Cytogenetic Studies in *Papaver*
VI. Chromosome relationships between *Papaver* species
of the Section *Orthorhoeades* (*P. syriacum* f. *adpresso*
***setulosus* and *P. rhoeas* and their amphiploids)**

C. P. Malik and T. N. Mary

Department of Botany, College of Basic Sciences, Punjab
Agricultural University, Ludhiana, India

Received October 16, 1973

The need for undertaking cytogenetic relationships of the *Papaver* species is generally felt but has not been realised due to the paucity of the availability of basic species. Very little work has been done on the cytogenetics of the genus. Some of the noteworthy contributions are those of Yasui (1940, 41), Koopmans (1955, 70), Knaben (1959), Hrishii (1960), McNaughton and Harper (1964). Thus, while the several species are important economically their cytogenetic architecture remains unmasked. Therefore, a study was initiated by the senior author to elucidate the cytogenetic make up and relationships of several *Papaver* species with a hope that such studies would help in understanding the mechanisms leading to their speciation. A series of papers regarding karyomorphology, cytology of autotetraploids, interspecific hybrids, trisomics have appeared or communicated (Grover and Malik 1969, Malik and Grover 1971, 73, Grover *et al.* 1973, Malik and Mary 1973). The present study deals with crossability of two species i.e. *Papaver rhoeas* and *P. syriacum*, their meiotic analysis and detailed cytogenetic studies of their hybrids and amphiploids. Both the species belong to the section *Orthorhoeades* (Fedde 1909). The genomic relationships of the species are deduced from the chromosome pairing in their amphiploids and F_2 plants.

Materials and methods

The origin of the two species used in the present studies is given below:

Species	Origin	Source
<i>Papaver rhoeas</i> L.	Udaipur (India)	Cultivated
<i>P. syriacum</i> Boiss et Bl.f. <i>adpresso-setulosus</i> Fedde.	Jerusalem (Israel)	Prof. N. Feinbren

The two species were successfully crossed. Emasculations were done while the anthers were green and great care was taken not to injure the ovary during this process. The emasculated buds were covered with glassine bags. After a day or two, artificial pollinations were accomplished and bags were replaced. The F_1 hybrids were successfully doubled following colchicine-agar treatment as described by Grover (1970).

For meiotic studies, the flower buds at suitable stages were gently punctured and their anthers were fixed in Carnoy's solution (6: 3: 1). Anthers were stained in iron-acetocarmine solution after four to six days of fixation and chromosome pairing in twenty PMC's was studied in their squash preparations.

Observations

A. Parents

a) *Morphology*: The morphological characters of different species together with their hybrids have been summarized in Table 1. Figures 1–2 illustrate flower buds and leaves typical of the species and their hybrids.

b) *Cytology*: Seven bivalents were regularly formed at Metaphase-I of the two species. Table 2 gives data regarding mean frequencies of ring and rod bivalents and chiasma frequency per cell. Comparison between the two species with regard to their mean chiasmata and ring bivalents yielded some interesting conclusions. For example, *P. syriacum* had low value of ring bivalents. In fact this species had also low chiasma frequency of chiasma per cell and differed significantly when compared to *P. rhoeas*.

c) *Pollen fertility*: The pollen fertility among the species varied from 92.4–95.5% while the diameter of the pollen was 25.84–27.36 μ . Table 3 includes pertinent data from the F_1 and amphiploids.

Table 1. Morphological characters of the parental species and their hybrid

Characters	Syriacum	F_1	<i>rhoeas</i>
Latex colour	White	Light Yellow	Yellow
Bristles on peduncle	adpressed	spreading	spreading
Leaf shape	Lower leaf lyrate, long petioled, upper leaves sessile, narrowly segmented	as in <i>syriacum</i>	Lower leaf petioled; upper ones sessile, lobing variable.
Floral bud	Narrowly elliptical with short bristled without tubercles	intermediate	Broadly elliptical, bristles arising from thick tubercles.
Guard cell L/W (μ)	$35.10^\circ \times 16.76$	$35.7^\circ \times 18.62$	$34.0^\circ \times 12.92$
Stomata/sq.mm.	118	138	186
Capsule shape	Oblong or clavate, umbonate disc in the centre of capsule	as in <i>syriacum</i>	subglobose to broadly ovoid, disc rounded.

