaphase II several types of orientation were observed. Two cells showed irregular arrangement of the chromosomes on the equatorial plate. Eleven cells showed one univalent at one pole and one cell showed two univalents at one pole. In seven cases cells showed one bivalent off the equatorial plate and the others regularly on the equatorial plate. One cell showed two bivalents off the equatorial plate and the others regularly on the equatorial plate.

Table 3. Chromosome count of triploid plant during meiosis in microsporocytes.

Meiotic stage	Diakinesis	Metaphase I	Anaphase I	Telophase I	Metaphase II	Anaphase II	Telophase II
Number of cells with 30 chromosomes	2	24	9	--	--	--	--
Number of cells with other chromosome numbers	0	3	0	--	--	2	--
Number of cells with regular orientation of chromosomes	2	27	0	0	0	0	0
Number of cells showing irregular orientation of chromosomes or laggards	0	0	9	17	22	2	7

Table 4. Chromosome orientation during meiosis in microsporocytes in triploid plant.

Meiotic stage	Diakinesis	Metaphase I	Metaphase II
10_{III}	--	2	--
$9_{III}, 1_{II}, 1_{I}$	2	8	--
$8_{III}\ 2_{II}, 2_{I}$	--	8	--
$7_{III}, 3_{II}, 3_{I}$	--	5	--
$6_{III}, 4_{II}, 4_{I}$	--	1	--
Irregularly on equatorial plate	--	--	2
1_{I} at pole, other chromosomes on equatorial plate	--	--	11
2_{I} at pole, other chromosomes on equatorial plate	--	--	1
1_{II} off equatorial plate, others regular	--	--	7
2_{II} off equatorial plate, others regular	--	--	1

Table 5 shows the chromosome distribution during meiosis in the microsporocytes in the triploid plant. The distribution was quite variable with from eight to 15 univalents going to the poles and from three to nine lagging univalents at anaphase I. At telophase I from one to seven laggards were observed with the frequency of the fewer laggards being the greater. At anaphase II one cell was found which showed 11 univalents moving to one pole, 13 to the other, and three laggards and one cell showed nine univalents moving to one pole, seven to the other, and 12 laggards. One cell was found at telophase II which showed seven laggards.

The frequency of occurrence of micronuclei in 25 quartet cells of the

Table 5. Chromosome distribution during meiosis in microsporocytes in triploid plant.

Meiotic stage	Anaphase I	Telophase I	Anaphase II	Telophase II
30 scattered univalents	1	--	--	--
13_I to each pole, 4 laggards	2	--	--	--
12_I to each pole, 6 laggards	1	--	--	--
12_I to one pole, 15_I to other, 3 laggards	1	--	--	--
12_I to one pole, 13_I to other, 5 laggards	2	--	--	--
11_I to one pole, 12_I to other, 7 laggards	1	--	--	--
8_I to one pole, 15_I to other, 9 laggards	1	--	--	--
11_I to one pole, 13_I to other, 3 laggards	--	--	1	--
9_I to one pole, 7_I to other, 12 laggards	--	--	1	--
1 laggard	--	6	--	--
2 laggards	--	5	--	--
3 laggards	--	3	--	--
4 laggards	1	3	--	--
6 laggards	--	1	--	--
7 laggards	--	1	--	1

triploid plant is shown in Table 6. Cells with from none to three micronuclei were more frequent than those containing fewer numbers of micronuclei. The meiotic index as determined from the data presented in Table 6 is one.

Table 6. Frequency of occurrence of micronuclei in quartet cells of triploid plant.

Number of micronuclei occurring	0	1	2	3	4	5	6
Number of cells of 25 quartets which contained the different numbers of micronuclei	42	27	18	9	2	1	1
Number of quartets with no micronuclei	1	--	--	--	--	--	--

Figure 3, Plate VII, is a photomicrograph of a microsporocyte of the triploid plant which shows the metaphase II stage of meiosis. Two micronuclei are visible near the place of the first division.

