

Desynapsis in *Coix lacryma-jobi* Caused by Genotype-Environment-Interaction

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Summary. Desynapsis leading to total sterility was observed in one plant of Job's tears, *Coix lacrymajobi* L., during summer months, while the other neighbouring plants were quite normal. Pachytene chromosome pairing in the desynaptic was apparently normal but a diakinesis and metaphase I several univalents were found. Perennial suckers of this plant in the rainy season showed regular meiosis and good fertility. It is probable that desynapsis was caused by an interaction of genotype and environment, in which the desynaptic gene became activated by the rapid increase in summer temperatures whilst its effect on chromosome synapsis was completely lost in the cooler periods.

Introduction

Desynapsis is the phenomenon in which the meiotic chromosomes pair at pachytene but begin to separate at diplotene and remain completely unpaired at diakinesis and metaphase I. Such a phenomenon has been reported in many plant species and is known to be governed by a single or a few pairs of genes (Beadle, 1930; Clausen, 1931; Bergner, Cartledge and Blakeslee, 1934; Richardson, 1935; Beasley and Brown, 1942; Prakken, 1943; Celarier, 1955, 1959; Swaminathan and Murty, 1959; Magoon, Ramanna and Shambulingappa, 1961; Koul, 1962; Het Ram Kalia, 1962; Sadasivaiah and Magoon, 1965; Stephens and Schertz, 1965; Vasudevan, Jos and Magoon, 1967 and others). In some cases, desynapsis is believed to be brought about by environmental conditions (Heilborn, 1930; Katayama, 1931; Sax, 1931; Darlington, 1937; Prakken, 1943; Johnsson, 1944; Li, Pao and Li, 1945; Ehrenberg, 1949; Wang, Yeh, Lee and Lee, 1965; Ahloowalia, 1969a,b; Sjödin, 1970; etc.). The available evidence suggests that lack of chiasma formation is the major, if not the only, factor involved in desynapsis (see Celarier, 1955). Crossing over involves breakage and reunion of deoxyribonucleic acid strands and presumably also breaking of protein chains in which several enzymes are involved. The absence of certain enzymes may interfere with these processes. Desynapsis probably also involves alterations in the chemical organization and function of nucleoproteins (Ahloowalia, 1969b). These factors may explain how genes governing desynapsis and environmental factors can influence chiasma formation.

Desynapsis has been observed in one plant of Job's tears (*Coix lacryma-jobi* L.) and the cytological studies made are reported below.

Materials and Methods

Some potted plants of Job's tears raised in June-December, 1966, from seeds originally collected from plants that ran wild in the University Campus; were inadvertently allowed to remain in pots even after the crop season was over. Since the species is perennial through basal stem suckers, new tillers came up in these as the old ones slowly dried away. A casual observation of these in midsummer, 1967, revealed that one plant had only sterile seeds, while others had apparently normal seed set. Except for the difference in sterility all looked alike.

Acetocarmine squash technique was invariably employed for cytological studies.

Self-pollinations were made by enclosing the whole plant in a large cloth pollination bag.

Results

Meiotic studies were made on the sterile plant, as well as on three other neighbouring plants having normal seed set. All four plants showed a diploid chromosome number of $2n = 20$. While the three fertile plants showed regular bivalent formation, the sterile plant exhibited abnormal meiosis with several univalents at diakinesis and metaphase I, although the chromosome pairing at pachytene was more or less complete. The frequency of univalents per cell varied from 12 to 20 with a mean of 15.4. Bivalents per cell varied between 0 and 4 with an average of 2.3. The plant apparently was a desynaptic. Chromosome associations at diakinesis and metaphase I are presented in Table 1. Only one nucleolus was found and two univalents were associated with it. Rod bivalents were more frequent (69.3%) than ring bivalents (30.7%). The number of chiasmata per cell varied between 0 and 6 with a mean frequency of 3.25.

