

# Apomictic Maternal Diploids in Tetraploid Job's Tears

J. VENKATESWARLU and PANUGANTI N. RAO

Department of Botany, Andhra University, Waltair (India)

**Summary.** Two cases of reversion to diploidy were observed in autotetraploid Job's tears (*Coix lacryma-jobi* L.  $4n = 40$ ) out of a total of 1,112 plants examined over a period of 7 years. One of these was a trisomic ( $2n = 21$ ) and the other a disomic ( $2n = 20$ ), derived from apomictic development of  $n + 1$  and  $n$  maternal gametes of the tetraploid, respectively. In some respects both these derivatives differed from the original diploid that gave rise to the tetraploid through colchicine treatment. The potentialities of such reversions in the evolution of new diploid races are discussed.

## Introduction

The occurrence in nature of a series of chromosome numbers,  $2x - 4x - 8x$  etc., is often believed to be a process proceeding in one direction only. Reversion from  $4x$  to  $2x$  also occurs occasionally through elimination of fertilization (see Randolph and Fischer, 1939; Müntzing, 1943; Hougas and Peloquin, 1958; Burnham, 1962; Raman, Krishnaswamy and Nayar, 1962; Ahloowalia, 1967; Srinivasachar, 1968, Bingham, 1969; Jauhar, 1970 and others) or through somatic reduction (see Huskins and Chouinard, 1950; Menzel, 1952; Menzel and Brown, 1952; Sanders and Franzke, 1962; Ross, 1962; Chen and Ross, 1963 and others). Such spontaneous diploids arising from tetraploids have been made use of in practical plant breeding in potatoes (Hougas and Peloquin, 1958), and their evolutionary importance has been stressed by Randolph and Fischer (1939) and Raven and Thompson (1964).

In many instances, the occurrence of diploid derivatives in tetraploid populations might escape attention unless (i) the diploids and tetraploids are easily distinguishable morphologically, (ii) a specific gene marker is involved in crosses between tetraploids and diploids, or (iii) chromosome counts are made. Cases of reversion to diploidy have been found in autotetraploid Job's tears (*Coix lacryma-jobi* L.) and the observations made in this case are presented below.

## Material and Methods

Colchicine-induced autotetraploids ( $4n = 40$ ) were obtained from a diploid strain of Job's tears ( $2n = 20$ ) that ran wild in the University Campus. Although tetraploids exhibit somewhat gigas characters while they are still young, at maturity they usually have the same dimensions as the diploids from which they arose. However, certain features of the inflorescences and false fruits are distinctive in tetraploids by virtue of which they can often be identified from the corresponding diploids. The lower glumes of the male spikelets in the tetraploid are larger with broader wings than in the diploid; the capsular spathes are larger and spherical compared with the slight-

ly smaller and ovoid spathes of the diploid; and the false fruits which maintain the same size and shape as the capsular spathes are coloured brownish-black in the tetraploid in contrast to bluish-white in the diploid.

These differences led to the belief that when a reversion to diploidy occurred in the tetraploid it might be identified tentatively on a morphological basis and later established by direct cytological examination.

## Observations

Colchicine-induced tetraploids obtained in 1966 produced plenty of open-pollinated seed in February, 1967. From these seeds a progeny of 278 plants was raised during June–December, 1967. 68 random plants of this population were cytologically examined.

Table 1. Frequency of reversion of tetraploids to diploidy in Job's tears

Year	No. of tetraploid plants raised	Reversion to diploidy
1967	278	1 (trisomic)
1968	325	1 (disomic)
1969	224	—
1970	146	—
1971	70	—
1972	42	—
1973	27	—
Total: 1,112		2

While 67 of them had a tetraploid chromosome number ranging from  $4n = 41$  to 39, one plant revealed a reduced but aneuploid number of  $2n = 21$  (trisomic) (Table 1). On closer examination, the trisomic plant had smaller lower glumes in the male spikelets and smaller, ovoid capsular spathes, coming close to the diploid form from which the tetraploid was derived. However, the false fruits unlike those of the diploid, were brownish-black in colour. Every other plant in the population was examined at maturity for possible diploid characters. Two plants generally had smaller, bluish-white, spherical false fruits and

larger lower glumes of male spikelets, but these showed a tetraploid chromosome number on cytological examination.