Meiosis in Trisomic Plants. Nine of the 25 surviving plants of the F_1 generation of the triploid x diploid cross were cytologically determined to be trisomics. As shown in Tables 7, 8, and 9, no cells were found in these plants which showed chromosome numbers other than 21. In trisomic plant 4 five cells at diakinesis were found which showed ten pairs of chromosomes and one univalent and in trisomic plant 16 two cells at diakinesis showed the same configuration (Table 7 and Table 10, respectively). Figure 1, Plate IV, is a photomicrograph of a microsporocyte at diakinesis in trisomic plant 25. Ten pairs of chromosomes and one univalent are visible. Figure 2, Plate IV, is a photomicrograph of a microsporocyte at diakinesis in trisomic plant 14. Nine bivalents and one trivalent lying near the nucleolus are visible. One cell showing this configuration was also found in plant 3 (Table 11).

Table 7. Chromosome count of plant 4 during meiosis in microsporocytes.

Meiotic stage	Diakinesis	Metaphase I	Anaphase I	Telophase I
Number of cells with 21 chromosomes	5	25	6	--
Number of cells with other chromosome numbers	0	0	0	--
Number of cells with regular orientation of chromosomes	0	13	1	0
Number of cells showing irregular orientation or laggards	5	12	5	20

Table 8. Chromosome count of plant 14 during meiosis in microsporocytes.

Meiotic stage	Diakinesis	Metaphase I	Anaphase I	Telophase I	Metaphase II	Anaphase II
Number of cells with 21 chromosomes	6	60	11	--	--	3
Number of cells with other chromosome numbers	0	0	0	--	--	0
Number of cells with regular orientation of chromosomes	6	59	12	89	1	3
Number of cells showing laggards	--	--	0	16	0	0

At metaphase I several different types of chromosome orientations were observed in the microsporocytes of the various trisomic plants. Ten bivalents and one univalent were observed in six cells of trisomic plant 3 (Table 11), in nine cells of trisomic plant 8 (Table 12), and in 13 cells of trisomic

Table 9. Chromosome count of plant 1 during meiosis in microsporocytes.

Meiotic stage	Metaphase I	Anaphase I	Telophase I
Number of cells with 21 chromosomes	24	1	18
Number of cells with other chromosome numbers	0	0	0
Number of cells with regular orientation of chromosomes	24	0	4
Number of cells with laggards	--	1	14

plant 16 (Table 10). Nine bivalents and one trivalent were seen in one cell of trisomic plant 3 (Table 11), in one cell of trisomic plant 8 (Table 12), in seven cells of trisomic plant 16 (Table 10), and in three cells of trisomic plant 22 (Table 13). Of the seven trivalents found in trisomic plant 16, six were J- or V-shaped and one was rod-shaped. Figures 3 and 4, Plate IV, and Figs. 1 and 2, Plate V, are photomicrographs of metaphase I plates of trisomic plant 1. In each the univalent is clearly visible.

Table 10. Chromosome orientation during meiosis in microsporocytes of plant 16.

Meiotic stage	Diakinesis	Metaphase I
$10_{II}, 1_{I}$	2	13
$9_{II}, 1_{III}$:		
J- or V-shaped trivalent	-	6
Rod-shaped trivalent	-	1

Table 11. Chromosome orientation during meiosis in microsporocytes of plant 3.

Meiotic stage	Diakinesis	Metaphase I
$10_{II}.1_{I}$	0	6
$9_{II}.1_{III}$	1	1

Table 12. Chromosome orientation and distribution during meiosis in microsporocytes of plant 8.

Meiotic stage	Metaphase I	Anaphase I	Telophase I
$10_{II}.1_{I}$	9	--	--
$9_{II}.1_{III}$	1	--	--
$10_{I}.11_{I}$	--	3	--
Equational division of lagging univalent	--	--	4

Table 13. Chromosome orientation and distribution during meiosis in microsporocytes of plant 22.

Meiotic stage	Metaphase I	Telophase I
10_{I} to each pole, 1 laggard	--	2
10_{I} to one pole, 11_{I} to the other	--	1
$9_{II}.1_{III}$	3	-

The chromosome distribution at anaphase I was somewhat variable. Ten univalents moving to one pole and 11 to the other were observed in three cells in trisomic plant 8 (Table 12), and in one cell of trisomic plant 4 (Table 14).

Ten univalents moving to each pole were seen in one cell of trisomic plant 4 (Table 14). One laggard was observed in five cells of trisomic plant 4 (Table 7), and in one cell of trisomic plant 1 (Table 9). In one cell of trisomic plant 4 six univalents moving to each pole and nine laggards were observed (Table 14). Figure 3, Plate V, is a photomicrograph of a cell of trisomic plant 14 at early anaphase I. Ten univalents are moving to one pole and 11 to the other.