B. Hybrids

a) *Morphology*: The salient morphological characters of the F_1 are shown in Table 1 and also Figure 1.

In the *P. syriacum* $\times$ *P. rhoeas* cross, hybrids were intermediate between the parents. For some of the characters such as leaf shape umbonate disc of the capsule and capsule shape, hybrid plants showed dominance of the *syriacum* parent. In the F_2 as many as 100 plants were sampled and there was segregation for almost

Table 2. Association and chiasma frequency at metaphase-I chromosome in the species and their hybrid

		I	II	Ring	Pod	Xta	
						1/X	cV
x=7							
<i>P. rhoeas</i>	$\bar{X}$	—	7	3.4	3.6	10.4	7.7
	Range	—	—	2-5	2-4	9.12	—
<i>P. syriacum</i>	$\bar{X}$	—	7	0.6	6.4	7.64	10.6
	Range	—	—	0-2	5-7	6-9	—
F ₁ hybrid	$\bar{X}$	.3	6.80	1.40	5.40	8.3	10.6
	Range	0-4	—	0.5	2-7	7-12	—

every character which demarcated the two species.

b) *Cytology*: i) *syriacum* × *rhoeas* (F₁). Details of meiosis in the F₁ hybrids are summarized in Table 2. During pachynema stage 1-2 bivalents had most of their segments in the two homologues unpaired. These differential segments were both interstitial and terminal. In some of the PMC's the terminal unpaired segments of two homologues were highly unequal. Rarely unpaired segments appeared as a loop suggesting duplication in one of the homologues. Interestingly enough cross-shaped configurations were not observed.

Majority of the PMCs had seven bivalents while in some association of a trivalent or a quadrivalent, besides 5 bivalents, was observed. However, all the cells had one multiple chromosome association only. The number and size of univalents varied (Fig. 1b). There was preponderance of rod bivalents and as many as 3 bivalents were distinctly heteromorphic. Heteromorphy was only prevalent in the rod types of

Fig. 1 a-m. a, metaphase I, seven bivalents of rod type. b, $3_{II}+8_I$. Note close associations of univalents. c, metaphase I with univalents and bivalents. d, anaphase I with a lagging bivalent. e, 7 rod bivalents; note some of the heteromorphic bivalents. f, heteromorphic bivalents at metaphase I. g, metaphase I with some heteromorphic bivalents. h, metaphase I with $I_{III}+5_{II}+1_I$.

bivalents (Fig. 1e, f). The quadrivalents were orientated in alternate sequence at metaphase I (Fig. 1h-j). At anaphase I, occasionally 2-3 bivalents exhibited delayed disjunction and were stretched between the two poles (Fig. 1d). Bridges appeared immediately after the disjunction of bivalents during anaphase I. Some of the bivalents displayed neocentric activity at this stage. About 40% of the cells examined had dicentric bridges. Usually a single bridge and a fragment per cell were present though some cells had only bridges. Measurements of bridges and fragments size made from photomicrographs of anaphase I indicated that the bridges varied in length and were either short, long or broken in different cells. Similarly the fragments were grouped into three sizes: small, medium, and large. Bridges and laggards were found at telophase II. In a tetrad 2-6 micronuclei of variable sizes were present. Fragments, both free and attached, were also observed at metaphase I. The mean chiasma frequency per cell was low.

