Cytogenetics of Polyploids

VI. Cytology of tetraploid and hexaploid *Cuscuta reflexa* Roxb.

M. L. H. Kaul¹ and A. K. Bhan²

Institute of Genetics, University of Bonn, Bonn, Germany

Received August 8, 1975

Cytogenetics of polyploids, despite its glamorous involvements, has remained much abinitio (Kaul 1974). Parasitic climbers are interesting because of their physiological novelties and ecological adjustments. However, their cytological features, especially of polyploids are not much documented. *Cuscuta reflexa*—a rootless, leafless, yellow, twining, parasitic climber grows almost all over India over hosts of diverse genera. Recently Bhattacharya (1971) has recorded 30 different hosts of *C. reflexa* from India. Also the parasite exhibits self parasitism with a compatible host-parasite relationship. In fact, the species is now recognised as combination of a few nearly different newly established taxa, viz. the Himalayan dodder, the reddish stem dark brown flowered Nepal dodder, the greenish stem leafy large flowered dodder and the original leafless, yellow, small flowered dodder. Furthermore, the species exhibits diversity in parasitism, ecological distribution, phenology, habitat preference, physiological set-up and cytological status (Kaul and Bhan 1974). Chromosomal races of this species having $2n=28$, 30 and 42 have been reported by Finn (1937), Sharma and Chatterjee (1957), Singh and Roy (1970) and Bhattacharya (1971).

The present paper puts on record the cytological features of two more additional cytological races of the species having $2n=32$ and 48 chromosomes. While the race with $2n=32$ was observed to grow parasitically on *Bougainvillea glabra* choisy, the race with $2n=48$ was found growing on *Clerodendron inerme*; the latter host for *C. reflexa* is not recorded by Bhattacharya (1971) and thus represents an addition to the hosts of *C. reflexa* as listed by the author. Some cytological features of the 32 chromosome race indicated earlier (Kaul and Bhan 1974) are also incorporated in this paper in order to compare the two races critically and to provide a useful addition to all that has already been learnt about this plant with a view to formulate a meaningful reference point for future work in this and other polyploid parasitic races.

Except for North American *Cuscutas* that possess $x=15$, other *Cuscutas* are reported predominantly to have $x=7$ and the two numbers are ascribed as the base numbers for this genus by Darlington and Wylie (1955). Nevertheless, the races worked out presently seem to be secondary polyploids with 8 ($7+1$) as the basic number. Accordingly, the cytotypes having $2n=32$ and 48 chromosomes are

¹ Present address: Cytogenetics Laboratory, Botany Department, BNC University, Kurukshetra 132119, India.

² LBS Nat. Acad. Adm., Mussoorie, India.

referred to as tetraploid and hexaploid, respectively in the text of this paper.

Material and Methods

The tetraploid and hexaploid races flower and fruit between October to April and between January to March, respectively. Though vegetative growth of both the races is luxuriant, flowering and fruiting of the hexaploid is scanty and majority of its fruits fall off prematurely in contrast to the tetraploid in which flowering and fruiting are normal. Somatic chromosome studies were made from shoot tips that were stained in 0.5% aceto-carmin after being fixed in 3:1 acetic-alcohol for 72 hours. Classification of the chromosomes was made using the standards laid by Lavan *et al.* (1964). The somatic chromosomes exceeding more than twice and one and half times the length of the smallest chromosome of the complement are designated as long and medium chromosomes, respectively and those exceeding less than 1.5 times the length of the smallest chromosome of the complement are designated as short chromosomes. For karyotype studies, use of pre-fixatives was avoided in order to minimise possible errors in evaluating chromosome length. For meiotic studies flower buds were utilized. These were squashed in 0.5% aceto-carmin after being fixed in 1:3 acetic-alcohol for 72 hours. Pollen viability was determined by using iodine-lactic acid staining procedure. For evaluating the significance of difference between the various morphological parameters of somatic chromosome groups of tetraploid and hexaploid race, analysis of variance was used.