Table 14. Chromosome distribution during the first anaphase stage of meiosis in microsporocytes of plant 4.

Chromosome distribution	Number of cells showing distribution
10_I to each pole, 1 laggard	4
10_I to one pole, 11_I to the other	1
6_I to each pole, 9 laggards	1

At telophase I in trisomic plant 22 one cell was found which showed ten univalents at one pole and 11 at the other (Table 13). Two cells of the same plant showed ten univalents at each pole and a lagging univalent. Lagging univalents were found in 20 cells of trisomic plant 4 (Table 7), in 14 cells of trisomic plant 1 (Table 9), in 16 cells of trisomic plant 14 (Table 8), and in four cells of trisomic plant 8 (Table 12). The four lagging univalents observed in cells of trisomic plant 8 were in the process of dividing equationally. Figure 4, Plate V, is a photomicrograph of a microsporocyte of trisomic plant 1 at telophase I. There are ten univalents at each pole and a lagging univalent which is dividing equationally.

No laggards were observed during the second meiotic division of the microsporocytes of the trisomic plants.

EXPLANATION OF PLATE IV

Fig. 1. A pollen mother cell of trisomic plant 25 showing 10_{II} and 1_{I} at diakinesis. 3325X

Fig. 2. A pollen mother cell of trisomic plant 14 showing 9_{II} and 1_{III} at diakinesis. 3325X

Fig. 3. A pollen mother cell of trisomic plant 1 showing 10_{II} and 1_{I} at metaphase I. 3610X

Fig. 4. A pollen mother cell of trisomic plant 1 showing 10_{II} and 1_{I} at metaphase I. 3615X

PLATE IV

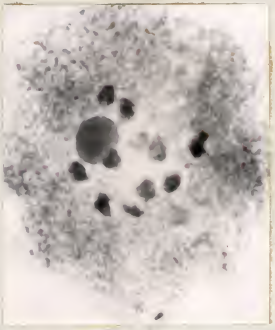

Fig. 1

Fig. 2

Fig. 3

Fig. 4

EXPLANATION OF PLATE V

Fig. 1. A pollen mother cell of trisomic plant 1 showing 1_I and clear and partially obscured bivalents at metaphase I. 3610X

Fig. 2. A pollen mother cell of trisomic plant 1 showing 1_I and clear and partially obscured bivalents at metaphase I. 3610X

Fig. 3. A pollen mother cell of trisomic plant 14 showing 21_I at anaphase I. 3325X

Fig. 4. A pollen mother cell of trisomic plant 1 showing 10_I at each pole and a lagging univalent which is undergoing equational division at telophase I. 2216X

PLATE V

Fig. 1

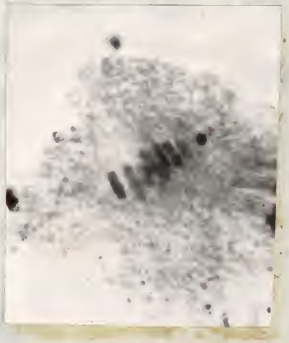

Fig. 2

Fig. 3

Fig. 4

Meiosis in 2n+2 and 2n+1+1 Plants. Four of the 25 surviving plants of the F_1 generation of the triploid x diploid cross, by cytological examination, were found to have two chromosomes more than the usual number of 20. No cells were found which had a deviating chromosome number. One cell at diakinesis in plant 2 showed scattered univalents, but in most cases the chromosomes regularly formed 11 pairs (Table 15). This was contrary to what was usually found at diakinesis in plants 9, 12, and 21. They most often formed ten pairs and two univalents with occasional instances of trivalent associations being seen.

Table 15. Chromosome count of plant 2 during meiosis in microsporocytes.