Regression analysis of chiasmata on rod bivalents was worked out. It indicated a highly significant negative correlation (-0.884^{***} ; $P=0.001$) when chiasmata were plotted against rod bivalents. Apparently rod bivalents caused effective reduction of chiasmata. The two parents exhibited highly significant differences between themselves with regard to two meiotic metrics (mean chiasmata and ring bivalents) when assessed by t-test. The F_1 hybrid simulated *syriacum* parent in average chiasma frequency and ring bivalents. However, it differed significantly from *rhoeas* ($P=0.05-0.001$). F_2 : During pachynema loose pairing was observed and in some of the bivalents homologues were unequal. At metaphase I, 2-4 univalents were found and some of the bivalents were heteromorphic. In addition trivalents and quadrivalents were also observed in many cells. The trivalents were mainly of 'V' shape while the quadrivalents were of chain type (Fig. 1j). Figure 1 shows preponderance of rod bivalents. The mean chiasma frequency was low and the mean chromosome pairing per cell was $.2_{IV} + .35_{III} + 5.50_{II} + 1.15_I$. Figure 1m is anaphase I with a bridge and a fragment configuration. Sometimes chromosomes lagged and divided precociously. At telophase II micronuclei were present.

Table 3. Pollen diameter and their fertility in the species, their F_1 and amphiploids

		Pollen grain size (μ)	Fertility (%)
<i>rhoeas</i>	$\bar{X}$	25.84	95.5
	Range	19.0-30.40	—
<i>syriacum</i>	$\bar{X}$	27.36	—
	Range	19.0-33.80	92.4
<i>syriacum</i> $\times$ <i>rhoeas</i>	$\bar{X}$	26.75	—
	Range	22.8-34-2	66.5
<i>syriacum</i> $\times$ <i>rhoeas</i> (amphiploid)	$\bar{X}$	30.4	—
	Range	22.82-38.0	75.8

i, $I_{IV} + 5_{II}$. j, $I_{IV} + 5_{II}$. k, amphiploid, metaphase I with majority of rod bivalents and quadrivalents. l, metaphase I in amphiploid with variable bivalents and quadrivalents. m, anaphase I in F_2 with lagging chromosomes and a bridge.

Figs. 2 a-i. a, amphiploid, anaphase-I stages. 14/14 distribution. b, 10/10 distribution with two bivalent bridges and three laggards. Mark one fragment near the lagging bivalent. c, 13/13 distribution with one bivalent showing delayed disjunction. Note one free fragment. d, lagging chromosomes and bivalent bridges of unequal thickness. e, one bivalent bridge with an attached fragment. f, lagging bivalents with attached and free fragment. g, bridge and a fragment configuration. h, bridge-fragment configuration, note attached fragment. i, 14/14 distribution.

C. Amphiploids

The hybrids were successfully doubled and amphiploids ($2n=28$) having morphological characters simulating F_1 's were secured. They were gigas and had profusion of vegetative parts and flowered late in the season. The mean chromosome pairing per cell in the amphiploid is given in Table 5. It was typified by $1.54_{IV} + .78_{III} + 8.25_{II} + 3.0_I$. Metaphase I stage had variable number of paired chromosomes (Figs. 1k, l) and univalents of unequal sizes. Nearly 59% of the chromosomes were associated as bivalents and the majority of them were of rod type ($x=6.0$ per cell). Nearly 30.5% chromosomes were involved in multivalents formation. In most of the cells a few laggards as well as bridges/or fragments were observed at anaphase I (Figs. 2a-h). The bridges varied in number (Figs. 2b-e) and thickness and also the fragments (Figs. 2b,c,g). Moreover, the fragments were either free (Fig. 2b,f,g) or attached (Fig. 2e). Figure 2f shows two fragments. The telophase II was completely abnormal and there were indications of aberrant spindle mechanism. Micronuclei (2-4) were also observed. Statistical tests were performed to determine the relationships between chiasma formation and the pairing pattern at metaphase I and the following correlations were observed.

1. *Multivalents*: (IV, III). A negative correlation was observed which was significant at 1 percent level.

2. *Bivalents and univalents*: Here again negative correlations were observed and the differences were highly significant ($P=.001$). When the average frequency of chiasmata was plotted against the number of chromosome configurations, the correlation showed that the type of chromosome pairing depended upon the chiasmata.