Results

Morphology

a. *Tetraploid*: The plant is a leafless, yellowish-green parasitic climber with thread like stem extruding haustoria, flowers white sub-racemose, fascicled, short pedicelled; sepals 5, subequal; petals 5, lobed campanulate; stamen 5, inserted near the throat, anthers yellow and inflated; ovary 3-celled, 4 ovuled; fruit globose and succulent.

b. *Hexaploid*: The plants are leafless, green with stout branches attached to the host by means of minute succulent disk like structures; these stems bear green fine branches that are extremely coiled around the host. From these branches closely placed *haustoria* emerge that penetrate the host. The flowers are sporadically produced in comparison to an extremely luxuriant reproductive growth observed in the corresponding tetraploid plants. The flowers are waxy, white, fragrant, shortly stalked, borne in small lax racemes and are 5-merous; calyx 5 lobed blunt, ovate; corolla subcylindric, lobes triangular, reflexed; scales prominent, emarginate, fimbriate deciduous; stamens 5, attached to the throat of corolla tube, anthers pale white and wrinkled; ovary 2-celled, narrowed upwards into a style which terminates into 2 widely apart placed wiry stigmas.

In both the chromosomal races described above, hyphae or modified root hairs were never observed, instead numerous haustoria were detected. These penetrate deep into the xylem core of the host and develop firm connections. On extraction

with alcohol, the pigment of both these races exhibited an absorption-spectrum similar to that of chlorophyll with absorption maxima at the red and blue regions of the spectrum, thereby, indicating the chlorophyllous nature of the pigment.

Cytology

a. *Somatic chromosomes of the tetraploid*: The chromosomes 32 in number (Fig. 4) vary at somatic metaphase from 10.42 to 23.06μ in length, and the length gradations between the chromosomes are gradual (Table 1). The chromosomal complement comprises of 28 metacentric and 4 submetacentric chromosomes (Fig. 1).

Figs. 1-2. Karyotype of tetraploid (1) and hexaploid (2) *C. reflexa*; each bar represents homologous chromosome pair.

While the long chromosome group, measuring 23.06μ in length comprises exclusively of 8 metacentric chromosomes, the medium group, measuring 20.02 to 17.36μ in length, consists of 12 metacentric and 4 submetacentric chromosomes and the short group, measuring 12.02 to 10.42μ in length, consists of 4 metacentric and 4 submetacentric chromosomes (Table 1). On the basis of general chromosome

Table 1. Morphological features of somatic metaphase chromosomes of tetraploid *C. reflexa*

Group	Pair number	Designation*	Total length (μ)	Relative length	Arm ratio (L/S)	Shape
A	1	L ₁	23.06	2.21	1.08	Metacentric
	2	L ₂	22.63	2.17	1.06	Metacentric
B	3	L ₃	21.36	2.05	1.03	"
	4	L ₄	21.36	2.05	1.06	"
C	5	M ₁	20.02	1.92	1.04	"
	6	M ₂	19.96	1.91	1.04	"
D	7	M ₃	18.28	1.75	1.08	"
	8	M ₄	18.12	1.74	1.08	"
E	9	M ₅	18.02	1.73	1.17	"
	10	M ₆	18.02	1.73	1.15	"
F	11	M ₇	17.36	1.67	1.17	"
	12	M ₈	17.84	1.71	1.16	"
G	13	S ₁	12.02	1.15	2.34	Submetacentric
	14	S ₂	11.96	1.15	2.26	"
H	15	S ₃	10.46	1.00	1.61	Metacentric
	16	S ₄	10.42	1.00	1.54	"

* L, M and S represent long, medium and short chromosome groups, respectively.

morphology and shape, the somatic chromosome of the complement could be grouped into 8 sets, each set comprising of 4 chromosomes that resemble each other in total chromosome length per nucleus, relative length and arm ratio (Tables 1, 3); the differences observed in these parameters within the chromosomes of each set are statistically insignificant at 5 per cent level of probability.