In 1967, interspecific crosses were attempted between tetraploid Job's tears and *C. aquatica* Roxb. ( $2n = 10$ ), using the former as female parent. Of the 18 seeds obtained and sown in June, 1968, 12 germinated. 8 of them turned out to be triploid  $F_1$  hybrids with  $2n = 25$  or 26 chromosomes (5 of *aquatica* and 20 or 21 of *lacryma-jobi* chromosomes respectively) and among the rest, 3 showed  $4n = 40$  and one  $2n = 20$  chromosomes of the maternal parent (Table 1). The false fruits in the latter were smaller, ovoid and brownish-black in colour. Since seeds from the tetraploid female parent were harvested by hand and sown in germinator trays filled with fine soil free from self-sown seeds, and false fruits of the diploid-derivative were brownish-black in colour, the possibility that it might be a contaminant was ruled out.

Every year from 1968 onwards tetraploid populations, raised both from self- and open-pollinations, were carefully examined at flowering and seeding to locate possible reversions to diploidy. On 3 different occasions, plants resembling the original diploid in one or other of the characters were found but a cytological check revealed only a tetraploid chromosome number. Thus during a period of 7 years, out of a total of 1,112 plants raised from seeds collected from tetraploids examined, only two cases of reversion to diploidy were found (Table 1).

Since the trisomic was obtained for the first time in Job's tears, observations on the behaviour of chromosomes during meiosis were made. Chromosome associations occurred at diakinesis and metaphase I as 9 II and 1 III or 10 II and 1 I (Table 2). The average chiasma frequency per cell worked out at 19.61. At anaphase I, a chromosome distribution of 10:11 was found in 38 (63.3%) of the 60 cells studied, and in the rest of the cells the extra chromosome remained as a laggard. Division of the lagging univalent was observed in 3 of the 42 cells examined at telophase I. Persistent laggards organised themselves into micronuclei. In 57.14% of the pollen tetrads examined, a micronucleus was present. Pollen fertility was 60.8% and the plant set 42 seeds under open-pollination.

The diploid obtained from tetraploid showed normal meiosis, good pollen fertility and seed set.

Table 2. Chromosome associations at diakinesis and metaphase I in a trisomic ( $2n = 21$ ) of Job's tears

Chromosome associations			No. of cells	Per cent
III	II	I		
1	9	—	39	70.9
—	10	1	16	29.1
Total: 55				

## Discussion

The two reversions from tetraploidy observed in the present study are obviously derived from apomictic development of an unfertilized egg or some other nucleus of the embryo-sac. Since, in the tetraploid, the anaphase I distribution of chromosomes varies from 20:20 to 18:22, and the chromosome numbers in the progeny range between 39 and 41 suggesting that aneuploid gametes also are functional, the occurrence of a trisomic through apomictic development of a  $n + 1$  maternal gamete of the tetraploid is not wholly unexpected. The importance of trisomics in any crop species, for identifying particular genes with specific chromosomes, is well known. Their origin through reversion from a tetraploid serves as an additional way of obtaining them.

The diploid and trisomic derivatives in the present study were both different from the original diploid that gave rise to the tetraploid in having brownish-black false fruits. The fact that the triploids, obtained from crossing tetraploids and diploids with the latter as male, and also several of the open-pollinated progenies of the triploids, containing diploids, trisomics and multiple trisomics, have brownish-black false fruits suggests that the brownish-black colour of false fruits in the tetraploids does not merely result from the doubled number of chromosomes but may be induced by some genotypic changes during chromosome doubling. Since colchicine is known to induce mutagenic changes (see Ross, 1962), and the tetraploids were originally derived through colchicine treatment, it is conceivable that whatever genetic changes might have occurred were brought about by colchicine. However, the fact that one other diploid reversion that occurred through androgenesis in the tetraploid Job's tears (Rao, unpublished) had bluish-white false fruits, and that some of the false fruits in the tetraploids, and those of diploids and trisomics produced from open-pollination of triploids also were small and bluish-white, suggests that either the genotypic changes involved are not quite stable or are variable in their expression.

The evolutionary potentialities of such reversions to diploidy seem to be far reaching. From the occurrence of diploid derivatives having a different morphology of the false fruit in the present study, it is apparent, as suggested by Randolph and Fischer (1939), that the evolutionary trend among autotetraploids is not necessarily unidirectional but may be in either direction. Thus in any plant species where autotetraploids occur, considering the number of tetraploid individuals in nature and the time span involved, the occurrence of reversions, even in low frequencies, would provide ample opportunity for new diploid races to arise from them. It even appears possible that the original diploids in certain types of polyploid complexes might become extinct, only to be produced at a later time. The shift back and forth

between the diploid state and the tetraploid state might serve as a mechanism for adjusting the balance of fitness and flexibility for the organisms of that group through selection (Raven and Thompson, 1964).

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J. Venkateswarlu  
Panuganti N. Rao  
Department of Botany  
Andhra University  
Waltair (India)