Table 4.

	10	10	10	11	11	11	12	12	13	13
Distribution	6	—	7	4	—	2	—	2	1	—
	11	17	17	12	16	14	15	13	13	14
No. of cells	2	2	2	2	2	2	2	4	4	4

One hypotetraploid ($2n=27$) amphiploid had the mean chromosome pairing of $.3_{IV} + .30_{III} + 11.15_{II} + 2.61_I$. Here only 4% chromosomes contributed towards IV formation though as many as 83.5% were associated as bivalents. Data on detailed chromosome pairing is given in Table 5. Table 4 shows an analysis of 26

Table 5. Chromosome association and chiasma frequency at metaphase-I in the *syriacum* × *rhoeas* amphiploids

Combination		I	II	II		III	IV	Xta ($\bar{x}$)	
				Ring	Rod			5d	cv
<i>syriacum</i> × <i>rhoeas</i> ($2n=28$)	$\bar{x}$	3.0	8.25	2.25	6.00	0.75	1.54	16.6	7.9
	Range	0.6	2.14	0.6	1-10	0.4	0-2	13-20	—
	%	10.7	58.8	—	—	—	—	—	—
(2n=27)	$\bar{x}$	2.6	11.5	1.9	4.5	0.3	0.3	14.54	14.6
	Range	0.5	9-11	0-3	8-12	0-2	0-3	11-18	—
	%	9.5	83.5	—	—	—	—	—	—

PMC's at anaphase I. There were irregular disjunctions, lagging chromosomes and bridges were observed at this stage. Micronuclei were also present in the tetrads. Comparisons in respect of IV,II as well as chiasma frequency were made between the autotetraploid of *syriacum* and the amphiploid from *rhoeas* × *syriacum* hybrid. The values calculated significantly differed with regard to rod bivalents. For instance *syriacum* autotetraploids had 67% of the chromosomes participating in the formation of rod bivalents—a value higher than the amphiploids ($P=.001$).

Discussion

The basic chromosome numbers reported for the genus *Papaver* are $x=6,7,11$. Sugiura (1940) suggested that the genus *Papaver* arose together with *Argemone*, *Meconopsis*, *Roemeria* and these were derived from *Corydalis* and *Chelidoniaeae*; the former having the basic number $x=4$ and the latter as $x=3$. Both diploid and polyploid species are reported in the genus. So far, very few species have been investigated karyomorphologically (Yasui 1940, Koopmans 1955, Hrishi 1960, Grover and Malik 1969). Many intraspecific and interspecific hybrid combinations have been studied cytogenetically (Yasui 1941, '43, Hrishi 1960, McNaughton and Harper 1960, Koopmans 1970, Malik and Grover 1973). Hybrids were raised between the species of the same (Hrishi 1960) or different sections (McNaughton and Harper 1964, Malik and Grover 1973). Works of Yasui (1941, '43) were interesting and dealt with genomic relationships of *P. somniferum* and *P. orientale*. Her two papers described series of references on the cytology of the *Papaver* species carried out by her. The two species currently investigated belong to the same section *Orthorhoeades* of the genus *Papaver*. Both the species had annual habit, non-clasping leaves and glabrous capsules. Feinbrun (1963) in his taxonomic studies on *Papaver* sect. *Orthorhoeades* of Palestine and some other Mediterranean countries, confirmed this classification but experienced general difficulty in the delimitation of species in the section *Orthorhoeades*. This was because of the overlapping of distinctive characters due to occasional interspecific hybridization. The two species investigated currently are clearly distinguishable on the basis of several characters e.g. the shape of capsule and its umbonate disc present in *P. syriacum* but absent in *rhoeas*. As regards other characters even under uniform garden conditions, wide variations in growth habit and flower colour were seen. However, some of these characters were controlled by separate simple Mendelian factors. According to Feinbrun (1963) *P. syriacum* had a restricted area of distribution e.g. Lebanon, Palestine (Israel, Jordan) and Cilicia (Asia Minor) while *rhoeas* was wide spread in Europe, Central and Northern Asia, etc. (McNaughton and Harper 1964). The two species formed allopatric pattern of distribution. It is interesting to note that the species were cross-compatible though their F_1 hybrids were semi-fertile and sufficient percentage of seeds obtained from interspecific crosses failed to germinate. Many of the F_1 's died at the seedling stage. The F_1 's which survived set reasonable amount of seeds and yielded F_2 progeny. Apparently internal sterility barriers to crossing existed between them and such barriers could be genic or even chromosomal.