b. *Somatic chromosome of the hexaploid*: The chromosomes in this race, 48 in number, vary in length from 6.08 to 13.67 μ and the length gradations between various somatic chromosomes are gradual (Table 2). The somatic chromosome

Table 2. Morphological features of somatic metaphase chromosomes of hexaploid *C. reflexa*

Group	Pair number	Designation*	Total length (μ)	Relative length (μ)	Arm ratio (L/S)	Shape
A	1	L ₁	13.67	2.27	1.04	Metacentric
	2	L ₂	13.40	2.22	1.08	"
	3	L ₃	13.40	2.22	1.04	"
B	4	L ₄	12.86	2.13	1.08	Metacentric
	5	L ₅	12.73	2.11	1.11	"
	6	L ₆	12.73	2.11	1.11	"
C	7	M ₁	12.06	2.00	1.25	Metacentric
	8	M ₂	12.06	2.00	1.25	"
	9	M ₃	12.06	2.00	1.25	"
D	10	M ₄	11.66	1.93	1.17	Metacentric
	11	M ₅	11.39	1.88	1.12	"
	12	M ₆	11.39	1.88	1.12	"
E	13	M ₇	10.85	1.80	1.13	Metacentric
	14	M ₈	10.72	1.78	1.05	"
	15	M ₉	10.72	1.78	1.11	"
F	16	M ₁₀	9.38	1.55	1.92	Submetacentric
	17	M ₁₁	9.38	1.55	2.19	"
	18	M ₁₂	9.11	1.51	2.09	"
G	19	S ₁	8.98	1.49	1.39	Submetacentric
	20	S ₂	8.71	1.44	1.32	"
	21	S ₃	8.44	1.40	1.42	"
H	22	S ₄	6.43	1.07	1.29	Metacentric
	23	S ₅	6.03	1.00	1.25	"
	24	S ₆	6.03	1.00	1.25	"

* L, M and S represents long, medium and short chromosome groups, respectively.

complement comprises of 36 chromosomes with median and 12 chromosomes with submedian centromere (Fig. 2). The long chromosome group, measuring 2.27 to 2.11 μ in length, comprises of 12 chromosome all having a median centromere; the medium chromosome group, measuring 2.0 to 1.53 μ in length consists of 24 chromosomes in all, out of which 6 chromosomes are submetacentric and the rest 18 metacentric; the short chromosome group, measuring 1.49 to 1.0 μ in length, comprises of 6 metacentric and 6 submetacentric chromosomes. On the basis of general chromosome morphology and shape, the somatic chromosomes complement of this race could be grouped into 8 sets, each set comprising of 6 chromosomes that

resemble each other in arm ratio, relative length and total chromosomal length per nucleus (Table 2); the differences observed in these parameters within the chromosomes of each set are statistically insignificant at 5 per cent level of probability.

The total and relative chromosomal lengths between each chromosome group in each race differ significantly except that between the group D and E in the tetraploid race (Table 3); this difference is significant without exception in the hexaploid race (Table 3). Not only the

chromosomes of the tetraploid race are longer than those of the chromosomes of the hexaploid race, but also the generalised pooled mean values obtained for the chromosomal length of medium and submedium chromosomes of the former race are significantly higher than that of the latter race (Fig. 3). Also a similar differentiation is observed between the chromosome groups of the two races when represented similarly (Fig. 3).