Meiotic stage	Diakinesis	Metaphase I	Anaphase I
Number of cells with 22 chromosomes	15	34	1
Number of cells with other chromosome numbers	0	0	0
Number of cells with regular orientation of chromosomes	14	33	1
Number of cells with irregular orientation of chromosomes	1	1	0

At metaphase I in plant 2, 11 bivalents regularly lined up on the equatorial plate. One instance was found in which the bivalents were more widely scattered in the cell than was usual (Table 15). In plants 9, 12, and 21 the orientation of the chromosomes at metaphase I was a little different from that found in plant 2. In plant 12 four cells were observed which showed eight bivalents and two trivalents. Figure 1, Plate VI, is a photomicrograph of a microsporocyte at metaphase I from plant 12. Visible are eight bivalents and two trivalents. One cell of plant 12 showed nine bivalents, one trivalent, and

EXPLANATION OF PLATE VI

Fig. 1. A pollen mother cell of 2n+1+1 plant 12 showing 8_{II} and 2_{III} at metaphase I. 3325X

Fig. 2. A pollen mother cell of 2n+1+1+1 plant 13 showing 7_{II} and 3_{III} at metaphase I. 3325X

Fig. 3. A pollen mother cell of 2n+1+1+1 plant 13 showing 10_{I} and 13_{I} at anaphase I. 3325X

Fig. 4. A pollen mother cell of 2n+1+1+1 plant 13 showing 10_{I}, 11_{I}, and 3 lagging univalents, 2 of which are dividing equationally, the third having already divided. 3420X

PLATE VI

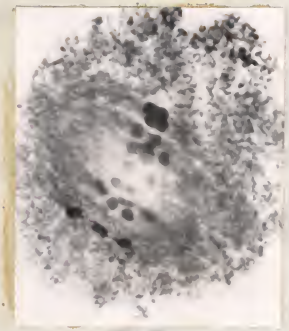

Fig. 1

Fig. 2

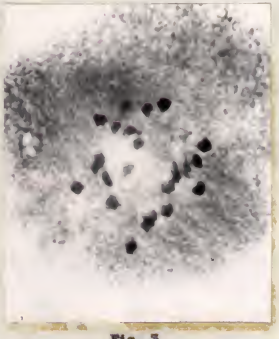

Fig. 3

Fig. 4

one univalent. There was one cell seen which showed nine bivalents and one quadrivalent (Table 16). Similar configurations were seen in the other 2n+1+1 plants.

Table 16. Chromosome orientation during meiosis in microsporocytes of plant 12.

Meiotic stage	Metaphase I	Metaphase II
$^{8}_{II},^{2}_{III}$	4	--
$^{9}_{II},^{1}_{III},^{1}_{I}$	1	--
$^{9}_{II},^{1}_{IV}$	1	--
3_{I} out in cytoplasm	--	1

In plant 2 only one cell was observed at anaphase I. No laggards were seen (Table 15). Of the two cells observed at anaphase I in plant 21, one showed a distribution of 11 univalents moving to each pole, and the other showed 12 univalents moving to one pole and ten to the other (Table 17). No cells at anaphase I were seen in the other 2n+1+1 plants.

At telophase I in plant 21, 20 cells were observed which showed laggards (Table 17). No cells at this stage were observed in the other 2n+1+1 plants.

Table 17. Chromosome distribution during meiosis in microsporocytes of plant 21.

Meiotic stage	Anaphase I	Telophase I
Number of cells showing laggards	--	20
Distribution:		
$^{11}_{I},^{11}_{I}$	1	--
$^{12}_{I},^{10}_{I}$	1	--

One cell at metaphase II in plant 12 was found which showed three univalents out in the cytoplasm of the cell (Table 16). No cells at this stage were observed in the other 2n+1+1 plants.

Meiosis in the 2n+1+1+1 Plant. Cytological examination of microsporocytes of plant 13 showed it to have three chromosomes more than the usual number of 20 for Sorghum vulgare. Figure 2, Plate VI, is a photomicrograph of a microsporocyte of plant 13 at metaphase I. Seven bivalents and three trivalents can be seen. Figure 3, Plate VI, is a photomicrograph of a microsporocyte of plant 13 at anaphase I. Thirteen univalents are moving to one pole and ten to the other. Figure 4, Plate VI, is a photomicrograph of a microsporocyte of plant 13 at telophase I. Ten univalents are visible at each pole. Lagging in the center of the cell are three univalents, two of which are dividing equationally and the other of which has already divided equationally, one half evidently having moved to a pole. Further study of this plant was not possible.