Meiotic data obtained from the F_1 's indicated that structural differences were common within the chromosomes of the two species. Since no structural heterozygosity was encountered in the parental species; the absence of structural heterozygotes in nature would be expected in the inbreeding population of both the species. Thus the presence of trivalents and quadrivalents in the diploid hybrids could be attributed to heterogeneity for segmental arrangements within the two species. Furthermore, pachytene data from F_1 's obtained thus far lent added support and confirmed the structural differences between the paternal genomes. The presence of a univalent proximal to the trivalent in many cells with III+I supported their origin due to desynapsis. In the F_1 pachynema studies loose pairing, size variations in some of the paired chromosomes suggested structural differences in the chromosomes of the two species. Such chromosomal divergences pointed towards structural differentiation of their genomes. At metaphase I there were unequal univalents and heteromorphic bivalents and these data closely supported the early observations. Both, the pairing pattern at pachynema and different sizes of univalents at metaphase I indicated major structural differences between some of the chromosomes of the two species. Some of the univalents disjoined early and presumably this happened due to genic differences.

From the chromosomal point of view the inevitable conclusion is that the two species appeared not to be structurally perfectly homologous. The average chiasma frequency and ring bivalents in the F_1 coupled with errors in chiasma formation provided compatible support. Furthermore, it is reasonable to assume that anaphase bridges during both the meiotic stages could be due to errors in chiasma formation.

The genetic differentiation of the two species paralleled their differentiation phenotypically. Moreover, the formation of chiasma and ring bivalents was lower in the hybrids compared to the parental species and these characters displayed continuous variation, envisaging a complex genetic control. Thus, reduction in effective pairing in the F_1 was obvious. There was also an increase in the frequency of cells with univalents and those having meiotic irregularities.

At this point of time it is worth recalling that *P. syriacum* though autogamous, has extremely low chiasmata frequencies. To us it seems that in this species the function of chiasmata must be just mechanical—a way to hold chromosomes together till metaphase I and not a source to affect recombination.

Furthermore, hybridization did not increase the chiasmata frequencies. In all likelihood a gene(s) complex operating in *syriacum* promoted preponderance of rod bivalents and such a system reduced chiasmata formation in the F_1 .

Results when considered in conjunction with the data from their amphiploids the interpretations become more rational. The more interesting point is that compared to the autotetraploid of *rhoeas* (Mary and Malik 1973) having 2.42_{IV} per cell, *syriacum* autotetraploid had low multivalents ($.72_{IV}/cell$) and same was true of *syriacum* $\times$ *rhoeas* amphiploids ($1.54_{IV}/cell$) where as low as 30.5% chromosomes participated in multivalent associations. Also in the F_1 supposed dis-organization of the genetic control system did not proceed for instance there was decrease in the variability of chiasma frequency. In fact one expected variations in expression to

increase. In the autotetraploid *rhoeas*, the mean frequency of multivalents was high. *Papaver syriacum* was a natural autogamous species and produced artificial hybrids when crossed with *rhoeas*. This would suggest that the degree of control of developmental stability, achieved by the particular homozygous gene systems of the *P. syriacum* was exceeded by that of the heterozygotes. The larger significance of heterozygosity in increasing developmental stability in allogamous forms is well accepted; it seems that such a phenomenon could function in a raw artificial hybrid raised from autogamous species. However, the precise implications of this should be carefully investigated. The chiasma frequency was also drastically affected in the F_2 populations and it exhibited increased variation. Some of the plants had translocations and possibly they arose as a consequence of recombination in the F_1 .