In the staining techniques followed presently, satellites of the somatic chromosomes of both the races could not be observed uniformly in all the preparations. However, it is not at all claimed that these are absent but it seems that either

they are obscure or weakly differentiated, both morphologically and physiologically, because the nucleolus remains very lightly stained even at diakinesis stage.

c. *Meiosis in the tetraploid*: In this race, the meiotic events are normal, metaphase being characterised by a normal bivalent formation and anaphase by a regular disjunction of the chromosomes and their symmetrical movement to the poles. Both terminal and interstitial chiasmata between the pairing chromosomes are observed at mid prophase (Fig. 5) and majority of the chiasmata observed at diplotene are interstitial; the chiasma frequency per bivalent being 2.06 ± 0.6 . Furthermore, the chiasma terminalization is rapid in the subsequent stage. Nucleolus is indistinct even at early stages of prophase I and disappears at diakinesis stages where normally it should have been quite prominent and distinctly stainable. Further meiotic stages are normal except that in a few PMCs (about 6%) chromosome bridge like structures at telophase I were observed. Each pollen mother cell lodges 4 microspores at the end of microsporogenesis. 87.6 ± 4.9 per cent pollen grains are fertile and stainable.

d. *Meiosis in the hexaploid*: Because of the paucity of the fixed floral buds and scanty division in these, meiosis could not be studied extensively. The long and tangled nature, increased number and overcrowded pattern of the chromosomes precluded their study at early prophase stages. A great proportion of meiocytes

Fig. 3. Histogram for the chromosome form (m=medium, sm=submedian) and group (L=long, M=medium and S=short of the tetraploid (A) and hexaploid (B) *C. reflexa*; pooled mean values utilized.

were observed in various stages of heterotypic division and hence as such an exact identification of a definitive stages is comparative. Though at diakinesis the chromosomes are spread a little, at prometaphase the configurations form compact structures. The congression of the chromosomal associations at metaphase plate was

Figs. 4-8. 4-5. Tetraploid *C. reflexa*. 4, somatic chromosomes. 5, diplotene stage. 6-8. Hexaploid *C. reflexa*. 6, somatic chromosomes. 7, metaphase I. 8, anaphase I.

imperfect, probably because of a poorly formed spindle. At metaphase I, an absence of bivalent formation, presence of multivalents and univalents and their non-orientation to the imperfectly formed spindle apparatus was observed. Further-

Table 3. Statistical significance of difference between the morphological parameters of somatic chromosome groups of tetraploid and hexaploid *Cuscuta reflexa*

Chromosome group	Tetraploid			Hexaploid		
	Total length (μ)	Relative length	Arm ratio (L/S)	Total length (μ)	Relative length	Arm ratio (L/S)
A	22.84	2.19	1.07	13.49	2.23	1.05
B	21.36	2.05	1.04	12.77	2.11	1.10
C	19.99	1.91	1.04	12.06	2.00	1.25
D	18.20	1.74	1.08	11.48	1.89	1.14
E	18.02	1.73	1.16	10.79	1.78	1.10
F	17.60	1.69	1.16	9.29	1.53	1.40
G	11.99	1.15	2.30	8.71	1.44	1.38
H	10.64	1.00	1.57	6.16	1.23	1.26
C. D. at 5% level	0.45	0.11	—	0.357	0.005	—

Pooled mean values utilized; differences significant except between the groups D and E of tetraploid *C. reflexa*.

more, the non-orientation could be also due inter-chromosomal repulsion existing at the crowded plate. This non-orientation leads to the formation of incipient spindle like structures (Fig. 7) that probably could function as independent microspindles later.

An analysis of chromosomal configurations comprising each association could not be made with exactness, but majority of these comprised of 4–6 chromosomes. Perfect bivalency was never observed. In most of the PMCs, anaphasic separation of chromosomes was not observed instead there was a compact mass of chromatin at late metaphase. However, in a few ($12.3 \pm 4.6\%$ PMCs) such a separation was observed but it was highly irregular and erratic (Fig. 8). Anaphase in them was characterised by variable number of laggards and chromosomal stickiness leading to the formation of unevenly thickened anaphase-bridges. Many univalents lag on the spindle-like structure and their presence affects the spindle elongation and cell cleavage. In 2.7% PMCs, two separated groups of chromosomes lying at two opposite poles were observed; these groups were unequal in size and accompanied by univalents and club like chromatin extensions.