At anaphase I also, there were many abnormalities, such as irregular distribution of chromosomes at either pole, laggards, bridges, division of univalents etc. (Ta-

Table 1. Chromosome associations at diakinesis and metaphase I in the desynaptic plant of Job's tears ($2n = 20$)

Chromosome associations		No. of cells	Per cent
II	I		
4	12	8	18.2
3	14	11	25.0
2	16	15	34.1
1	18	6	13.6
-	20	4	9.1
		Total: 44	

Table 2. Chromosome distribution at anaphase I in the desynaptic plant of Job's tears ($2n = 20$)

Chromosome distribution	No. of cells	Per cent
10:10	1	1.25
9:11	5	6.25
8:12	8	10.00
7:13	8	10.00
6:14	14	17.50
5:15	15	18.75
10:9 + 1L	2	2.50
9:9 + 2L	4	5.00
9:8 + 3L	2	2.50
8:8 + 4L	3	3.75
7:8 + 5L	5	6.25
7:7 + 6L	9	11.25
9:9 + 1B	2	2.50
8:9 + 1B + 1L	1	1.25
8:8 + 1B + 2L	1	1.25
Total: 80		

L = Laggard; B = Bridge.

ble 2). Regular distribution of 10:10 chromosomes was found in only one cell. Laggards ranging from 1 to 6 occurred in 33.5% of the cells, and bridges with and without laggards were found in 5.0% of the cells studied. Many cells with persistent laggards were observed at telophase I. Second meiotic division was also characterised by similar irregularities. The distribution of chromosomes on the second metaphase plate and at anaphase II was highly variable with some of them staying outside the spindle, so that when the pollen quartet was formed these chromosomes often were not included in the daughter nuclei, resulting in spores with unbalanced chromosome numbers. Persistent laggards organized themselves into micronuclei. In 53.3% of the 60 pollen tetrads studied, micronuclei were present, varying from 1 to 3 per tetrad.

By July, 1967, as the old tillers started drying, new tillers began coming up. When florets from these, in the desynaptic plant, were cytologically examined at the end of the rainy season in October, 1967, they showed normal meiosis and, subsequently, good seed set on selfing. Twenty-three plants of the selfed progeny were examined cytologically in October, 1968. All showed normal meiosis and good fertility.

Discussion

Since one or more bivalents were present in a majority of the cells, the desynapsis observed belongs to the "medium-strong" type of Prakken (1943), and the other irregularities were obviously a consequence of univalent formation, which ultimately culminated in total sterility. Desynapsis leading to complete sterility was also observed by Whittington (1958) in red clover. As the pachytene studies strongly suggest that there is no hindrance to pairing, the occurrence of a large number of univalents at diakinesis and metaphase I must have been due to failure of chiasma formation. Environmental factors like summer temperature can not alone account for the observed deviation from regular bivalent formation, since the desynaptic and the normal plants were growing under similar conditions and fixation of materials was done at the same time on the same day. Nor can this be accounted for entirely on the basis of a gene mutation, as regular bivalent pairing was observed in the same plant subsequently.

That a genotype-environment interaction was probably involved in causing desynapsis seems to be a more plausible explanation. Darlington (1958) presumes that mutant genes are less buffered against environmental fluctuations. Sensitivity of synaptic genes to variations in temperature has been reported more recently by Ahloowalia (1969a,b) and Sjödin (1970). The ultrasensitivity of these genes to environmental changes implicates gene products, such as a histone, of relatively short life (see Ahloowalia, 1969b). It is, therefore, conceivable that the occurrence of a temperature sensitive gene mutation was responsible for the failure of chromosome synapsis at diakinesis and metaphase I in Job's tears. This gene was probably triggered into action by the rapid rise in summer temperatures from the month of March onwards, causing desynapsis, but with the onset of rains and fall in temperatures through the winter months, its effect was completely lost and normal chromosome pairing restored.

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