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Report on Desynaptic Mutants among the Progeny of Artificial Interspecific Hybrid of *Coix*

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ABSTRACT

A premature disjunction of few to all bivalents during Meiosis-I is reported here in the genus Coix. This is a classic case of desynapsis type of mutation. The two species of Coix, Coixaquatica (2n=10) and nullisomic Coix gigantea Roxb. (2n=18) were artificially crossed. A range of interspecific hybrids from 2n=11 to 2n=26 was produced with varying numbers aquatica and gigantea chromosomes. Some hybrids were partially fertile and were selfed to study the inheritance of parental chromosomes in hybrids. Among the selfed progeny of hybrid with 2n=11 and tetrasomic C.gigantea (2n=22) two desynaptic mutants, one with 2n=11 chromosomes and another with 2n-22 chromosomes were obtained. Their detailed cytology and probable cause of this mutation is discussed.

Key words: Artificial interspecific hybrids, desynaptic mutants, Nullisomy, Chromosomal inheritance.

INTRODUCTION

Genus *Coix (L)* is a wild relative of Maize belonging to tribe Maydeae of family Poaceae. Among the nine species of the genus *Coix*, *C. lacrymajobi* L.and

C. gigantea Koen. have 2n = 20 small chromosomes and *C. aquatica* Roxb. 2n = 10 large chromosomes, and are widely distributed in South and South East Asia, the first is cultivated and spread to all warmer parts of the world. Aneuploid and polyploid races occurred through chromosome nondisjunction and genome doubling in *C. gigantea* and *C. aquatic*a. The other species have restricted localized distribution. *C. puellarum* Balansa, *C. ouwehandii* Koord. and *C. poilanei* Mimeur are speculated to have originated from the three established species, through chromosomal changes and gene mutations and adapted to restricted localized areas, and *C. gasteenii* Simon, an allopolyploid form of *C. lacrymajobi* and *C. gigantea*[16(b)].Apart from being economically important but underutilized plant, this genus was shown to be interesting cytologically. Aneuploids and interspecific hybrids are of common occurrence in the wild populations of all the 3 species[1, 13,17-26]. Populations of *C. aquatica* and *C. gigantea*, when grown side by side produced a range of hybrids from 2n=10 to 2n=28[26]. *C. gigantea* produced aneuploids ranging from 2n-2 to 2n+6. Artificial crosses between *C. aquatica* and *C. gigantea* also produced similar hybrids[13]. Some semi-fertile and interesting hybrids were self-pollinated and progenies were cytologically screened to study the inheritance of *aquatica* and *gigantea* chromosomes. Two plants from such crosses, one with 2n=11(10 aquatica+1 gigantea) chromosomes and one tetrasomic of *C. gigantea* (2n=22)showed peculiar chromosome behavior in the form of desynapsis, which are being reported. A case of desynapsis in case of the natural population of species *Coix lacryma-jobi*[16]. Desynapsis is being reported in the population of interspecific hybrid of other two species of *Coix*, for the first time.

MATERIALS AND METHODS

Artificial cross-pollinations were performed involving *Coix aquatica* (2n=10) and established nullisomic of *Coix gigantea* (2n=18). Seeds were collected and sown in the subsequent year to raise F_1 progeny. The resulting plants

were cytologically screened for chromosome numbers and meiotic behavior. The hybrids obtained were selfed to produce F_2 generations. Further, F_3 and F_4 generations were obtained in a similar fashion and cytologically screened by conventional methods. Important stages of meiosis were micro-photographed.