A cell wall like structure was found to be formed around each meiocyte and further continuance of meiosis in these seems to be arrested. Numerous attempts to find later stages of meiosis in the available material revealed that these meiocytes are unable to undergo through further stages of meiosis or even to complete the first division stage of meiosis. In majority of the cases, branched fibrillous attachments projecting out from the degenerated PMCs were observed. These are probably formed by the disintegration of cell walls between the gonads. Finally, these

filaments form a net-work like structure within the pollen sac and the cells are in a process of further degeneration.

In a few anther sacs, highly enlarged polynucleate tapetal cells move freely into the centre of the pollen sacs. Cell wall disintegration process in an advanced state leads to the dissolution of the wall even between the two pollen sacs of an anther. In late stages, the contents of the pollen sacs are transformed into a fibrous mass like structure. Very rarely, few pollen grain like structures were also observed but whether they are viable or not could not be determined.

Discussion

Cuscuta in comparison to other members of the family Convolvaceae, possesses unusually long chromosomes and possesses species having the lowest chromosome number ($2n=14$) in the family. The material studied presently appears to be a secondary polyploid originating from a base number 8 ($7+1$). Thus, three base numbers (viz. $x=7$, 8 and 15), and not two ($x=7$, 15) as documented by Darlington and Wylie (1955), exist for the genus *Cuscuta*. Nevertheless, the exact nature of polyploidy of the races cytologically worked out presently is not possible to state with certainty unless other races of the species and their immediate relatives are not thoroughly analysed from cytogenetic and morphological point of view.

However, the chromosomal race with $2n=32$ appears to be tetraploid originating from a base number $x=8$. This contention is supported by the fact that chromosome pairs 1 and 2, 3 and 4, 5 and 6, . . . 15 and 16 resemble each other very closely in general morphology, arm ratio, relative-length and total chromosome length (Table 1). This grouping of somatic chromosomes into sets of four indicates this race as an autotetraploid rather than of hybrid origin. But the fallacy of this interpretation lies in the fact that metaphase chromosomes are simply the outer shells of genetic material, and do not reveal their contents any more than the outer aspects of two identically designed suburban tract houses having internal differences in their furniture, decoration and the people inhabiting them.

Absence of multivalents and presence of regular bivalent formation in a polyploid species normally indicates its allopolyploid nature. But the presence of multivalent association at meiosis cannot necessarily be treated as the sole evidence of autopolyploidy in a taxon because the genotypically controlled tendency to form only bivalents is found in a autopolyploid *Phleum pratense* (Müntzing and Prakken 1940). Also with evolution, a significant reduction in multivalent frequency occurs in the colchicine induced tetraploid of *Zea mays* and *Brassica campestris* var. *toria* (Giles and Randolph 1951, Swaminathan and Sulbha 1959). Furthermore, specificity of synapsis can be induced or narrowed by gene action to permit the pairing of chromosomes related genetically or evolutionarily (Riley and Law 1955). Hence chromosome pairing and in fact all the events of meiosis are under some form of genetic control.

Thus, the apparent diploid like behaviour of this tetraploid race can be explained when it is realised that in some classical examples of polyploids, the failure of pairing between genomes is not due to the lack of homology between constituent genomes, but due to genetic mechanism suppressing pairing between homologous or