Coming back to the conclusions regarding chromosomal differences between the two species, it is significant to recall the presence of bridges+fragments as well as multiple bridges at anaphase I, II of the F_1 's. In general the presence of such configurations at anaphase I was taken to indicate the occurrence of paracentric inversions. However, such inferences were infallible only if confirmed by the demonstration of inversion loops during pachynema. Matsuura (1950) proposed breakage-fusion hypothesis to account for meiotic bridges and fragment configurations. There is good possibility that bridges and fragment configurations resulted from chromosome breakage and not through inversion heterozygosity in our material. It is now widely recognised that bridge-fragment configurations could arise through two main ways; crossing over between inverted segments or due to spontaneous breakage and reunion of chromatids during early prophase I. There are certain diagnostic cytological features which offer distinction between two types fairly accurately. However, before accepting a general interpretation of the results based on breakage-reunion theory a qualification concerning its general validity is necessary. For instance in the inversion process, pachynema stages display reverse pairing configurations i.e. loops and subsequently at anaphase I, bridges and fragments involving the same chromosome are visible. Moreover, the size of the fragment at anaphase I, should be reasonably constant. In contrast, the breakage-reunion phenomenon leads to univalent bridges and exhibits variability in the size of the fragment. There is also appearance of bridge+fragment during the anaphase II. It is significant to mention that breakage-reunion occurred due to the errors in crossing over and according to Lewis and John (1966) such configurations resulted from U-type exchange. Most recently, Jones (1968) has furnished evidence in favour of this hypothesis. For instance in his studies he observed that chiasma frequency closely followed variations in frequency of bridge+fragment configurations; distribution of chiasmata in a bivalent was correlated with U-type exchange especially in the species having localized chiasmata. Thus while distal chiasmata produced small fragment proximal ones yielded long ones. Cytological inferences included occurrence of fragments during metaphase I, variation in fragment size, bridges without fragments, variations in the size and thickness of bridges, and a higher percentage of bridges during anaphase II. All that can be deduced further for the moment, is that the appearance of bridges and acentric fragments at meiosis could be traced to genetic unbalance as a consequence of hybridization. With

these qualifications in mind, the overall implications of the occurrence of bridge+fragment configurations be considered now. Lack of inversion loops during pachynema; variations in the number, size and structure of bridges at anaphase I, variability of fragment sizes, its appearance or absence, types of anaphase II bridges add weight against the probable role of inversion heterozygosity in differentiation of the two species. The thinking is therefore, inevitably inclined towards breakage-reunion concept, as proposed by Lewis and John (1966). These authors as well as Jones (1968) further suggested that spontaneous chromosome breakage is a common meiotic syndrome which reflected mistakes in chiasma formation. Moreover, the position of chiasmata was vital and this resulted in the variability of bridge types. The overall discussion so far allows, the acceptance that precisely such errors would occur at a higher rate in hybrids especially those having slight structural divergences between chromosomes of parental species. Perhaps yet another interesting aspect of our assumption is that such differences were not large enough to restrict pairing but sufficient to cause errors in chiasma formation leading to breakage reunion phenomenon. At any rate, some amount of non-homology between the paired chromosomes is also envisaged. Fortunately presence of univalents and heteromorphic bivalents, as mentioned earlier did support this assumption. One may go a step further to suggest that even "cryptic" structural hybridity (sensu Stebbins 1950) might have been involved. Moreover, presence of fragments at metaphase I provides additional evidence.

Perhaps the most compelling evidence in favour of above comes from the amphiploid where similar bridges+fragments were encountered. If the bridge+fragment configurations really owed their origin to inversion heterozygosity, in the amphiploid, with full genomes of *syriacum* and *rhoeas*, such types of bridges should not have appeared. In fact by comparison of chromosome breakage in the 2x hybrid and its persistence in the tetraploid derivative (i.e. amphiploid), it is reasonable to support the earlier hypothesis based on breakage-reunion and possibly affected by hybridity.