RESULTS

Table-1: Result of selfing2n=11

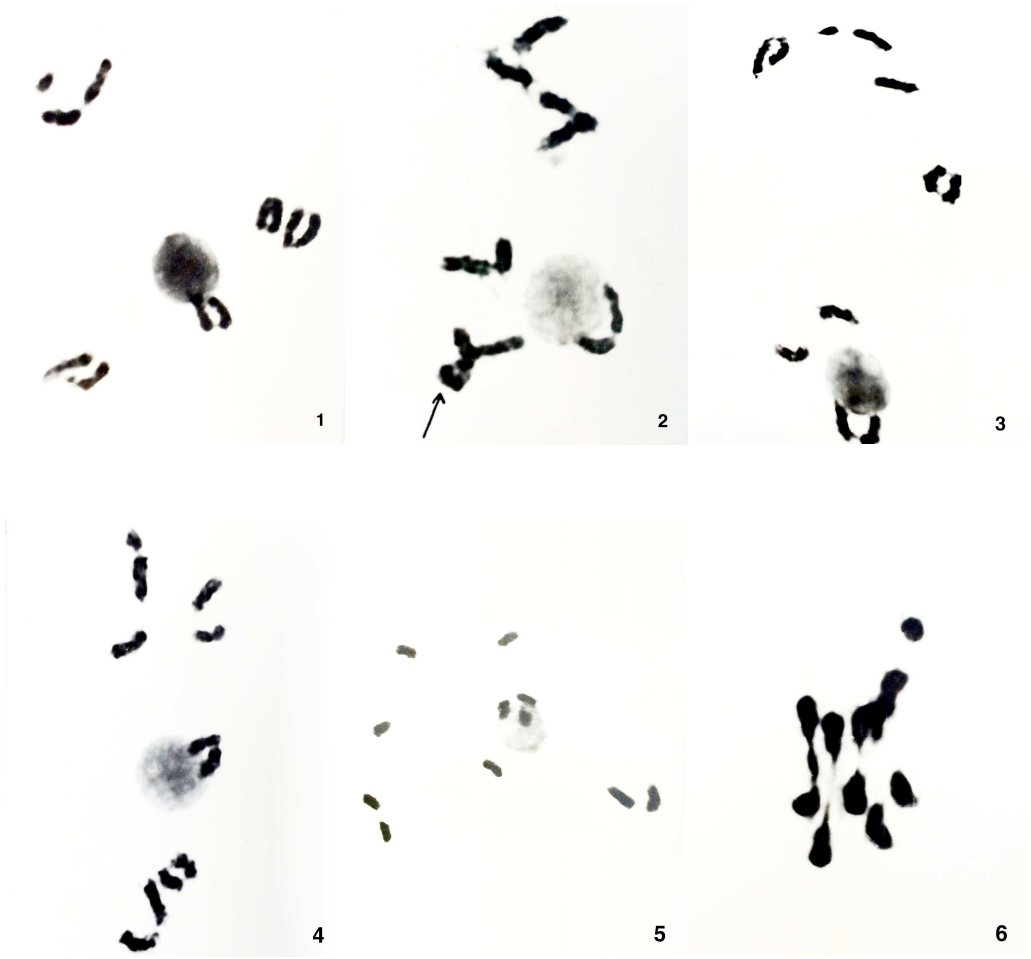
Number of plants obtained and screened	Plants with chromosome number	
	2n=10	2n=11
09	07	02

Table-2: Result of selfing 2n=22

Plants Screened	Plants with chromosome number							
	2n=18	2n=19	2n=20	2n=21	2n=22	2n=23	2n=24	2n=26
67	08	31	01	01	21	03	01	01

One plant with 2n=11 obtained from selfed progeny of 2n=11 of F_3 and 2n=22 obtained from selfed progeny of 2n=22 of F_3 showed interesting cytological behavior in the form of variable degrees of desynapsis.