Meiosis in the 2n+2+1+1+1+1 Plant. Cytological examination of microsporocytes of plant 10 revealed that it had six extra chromosomes. At diakinesis a number of different configurations of chromosomes were found as shown in Table 18. In the cases where there was just one nucleolus, from four to eight pairs of chromosomes were attached to the nucleolus and correspondingly, from nine to five pairs of chromosomes were scattered about in the cytoplasm. In three cells it was found that the bivalents were completely disjoined. Two cells were found in which two nucleoli were present. In one case four pairs of chromosomes were attached to one nucleolus, five pairs were attached to the other, and four pairs of chromosomes were scattered about in the cytoplasm. In the other where there were two nucleoli present, four pairs of chromosomes were attached to one nucleolus, three pairs were attached to the other, and six pairs were scattered about in the cytoplasm.

Table 18. Chromosome orientation during diakinesis stage of meiosis in microsporocytes of plant 10.

Chromosome arrangement	Number of cells showing arrangement
5 scattered pairs, 8 pairs attached to nucleolus	8
6 scattered pairs, 7 pairs attached to nucleolus	8
7 scattered pairs, 6 pairs attached to nucleolus	15
8 scattered pairs, 5 pairs attached to nucleolus	11
9 scattered pairs, 4 pairs attached to nucleolus	1
2 nucleoli, 4 scattered pairs, 4 pairs attached to one nucleolus, 5 pairs attached to other	1
2 nucleoli, 6 scattered pairs, 4 pairs attached to one nucleolus, 3 pairs attached to other	1
Split bivalents	3

In the 18 metaphase I cells observed the chromosomes were regularly oriented on the equatorial plate (Table 19). Figure 1, Plate VII, is a photomicrograph of a cell from plant 10 at metaphase I. Visible are 11 bivalents, two trivalents, and two univalents.

Six anaphase I cells were observed which showed lagging chromosomes (Table 19). Figure 2, Plate VII, is a photomicrograph of a microsporocyte of plant 10 at late anaphase I. Cleanly visible are several lagging univalents which are dividing equationally.

An equal number of cells of plant 10 at telophase I were observed to have laggards and to have no laggards (Table 19).

Of the seven second division cells observed in plant 10 five showed lagging chromosomes (Table 19). Five of the seven observed quartets showed micronuclei.

Table 19. Chromocome count of plant 10 during meiosis in microsporocytes.

Meiotic stage	Diakinesis	Metaphase I	Anaphase I	Telophase I	Metaphase II	Anaphase II	Telophase II	Quartet
Number of cells with 26 chromosomes	48	34	10	--	--	--	--	--
Number of cells with other chromosome numbers	0	0	0	--	--	--	--	--
Number of cells with regular orientation of chromosomes	48	18	4	40	1	1	0	2
Number of cells showing laggards	--	--	6	40	--	3	2	5[1]

[1] Actually the number of quartets showing micronuclei.

EXPLANATION OF PLATE VII

Fig. 1. A pollen mother cell of 2n+2+1+1+1+1 plant 10 showing 11_{II}, 2_{III}, and 2_{I} at metaphase I. 3325X

Fig. 2. A pollen mother cell of 2n+2+1+1+1+1 plant 10 showing 6 laggards at telophase I. 3325X

Fig. 3. A pollen mother cell of triploid plant showing 2 micronuclei at metaphase II. 3000X

PLATE VII

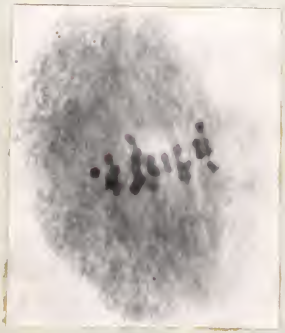

Fig. 1

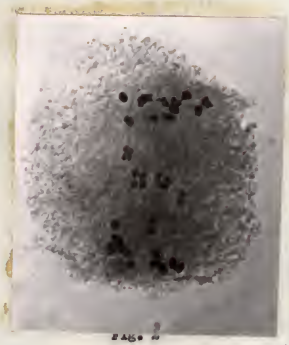

Fig. 2

Fig. 3

Meiosis in the Remaining F_1 Plants. Cytological examination of the microsporocytes of nine of the ten remaining plants of the F_1 generation showed them to go through meiosis as do the diploid plants, so they were considered to be normal.

No microsporocytes at the proper stage for determination of chromosome number could be obtained for plant 17, so at the present time its chromosome number is unknown.