homeologous chromosomes. For instance in well understood situations as in *Triticum aestivum* ($2n=6x=42$), the apparent diploid like behaviour in the hexaploid is due to a gene located on chromosome 5B which restricts the chromosome pairing at meiosis to fully homologous partners (Riley and Chapman 1958, Riley 1960). When this activity is removed or suppressed genetically, homoeologous chromosomes, which are genetically and evolutionarily related chromosomes of different genomes will pair with each other. Thus the effect of chromosome 5B on meiotic chromosome pairing is, therefore, responsible for the meiotic stability and disomic inheritance of hexaploid wheat. A similar gene controlled phenomena suppressing multivalent formation and permitting bivalent formation may be operating in the tetraploid race of *Cuscuta reflexa*. In fact, Riley (1960) postulated that the gene controlled diploidization mechanism is operative in some other polyploid plants other than wheat. Furthermore, in addition to a similar delicately balanced gene controlled homologous chromosome pairing, genes effecting, suppressing or promoting the pairing or crossing relationships as reported for wheat (Feldman 1966, Riley and Chapman 1967, Kempana and Riley 1972, Driscoll 1972, Mello-Sampaya 1971, Liang *et al.* 1972, Lang and Riley 1973) may also be present in this race.

Any one of the situations pointed out above may not be exclusively occurring in *Cuscuta* which is mainly propagated by vegetative means and is a poor seeder. When the young flowers of the hexaploid were emasculated and bagged, a normal seed set unlike in the tetraploid was obtained. Thus, the seed, whatever, is formed in the hexaploid, appears largely a product of apomictic reproduction. A shift from bivalent to multivalent type of chromosome association favoured by a selection, natural or human, may be possible in crops where the plant part of value is the seed. But this is not true for *Cuscuta*. Thus apomixis confers an added advantage to the hexaploid to accumulate, maintain and perpetuate any numerical or structural changes occurring in the chromosomes. However, such a type of mechanism appears to be absent in the tetraploid in which all the floral buds when emasculated and bagged or crossed with the hexaploid fall off prematurely without bearing viable seeds in 93 per cent of the cases. However, the few seeds that were formed after crossings, appeared normal but never germinated in seed germinators and TTC testing revealed nonviable and deformed embryo in these seeds.

Meiotic pairing, except for a few organisms, has been regarded as a reliable criteria of polyploidy involved. The presence of multivalents in the hexaploid race indicates a degree of homology between more than two chromosomes. A high frequency of multivalents accompanied by univalents indicates an autopolyploid nature of the hexaploid with $2n=48$ chromosomes. Though multivalent frequency is primarily a question of homology it becomes difficult to distinguish precisely between auto and segmental allopolyploid until a thorough experimental and systematic analysis is done. However, chiefly on cytological grounds, which though valuable are by no means infallible, one would ordinarily expect a much higher frequency of multivalents in autopolyploids in comparison to segmental allopolyploids. Thus, in the hexaploid unlike in the tetraploid *C. reflexa* and hexaploid Chinese Spring wheat, multivalent formations are observed. This indicates that there is either an absence of a homologous suppressor or bivalent regulator gene or the presence of another gene

that inhibits or suppresses the action of bivalent regulator gene in the hexaploid *C. reflexa* genome. A similar situation can be true for the hexaploid *C. reflexa* having $2n=42$ in which also a multivalent formation was observed by Sharma and Chatterjee (1957), thus suggesting an autopolyploid constitution of the cytological race.

While the somatic chromosome complement of the tetraploid comprises of 28 metacentric and 4 submetacentric chromosomes, the complement of the hexaploid consists of 36 metacentric and 12 submetacentric chromosomes. Thus the ratio of metacentric to submetacentric is increased from 3.5 in the former to 3.0 in the latter race. Hence the chromosomal symmetry is decreased with an increase in the level of ploidy. Chromosome length range in the tetraploid is from 10.42 to 23.06μ and in the hexaploid it is from 6.03 to 13.67μ , the gradation in chromosome length is gradual in both the races. Nevertheless, a decrease in chromosome length following increase in ploidy level in this species is distinctly evident. However, the total chromosome length in the two races is not much different (tetraploid = 563.78 and hexaploid = 507.84). Furthermore, not only the somatic chromosome of the tetraploid race are longer than those of hexaploid race, but the mean chromosome length of the metacentric and submetacentric chromosome of the former is significantly larger than that of the latter race. A similar differentiation is evident between the chromosomal groups of these two races. The somatic chromosomal length variation in the hexaploid race of *C. reflexa* having $2n=42$ chromosomes which is from 4.4 to 18.3μ (Sharma and Chatterjee 1957) is greater than that observed in the hexaploid race investigated presently. Moreover, while the hexaploid race with $2n=42$ has 8 long, 28 medium and 6 short sized somatic chromosomes, the race with $2n=48$ chromosome has 12 long, 24 medium and 12 short sized chromosomes. Thus, the hexaploid material investigated presently possesses more long and short sized and less medium sized chromosomes than that of the hexaploid race worked out by Sharma and Chatterjee (1957).