Plate 1 – Cytology of the Mutant 2n=11



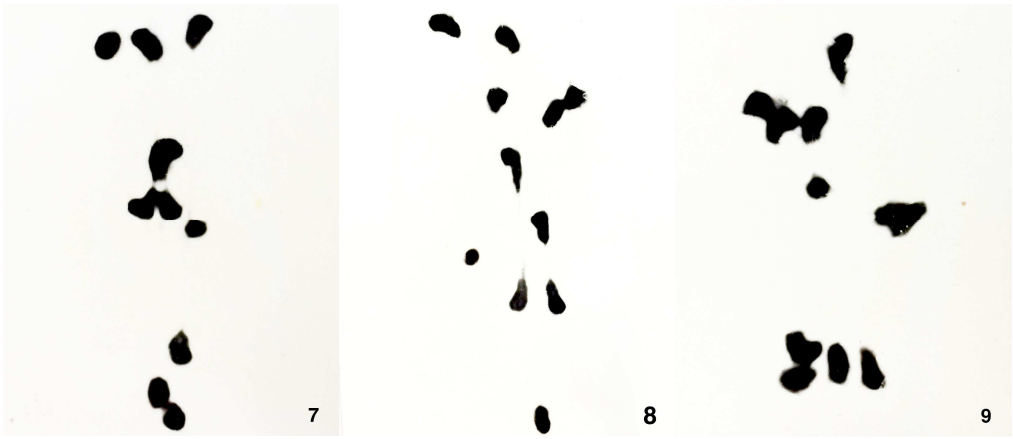
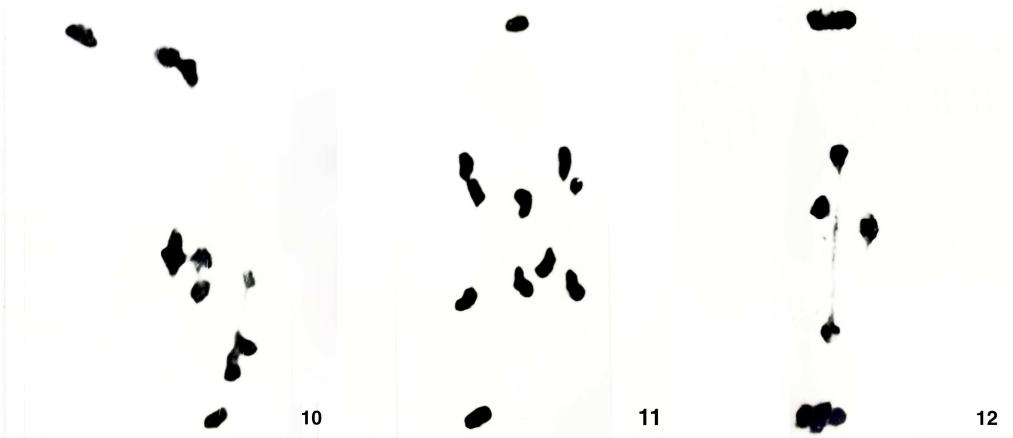
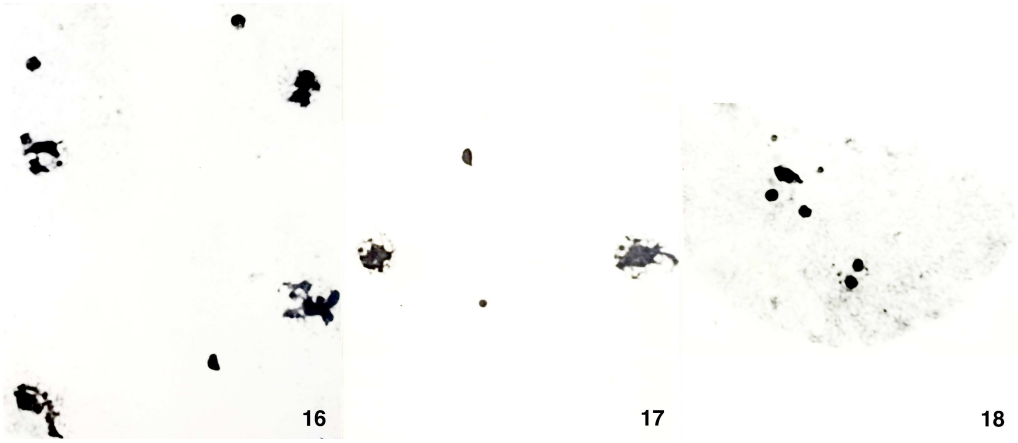