DISCUSSION

Although triploid plants have been previously reported in Sorghum vulgare (Chin, 24 and Kidd, 45), no crosses of triploid x diploid plants in the species have been reported, much less any studies of the aneuploid series resulting therefrom.

Nine of the 25 surviving plants of the triploid x diploid cross reported here were found to have the normal diploid number of chromosomes, while the remaining 16 plants had chromosome numbers ranging from 21 to 26. The vigor of these aberrant plants was not appreciably different from that of plants with a normal chromosome number. These facts would seem to indicate that Sorghum vulgare can tolerate several extra chromosomes without much loss in vitality. However, the triploid and all the plants in its progeny found to have extra chromosomes were completely sterile under selfing and had a greater or lesser degree of sterility when open-pollinated. The triploid and plants 2, 10, and 13 were highly sterile even under open-pollination. With the exception of plant 2, this would indicate that sterility increases with the number of extra chromosomes. The sterility of plant 2 is difficult to explain. It may possibly have some connection with the fact that the two extra chromosomes seem to pair regularly. Much less sterility was observed in the three plants whose two extra

chromosomes formed trivalent associations or univalents. No obvious connection between chromosome number of the aberrant plants and percent of good pollen was noted. The sterility of these plants can be circumvented because of the fact that Sorghum vulgare is a perennial and the aberrant plants, especially, tiller profusely. The various aberrants can be and some of them were cloned out to increase their number.

It would be difficult to attribute sterility and other observable differences in the various trisomic plants to different chromosomes being involved three times because of their probable hybrid origin, although some of the differences may be due to different chromosomes. Further study would determine the answer.

Trisomic Inheritance

Of all the aberrant plants obtained from the triploid x diploid cross, the trisomics are probably of the most value because it is expected that they can be used directly in the location of specific genes on specific chromosomes and the location of linkage groups. Monosomics and nullisomics could be of such use, but it is doubtful whether Sorghum vulgare is a sufficient enough polyploid to allow the loss of one or two chromosomes. The other aberrant plants could be crossed with diploid plants in the hope of producing additional trisomic plants, but the high degree of sterility in those with the higher chromosome numbers would be a limiting factor. Probably the best source of trisomics would still be the triploid x diploid cross. It would seem evident from the high percentage of trisomics obtained from such a cross, that a complete set of primary trisomics can be obtained with relatively little difficulty.

It is more than likely true that among the eight trisomic plants on hand are plants that may be trisomic for different chromosomes although some of them

may be of the same genetic constitution. The uncertain origin of the triploid parent would not cause any difficulty in using the various trisomics in crosses.

A factor influencing the percent of transmission of the trisomic chromosome would be the viability of the male and female gametes carrying the extra chromosome in the trisomic plants. Until definite studies and determination of the percent of transmission of the extra chromosome are made in the pollen and egg cells, it is to be assumed (on the basis of information gathered about trisomics and percent of transmission of the extra chromosome in other genera) that there would be very little, if any, transmission of the extra chromosome through the pollen in Sorghum vulgare. Consequently, the trisomic plants would have to be used as the female parent in crosses with normal diploid tester stocks. The percent of transmission of the extra chromosome through the female would be a matter of further study.

The following procedure would be followed in determining the genetic constitution of the various trisomics: use a particular trisomic plant as a female in a cross with a homozygous recessive diploid plant of known genetic background (a tester stock) as a male. If the trisomic plant is of the constitution AAA (letting A represent the dominant allele of any particular pair of alleles and a represent the recessive allele), all the plants of the F_1 generation, whether trisomic or diploid for the character being studied, will show the dominant condition of the character. However, in the next backcross generation, assuming no transmission of the extra chromosome through the pollen and complete transmission through the egg, there will be a 5:1 ratio of the A allele to the a allele if the chromosome carrying the factor being studied is present in the trisomic plant in triplicate. If the chromosome carrying the factor being studied is present in the trisomic plant only twice, then the ratio of the A to the a allele in the second backcross generation will be 1:1.

If the trisomic plant being studied is in the duplex (AAa) condition, a cross with a tester stock which is homozygous recessive for the triplicated chromosome in the trisomic would give a 5:1 ratio of the A to the a allele. Otherwise the normal 1:1 backcross ratio would appear.