Two kinds of adaptive advantages over tetraploid race exist for the type of karyotype asymmetry present in the hexaploid race. One concerns the cell dynamics, because smaller chromosomes of this race, whether metacentric or submetacentric will be able to complete the somatic metaphase separation of their chromatids more easily than the larger metacentric or submetacentric chromosomes of the tetraploid race. Consequently, the asymmetrical karyotype of the hexaploid might be expected to go through mitosis more rapidly than the symmetrical ones of the tetraploid, thus rendering the cells of the hexaploid capable of more rapid proliferation than that of the tetraploid. This easier separation could be based upon the fact that the final separation of chromosomes at prometaphase and metaphase involves proximal regions of chromatids. In the submetacentric, subtelocentric and small metacentric chromosomes of the hexaploid race, these regions are smaller than the larger metacentric and submetacentric chromosomes of tetraploid race, so that the chromosomes of the hexaploid race could be expected to separate more easily, freely and randomly to produce supernumerary chromosomes in some cells and in clones observed presently.

The intraspecific polyploidy in *C. reflexa* appears to confer two distinct advant-

ages over its other allies because these cytological races constitute new genetic types, which are likely to be particularly well adapted to colonization of newly available areas and hosts. This could explain the wide occurrence, host diversity, ecological amplitude of this species. Also since polyploidy is a way in which interspecific barrier can arise at one step, it has given an opportunity for the two new lines detected presently to evolve independently and to diverge from parental types.

Summary

Two cytological races having $2n=32$ and 48 and designated as tetraploid and hexaploid, respectively were found in *C. reflexa*. While somatic chromosome complement of tetraploid race comprises of 28 metacentric and 4 submetacentric chromosomes, the complement of hexaploid races consists of 36 chromosomes with median and 12 chromosomes with submedian centromere. On the basis of general chromosome morphology and shape, the somatic chromosomes of the complement could be grouped into 8 sets, each set comprising of 4 chromosomes in the tetraploid and of 6 chromosomes in the hexaploid race. The differences observed in these parameters within the chromosomes of each set are statistically insignificant but those between the sets are significant. Meiosis in the tetraploid race is normal leading to the formation of viable pollen grains. In the hexaploid race, meiosis is highly abnormal and is arrested before heterotypic division is completed. Immediately after the pollen mother cells degenerate, branched fibrilous attachments projecting out from the degenerated PMCs are observed. When the young immature anthers were clipped off and the flowers bagged, parthenocarpic seeds are produced in the hexaploid material. However, the seed set is poor. A gene controlled suppression of homeologous pairing in the tetraploid race has been postulated. This type of control is not operative in the two hexaploid races of the species. The implications of karyotype morphology and chromosome pairing behaviour in polyploids are critically discussed in general and the role of polyploidy in the species in particular.

Acknowledgments

We are extremely grateful to Prof. Dr. W. Gottschalk for his valuable suggestions and to Miss Dr. Dagmar Müller and Mrs. Ursula Laux of the Institute of Genetics, University of Bonn, for their kind and continued cooperation and help in preparation of this manuscript. Thanks are due to Miss Veronika Taudin of Botanical Institute, University of Bonn, for her help in drawings contained in this paper.