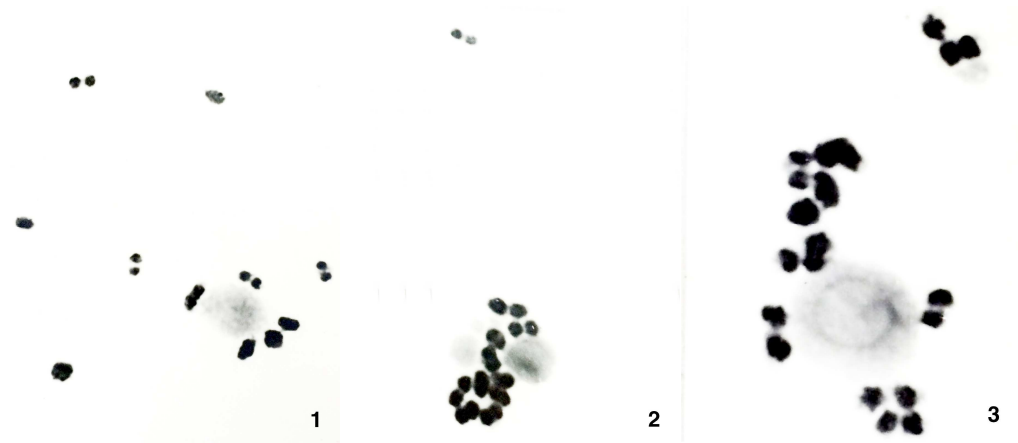
Plate 2

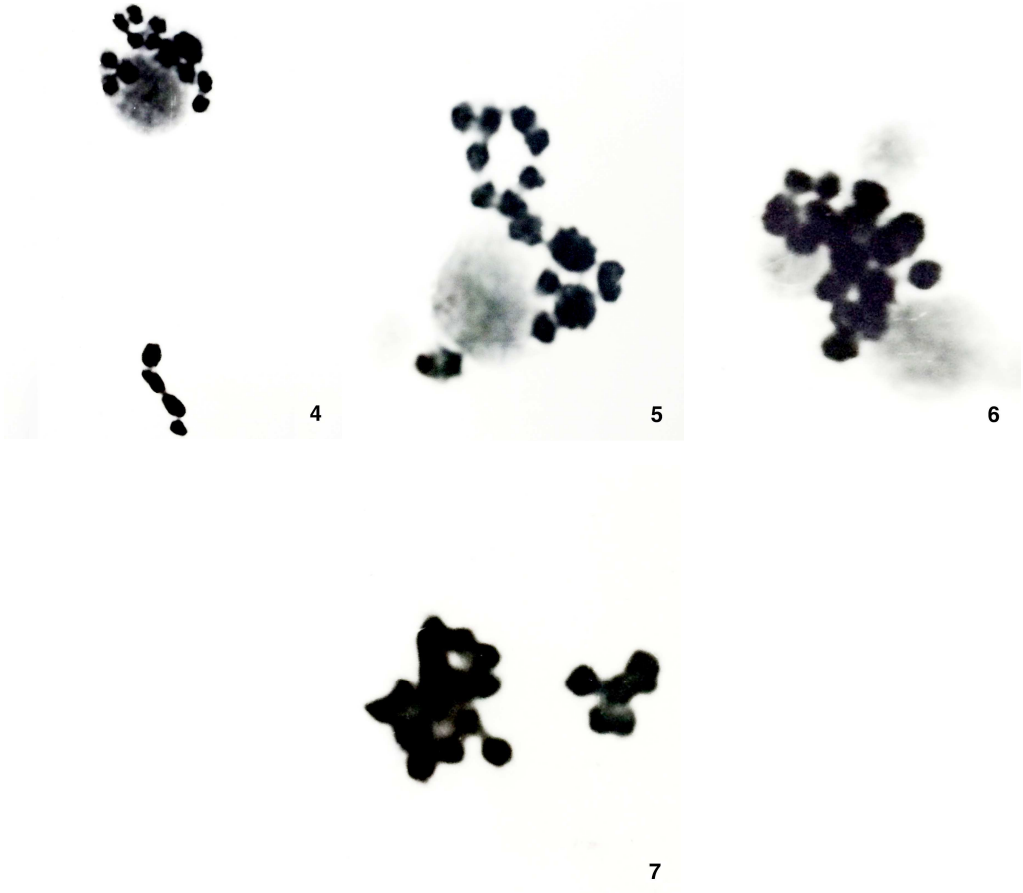




This plant carried 10 large chromosomes from *C. aquatica* and one small chromosome from *C. gigantea*. This plant showed partial desynapsis. Most of the PMCs showed poor pairing and reduction in the number of chaismata. The bivalents showed end-to-end pairing or simple terminal association probably without crossing over, majority of the times (Fig. 2). One small chromosome of *C.gigantea* formed heteromorphic bivalent with larger chromosome of *C. aquatica*. Variable numbers of *aquatica* chromosomes remained unpaired and in some PMCs 11 univalents (Fig.5) were recorded at diakinesis. Though the metaphase orientation of bivalents was normal (Fig. 6), in anaphase, distribution of univalents was noted to be irregular (Fig.7, 8-13). A bivalent (Fig. 9) two bivalents (Fig.10), a trivalent and a univalent (Fig.7) were found to be lagging, leading to unequal distribution of the chromosomes at poles (Figs.7, 9 &12). Univalents were also noted to be randomly distributed (Fig.11). In some PMCs, dicentric bridge formation was noted (Fig.12) in addition to pole-to-pole distribution of 9 univalents and a bivalent. (Fig.13). Rarely was seen 6-5 distribution univalent at anaphase -I (Fig.14). Dyads and tetrads frequently showed variable number of laggard univalent that normally turned pycnotic (Figs.15, 16,17 &18). The net result of this disturbed meiosis was deficient microspores with micronuclei leading to the formation of sterile pollen. The plant was weak and small with just a few tillers.

Plate 3 – Cytology of the Mutant 2n=22





This plant carried all the *C. gigantean* chromosomes. This too was a desynaptic mutant. The chromosomes formed bivalents very rarely (Fig.1) and most of the time showed variable number of univalents always in association with the nucleolus or nucleolar bits.(Fig.2 & 3). The univalent and bivalents were randomly placed in PMCs but most were attached to or close to the nucleolus (Figs. 3, 4 & 5). As PMCs approached metaphase, the chromosomes became sticky, globose and condensed forming clumps. (Fig. 6,7). Later this heavy clumping increasingly made it impossible to resolve them. Further stages were, therefore could not be analyzed. The plant was highly sterile.

DISCUSSION