In the literature several instances of interspecific hybrids are mentioned where chromosome breakages were pronounced e.g. *Bromus* (Walters 1958); *Elymus* (Haneen 1963) and *Festuca* etc. (Malik and Thomas 1966, Malik 1967).

Papaver syriacum Boiss has been treated as a synonym of *P. rhoeas* var. *syriacum* Boiss, as well as *P. obtusifolium* Deaf. var. *barbeyi* Fedde. In fact *P. syriacum* is a clearly demarcated species since it possessed umbonate disc. Indeed *P. syriacum* was accorded specific rank by Fedde (1909). There are other species e.g. *P. umbonatum* Boiss, *P. stylatum* Boiss et al. *P. clavatum* Boiss et Haussk which resembled *P. syriacum*. Crosses have not been made in order to evaluate their precise cytogenetic relationships. Incidentally all the umbonate species existed in palestinian area from where *P. rhoeas* was lacking. Recently Feinbrun (1963) suggested that *P. umbonatum* and *P. syriacum* were synonyms. Furthermore, the same author suggested that "in case of identity of both species . . . the name *P. syriacum* Boiss, to be changed to *P. umbonatum*". Nothing is known about the extent of natural hybridization in *P. syriacum* except a suggestive case with *P. rhoeas* L. var. *oblongatum* Boiss.

Papaver rhoeas and *P. syriacum* belong to the same section *Orthorhoeades*. It is interesting to mention that they produced semifertile hybrids. Earlier Malik and Grover (1973) succeeded in securing fertile intersectional hybrids (*rhoeas* × *glaucum*).

The evidences currently available allow the acceptance of a few deductions. For instance, the two species are differentiated genetically with regard to two meiotic characters (ring II and chiasma frequencies). There were evidences of structural differences between their genomes and their hybrids were semifertile.

The lack of increased fertility in the induced amphiploids raised from the present hybrid, provided strong support to the genetic nature of hybrid sterility as well. Almost complete bivalent pairing in a majority of the cells of the amphiploids, low multivalent frequency indicated the occurrence of preferential pairing.

Summary

Cytogenetic relationships between two diploid species belonging to genus *Papaver* section *Orthorhoeades* (*Papaver syriacum* f. *adpresso-setulosum* Boiss; *P. rhoeas* Lin.) is assessed using several parameters e.g. morphology, cytology, extent of crossing and cytogenetic display of hybrids and amphiploids. Even F_2 populations have also been analysed cytogenetically.

Both the species had normal meiotic course and 7 bivalents were formed at metaphase I; there was preponderance of rod bivalents in the *P. syriacum*. The hybrids between the two species had reduced chromosome pairing and less chiasma frequency compared to the parents. Univalents and heteromorphic rod bivalents were deciphered at metaphase I of the F_1 's. Our studies also indicated structural differences between chromosomes of two species. The presence of multivalents in the diploid hybrids suggested heterogeneity for segmental arrangements within the two species and pachynema studies supported such inferences. The genetic differentiation of two species paralleled phenotypic differentiation. The F_2 populations also exhibited meiotic disturbances and reduced fertility but increase in the variability of the chiasmata frequency. There were some plants with translocations also. The variability in size and number of fragments at anaphase I and anaphase II suggested their origin through chromosome breakage and reunion rather than inversion heterozygosity. The amphiploid had mean pairing as $1.54_{IV} + .78_{III} + 8.25_{II} + 3.0_I$. Multivalents were low in frequency and rod bivalents were in higher percentage. Persistence of bridge-fragment configurations at anaphase I, II of the tetraploid amphiploid derivative (i.e. amphiploid) supported their origin through breakage-reunion process. Detailed taxonomic relationships of two species within themselves and with other species in the section *Orthorhoeades* is further discussed.