References

- Bhattacharya, P. N. 1971. The botanical vicissitudes of taxon: *Cuscuta reflexa* Roxb. Sci. and Cult. 37: 251-255.
- Darlington, C. D. and Wylie, A. P. 1955. Chromosome Atlas of Flowering Plants. George Allen and Unwin Ltd., London.
- Driscoli, C. J. 1972. Genetic suppression to homeologous chromosome pairing in hexaploid wheat. Can. J. Genet. Cytol. 14: 39-42.

- Endrizzi, J. E. 1962. The diploid-like cytological behaviour of tetraploid cotton. *Evolution* **16**: 325-329.
- Feldman, M. 1966. The effect of chromosome 5B, 5D and 5A on chromosomal pairing in *Triticum aestivum*. *Proc. Nat. Acad. Sci. (USA)* **55**: 1447-1453.
- Finn, W. 1937. See Darlington and Wylie, 1955.
- Giles, A. and Randolph, L. F. 1951. Reduction of quadrivalent frequency in an autotetraploid maize during a period of 10 years. *Amer. J. Bot.* **38**: 12-17.
- Kaul, M. L. H. 1974. Cytogenetics of polyploids V. Induced breakdown in meiotic stability of *Ageratum conyzoides* Linn. *Cytologia* **39**: 27-39.
- and Bhan, A. K. 1974. Cytology of *Cuscuta reflexa*. *Cytologia* **39**: 493-498.
- Kempana, C. and Riley, R. 1962. Relationship between genetic effects of deficiencies for chromosome III and V on meiotic pairing in *Triticum aestivum*. *Nature* **195**: 1270-1273.
- Lang, W. and Riley, R. 1973. The position on chromosome 5B of wheat of the locus determining crossability with rye. *Genet. Res. Camb.* **22**: 143-153.
- Larsen, J. and Kimber, G. 1973. The effect of the genotype of *Triticum speltoides* on the pairing of homologous chromosomes. *Can. J. Genet. Cytol.* **15**: 233-236.
- Levan, A., Fredga K., and Sandberg A. A. 1964. Nomenclature for centromeric position on chromosomes. *Hereditas* **52**: 201-220.
- Liang, G. H., Deyoe, C. and Geng, H. Y. 1972. Genetic control of meiotic irregularities in Mediterranean wheat. *J. Hered.* **63**: 271-274.
- Mello-Sampyo, J. 1971. Genetic regulation of meiotic chromosome pairing by chromosome 3D of *Triticum aestivum*. *Nature, New Biol.* **230**: 22-23.
- Müntzing, A. and Prakken, R. 1940. The mode of chromosome pairing in *Phleum* twins with 63 chromosomes and its cytogenetic consequences. *Hereditas* **26**: 463-501.
- Riley, R. 1960. The diploidisation of polyploid wheat. *Heredity* **15**: 407-429.
- and Chapman, V. 1958. Genetic control of cytologically diploid behaviour of hexaploid wheat. *Nature* **182**: 713-715.
- 1967. The inheritance in wheat crossability with rye. *Genet. Res. Camb.* **9**: 259-267.
- and Law, C. N. 1965. Genetic variation in chromosome pairing. *Adv. Genet.* **13**: 57-114.
- Sears, E. R. 1969. Wheat cytogenetics. *Ann. Rev. Genet.* **3**: 451-468.
- Sharma, A. K. and Chatterjee, A. K. 1957. A cytological investigation of some convolvulaceae as an aid in understanding their lines of evolution. *Oryton* **8**: 143-157.
- Singh, V. K. and Roy, S. K. 1970. Cytology of *Cuscuta* Linn. *Sci. and Cult.* **36**: 567-568.
- Swaminathan, M. S. and Sulbha, K. 1959. Multivalent frequency and seed fertility in raw and evolved tetraploids of *Brassica campestris* var. *toria*. *Z. Vererb.* **90**: 358-392.
-