Desynapsis has been reported in as many as 20 plant families, 50 genera and 70 species. More recently, it has been shown to occur in 126 plants[11] and many more reports are available in the recent literature as well.Plenty of literature is available on the meiotic abnormalities in plants that focuses on the two important events, desynapsis and asynapsis. When the old literature was reviewed, it was noted that theoretically these two events are differentiated on the basis of chromosome behaviour at Prophase-I and metaphase-I of the reduction division of meiosis. Desynapsis is associated with appearance of univalents (formed as a result of precocious separation of bivalents) at the post pachytene stage. This probably occurs due to failure of crossing over. Asynapsis, on the other hand, has been linked with total prevention of chromosome pairing. Practically, in the absence of detailed study of Prophase-I it is difficult to show whether asynapsis has occurred or desynapsis, and hence it is hard to use either of these terms with accuracy. Soost[27] preferred to associate asynapsis with lack of chromosome pairing during first meiotic prophase and according to him this term is inappropriately used to indicate lack of chromosome pairing at any point during meiosis-I. Li, Pao and Lisuggested the use of term desynapsis for the condition where chromosomes synapse at pachytene but fail to sustain the pairing in further stages of prophase-I and metaphase-I

As a result of desynapsis, variable number of univalents are detected in the PMCs. Depending upon this number, 3 types of desynapsis has been described: weak, medium-strong and complete desynapsis[12]. The amount of unpairing of chromosomes is described as degree of desynapsis that can be calculated using the formula ***"d= r + i "*** where***r*** is the number of rod bivalents and ***i*** is the number of univalents[6]. Statistical analysis of the chaisma frequency for bivalents in PMCs has been done and correlated with the intensity of desynapsis.[4, 8, 28, and 29]. Pagliarini, M. S.[14] described three different patterns of desynapsis. This differentiation is made on the basis of, Pattern-1: presence of only univalents in most of the PMCs showing irregular segregation of chromosomes in meiosis I & II, or, Pattern-2:

most PMCs showing most or all univalent at diakinesis followed by their normal segregation during meiosis II and finally, pattern-3: sister chromatid cohesion at prometaphase-I with further irregular congression and distribution of the chromatids during both divisions.