If the trisomic plant is of the simplex (Aaa) constitution, a cross with a genetic tester of the constitution aa would give a 1:1 ratio of the A to the a allele whether or not the trisomic plant carries the factor being studied in triplicate. A second backcross would give the same 1:1 ratio. A cross with a tester of Aa constitution would give a 3:1 ratio if the factor being studied is represented in the trisomic in triplicate. A cross with a tester of AA constitution would give the dominant condition in all the progeny whether or not the chromosome carrying the factor being studied is represented in the trisomic two or three times.

If the trisomic plant is in the nulliplex condition (aaa), a cross with a tester aa would result in progeny showing the recessive condition whether or not the factor being studied is represented in the trisomic two or three times. In such a case the best way to determine the constitution of the trisomic would be to cross it with a trisomic in the simplex or duplex condition which would give, respectively, a 1:2 and a 2:1 ratio of the A allele to the a allele if the same chromosomes are involved three times.

Table 20 gives the trisomic inheritance of an allelic pair A and a in a trisomic when the extra chromosome is not carried by the pollen. The ratios would be modified if transmission of the extra chromosome is less than 100 percent through the female.

Table 20. Trisomic inheritance of an allelic pair A and a in a trisomic plant, assuming no transmission of the extra chromosome through the pollen, complete transmission through the egg, and random assortment in trisome.

Female parent	Male parent	2n offspring			2n+1 offspring				Ratio
		AA	Aa	aa	AAA	AAa	Aaa	aaa	A:a
AAA	AAA	1	--	--	1	--	--	--	1:0
	AAa	2	1	--	2	1	--	--	1:0
	Aaa	1	2	--	1	2	--	--	1:0
	aaa	--	1	--	--	1	--	--	1:0
	AA	1	--	--	1	--	--	--	1:0
	Aa	1	1	--	1	1	--	--	1:0
	aa	--	1	--	--	1	--	--	1:0
AAa	AAA	2	1	--	1	2	--	--	1:0
	AAa	4	4	1	2	5	2	--	17:1
	Aaa	2	5	2	1	4	4	--	8:1
	aaa	--	2	1	--	1	2	--	5:1
	AA	2	1	--	1	2	--	--	1:0
	Aa	2	3	1	1	3	2	--	11:1
	aa	--	2	1	--	1	2	--	5:1
Aaa	AAA	1	2	--	--	2	1	--	1:0
	AAa	2	5	2	--	4	4	1	5:1
	Aaa	1	4	4	--	2	5	2	2:1
	aaa	--	1	2	--	--	2	1	1:1
	AA	1	2	--	--	2	1	--	1:0
	Aa	1	3	2	--	2	3	1	3:1
	aa	--	1	2	--	--	2	1	1:1
aaa	AAA	--	1	--	--	--	1	--	1:0
	AAa	--	2	1	--	--	2	1	2:1
	Aaa	--	1	2	--	--	1	2	1:2
	aaa	--	--	1	--	--	--	1	0:1
	AA	--	1	--	--	--	1	--	1:0
	Aa	--	1	1	--	--	1	1	1:1
	aa	--	--	1	--	--	--	1	0:1
AA	AAA	1	--	--	--	--	--	--	1:0
	AAa	2	1	--	--	--	--	--	1:0
	Aaa	1	2	--	--	--	--	--	1:0
	aaa	--	1	--	--	--	--	--	1:0
Aa	AAA	1	1	--	--	--	--	--	1:0
	AAa	2	3	1	--	--	--	--	5:1
	Aaa	1	3	2	--	--	--	--	2:1
	aaa	--	1	1	--	--	--	--	1:1
aa	AAA	--	1	--	--	--	--	--	1:0
	AAa	--	2	1	--	--	--	--	2:1
	Aaa	--	1	2	--	--	--	--	1:2
	aaa	--	--	1	--	--	--	--	0:1

Meiosis and Other Characters

Meiosis in the triploid plant and in the aberrants corresponded to that in other triploids and aneuploids reported in the literature. There was much irregularity in all of them which would cause much irregularity in the progeny. The most frequent type of trivalent found in the plants in general was the rod type, with the V- and J-shaped trivalents being the next most frequent. Only one case, in the triploid, was found of the frying pan type of trivalent.

The fairly large percent of the progeny of the triploid x diploid cross having one and two extra chromosomes would indicate that possibly those plants or zygotes and gametes with the higher chromosome numbers are less viable than those with the lower chromosome numbers.