Most of the available literature on desynapsis has cited examples from those cases where complete genome was found to be affected (hologenomic dysnapsis). In this type, all the bivalents are affected by desynaptic mutation. R. C. Jackson[8] et el showed that desynapsis can also be chromosome-specific, as studied in the case of *Haplopappus gracilis,* where only some of the bivalents are affected. The entire process of meiosis, especially crossing over that results from successful chromosome pairing, is genetically controlled. In most of the cases that are reported, desynapsis has been shown to occur spontaneously. However in *Capsicum annum,* irradiation with ^{60}Co gamma radiations was shown to induce desynapsis[9]. Though this type of mutation resulted in good vegetative growth and normal flowering, the plants showed negligible fruit setting. Whether natural or induced, desynapsis in all the cases reported, always resulted in some or all of the following consequences: variable number of univalents, their unequal distribution in anaphase II, formation of unstable and aneuploid gametes, and sterile pollen grains and hence weak and sterile plants. Filho[5], et al, showed formation of diploid pollens and ovules as a result of this type of mutation. Animesh Datta[4] et al found that the chromosomes become sticky, globose and condensed due to desynapsis in case of diploid and hexaploid species of *Solanum.* Desynapsis is reported to affect microsporogenesis[15] as well megasporogenesis[7]. Calisto V. et al [3] reported occurrence of precocious cytokinesis in Metaphase-I of meiosis, as a result of desynapsis in *Brachiariahumidicola*.

Some probable causes that are thought to induce desynapsis as cited in the literarture, are, 1.Interspecific hybridization, 2.Nullisomy, and 3.Influence of external environmental conditions, 4.Apomixis and 5.Action of gene(s). Rao[16(a)]associated the occurrence of desynapsis in *Coix lacryma-jobi* with genotype-Environment interaction. Amongst all these reports the most accepted and established cause behind desynapsis is mutation of recessive gene(s) causing synapsis. Hernandez Soriano and Ramage[17] proposed that many loci must be involved in maintaining normal meiotic pairing. To explain desynaptic variation of B chromosomes in Maize[10], a genetic model was proposed in which transposable elements are suggested to be acting upon the genes controlling sister chromatid cohesion.

The parental artificial crossing in the present piece of work involved two species, *Coix aquatica (*2n=10)*&* *C. gigantea* (2n=18) that produced interspecific hybrid with 2n=14 chromosomes (5 aquatica+9giganea) in the F1. Which upon selfing produced a range of hybrids and some aneuploids, and those chromosomal variants of cytological interest were selfed to raise F2, next F3 and finally F4 generations for the study of inheritance of the chromosomes from these two species. When initially the cytological studies on this genus were undertaken, the material of the diploid species of *C. gigantea* carried *2n=20* chromosomes. Over the years of maintenance of the germplasm of the same, this diploid number was gradually seen to be replaced by nullisomics with 2n=18 chromosomes, to such an extent that they completely dominated the *Coix gigantea* population. These nullisomics not only replaced the disomics but despite the loss of two chromosomes, they were found to be robust and fully fertile. While discussing nullisomy as the reason to induce asynapsis in wheat, Bayliss and Riley[2] showed that nullisomy increases the sensitivity of chaisma frequency to temperature. The nullisomic chromosomes, according to them, activate the recessive allele on other chromosome, which controls stability of chaisma frequency to temperature. Thus in wheat, nullisomic condition where the deficient chromosome carried gene(s) for stabilizing the meiotic pairing against variations due to temperature differences created a genotype-environment interaction leading to desynapsis.

CONCLUSION

In the light of the literature study, the case of desynapsis in *Coix* (in 2n=11 interspecific hybrid and 2n=22 tetraploid of *C. gigantea)* falls under the category of medium-strong. Whether or not the nullisomics utilized in the production of artificial interspecific hybrids between *Coix gigantea* and *C .aquatica* have any similarity of action, to the nullisomics of wheat, (as per report[2)], as far as the induction of desynapsis is concerned, requires further detailed study.It may be tentatively concluded that in the genus *Coix*, nullisomy followed by artificial interspecific hybridization could be the triggering forces in inducing this mutation or at least seem to have added to the effect of action of mutant synaptic genes. Since these mutants appeared spontaneously in the populations and available material was inadequate, detailed study on meiotic behavior and inheritance pattern of desynaptic mutation could not be carried out. Further, these plants were sterile, so inheritance behavior of chromosomes from both species that were utilized in producing hybrids, could also not be studied. Detailed studies on the inheritance of desynaptic genes in *Coix*, to predict the cause of this type of mutation are required.

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