The most unusual plant of the aberrant progeny of the triploid x diploid cross was plant 2 which has two extra chromosomes which seem to pair regularly. It appears that this plant is a tetrasomic and that there is an additive effect of four chromosomes of the same type causing the extreme dwarf condition, profuse tillering, and high degree of sterility. These characteristics were not true of the three plants determined to be double trisomics.

Plant 10 was distinct from the standpoint of its extreme height. This was probably due to an additive effect of the six extra chromosomes. Indications from the associations at metaphase I of meiosis were that this plant is tetrasomic for one pair of chromosomes and trisomic for four other pairs.

SUMMARY

Of 25 surviving plants from the progeny of a triploid x diploid cross in Sorghum vulgare, nine were found to be normal diploids, nine were found to be primary trisomics, three were found to double trisomics, one was probably a

tetrasomic, one was a triple trisomic, one seemed to be a tetrasomic-quadruple trisomic complex, and one was of undetermined chromosome number.

Meiosis in the triploid plant and the aberrant progeny was found to correspond essentially to that reported in other triploids and aneuploids in the literature. The most frequent type of trivalent found was the rod type with the V- and J-shaped types being the next most frequent. Only one example, in the triploid, was found of the frying pan type of trivalent.

There was no correlation of chromosome numbers of the plants from the standpoint of morphological characters except that the percent of seed set on the triploid and three of its progeny, one with six extra chromosomes, one with three extra chromosomes, and one seeming tetrasomic, was very low. There was no noticeable increase or decrease in vitality due to extra chromosomes.

The high frequency of primary trisomics found in the progeny of the triploid x diploid cross indicated that a complete set of primary trisomics could probably be obtained without much difficulty. These primary trisomics would be of especial value in locating particular factors on particular chromosomes and in locating linkage groups. It is probable that Sorghum vulgare is not a sufficient enough polyploid to allow the loss of chromosomes necessary to produce the monosomics and nullisomics which are often used in the location of factors and linkage groups.

Trisomic inheritance was outlined and the method of determining the genetic constitution of the trisomics was discussed.

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A CYTOLOGICAL STUDY OF A TRIPLOID X DIPLOID CROSS OF SORGHUM VULGARE

by

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An off-type plant of Sorghum vulgare having slightly less than normal vigor, early heading, excessive side branches, many tillers, and very low seed set was found in a row of White Collier sorgo at the Fort Hays Branch Experiment Station in 1953. Cytological examination of the microsporocytes showed that it was actually a triploid. From an infinitely large number of florets about 100 seeds had been set from cross-pollination, presumably with White Collier lines and/or Waxy Atlas selections which were adjacent to the triploid. These seeds were red indicating that the triploid was probably of hybrid origin.

Fifty of the seeds planted in the greenhouse and moved in the seedling stage to the field yielded 27 plants, two of which were later destroyed by rabbits. Of the 25 surviving plants from this triploid x diploid cross, nine were found to be normal diploids, nine were primary trisomics, three were double trisomics, one was probably a tetrasomic, one was a triple trisomic, one seemed to be a tetrasomic-quadruple trisomic complex, and one was of undetermined chromosome number.

There was no obvious connection between chromosome number and the morphological characteristics of the various plants. Extra chromosomes did not seem to appreciably affect the vitality but there was a very much lower percent of seed set in the triploid, the tetrasomic, the triple trisomic, and the plant with the tetrasomic-quadruple trisomic chromosome complex.

The high frequency of primary trisomics found in the progeny of this triploid x diploid cross indicated that a complete set of primary trisomics could probably be obtained without much difficulty. These primary trisomics would be of especial value in locating particular factors on particular chromosomes and in locating linkage groups. It is probable that Sorghum vulgare is not a sufficient enough polyploid to allow the loss of chromosomes

necessary to produce the monosomics and nullisomics which are often used in the location of factors and linkage groups on chromosomes.

Trisomic inheritance was outlined and the method of determining the genetic constitution of the trisomics was discussed.

Meiosis in the triploid plant and its aberrant progeny was found to correspond essentially to that reported in other triploids and aneuploids in the literature. The most frequent type of trivalent found was the rod type with the V- and J-shaped types being the next most frequent. Only one example, in the triploid, was found of the frying pan type of trivalent.