Acknowledgement

We are thankful to Prof. N. Feinbrun, University of Jerusalem (Israel) for his help in supplying the seeds of *Papaver syriacum*.

Literature cited

- Fedde, F. 1909. *Papaveraceae* in das Pflanzenreich. Engelman, Leipzig 4: 209–326.
- Feinbrun, N. 1963. Taxonomic studies on *Papaver* sect. *Orthorhoeades* of Palestine and some other Mediterranean countries. *Israel J. Bot.* **12**: 74–96.
- Grover, I. S. 1970. Cytogenetical relationships in some *Argemone* and *Papaver* species. Ph. D. thesis, University of Udaipur, Udaipur, India. 1–237.
- , Mangat, G. S. and Malik, C. P. 1973. Cytogenetic studies in *Papaver* V. Cytogenetical relationships between *P. somniferum* ($2n=22$) and *P. setigerum* ($2n=44$). All India Symposium Cytogenetics in improvement and evolution of plants. Kashmir University, Srinagar, 28–29.
- and Malik, C. P. 1969. Karyological studies in some *Papaver* species. *Genetica Iberica* **21**: 105–113.
- Heneen, W. K. 1962. Chromosomal polymorphism and morphological diveristy in *Elymus Re-chingeri*. *Hereditas* **48**: 545–564.
- Hrishi, N. J. 1960. Cytological studies of *Papaver somniferum* and *P. setigerum* DC. and their hybrids. *Genetica* **31**: 1–130.
- Jones, G. H. 1968. Meiotic errors in rye related to chiasma formation. *Mutation Research* **5**: 385–395.
- Knaben, G. 1959. On the evolution of *radicatum* group of scapiflora *Papaver* as studied in 70 and 56 chromosome species. Part A—Cytotaxonomic aspects. *Opera Botanica* **2**: 1–74.
- Koopmans, A. 1955. A trisomic *Papaver rhoeas*. *Genetica* **28**: 35–41.
- 1970. Species differentiation in *Papaver dulium*. *New Phytologist* **69**: 1121–1130.
- Lewis, K. R. and John, B. 1966. The meiotic consequences of spontaneous chromosome breakage. *Chromosoma* **18**: 287–304.
- Malik, C. P. 1967. Desynapsis and formation of restitution nuclei in *Lolium multiflorum* $\times$ *Festuca arundinacea*. *Portugalia Acta Biolog.* **10**: 99–108.
- and Grover, I. S. 1970. Failure of chromosome pairing in opium poppy (*Papaver somniferum*) *Zeit. fur Biol.* **116**: 472–480.
- and — 1973. Cytogenetic studies in *Papaver* II. Hybrids between species with 7 as the haploid chromosome number. *Caryologia* **28**: 13–25.
- and Mary, T. N. 1973. Cytogenetic studies in *Papaver* IV. Trisomic in garden poppy. *Chromosome Information Service* **15**: 34–35.
- and Thomas, P. T. 1966. Chromosomal polymorphism in tall fescue (*Festuca arundinacea* Schreb.). *Chromosoma* **18**: 1–18.
- Mary, T. N. and Malik, C. P. 1973. Cytogenetic studies in *Papaver* III. Induced polyploids in some *Papaver* species. *ibid.* **15**: 27–29.
- Matsuura, H. 1950. Chromosome studies on *Trillium kamtschaticum* Pall. and its allies XIX. Chromatic breakage and reunion at chiasmata. *Cytologia* **16**: 48–57.
- McNaughton, I. H. and Harper, J. L. 1964. Biological flora of the British Isles No. 99. *Papaver*. *J. Ecol.* **52**: 767–793.
- Stebbins, G. L. 1951. *Variation and Evolution in Plants*. Columbia University Press, New York.
- Sugiura, T. 1940. Chromosome studies on *Papaveraceae* with special reference to the phylogeny. *Cytologia* **3**: 558–576.
- Walters, M. S. 1958. Studies of spontaneous chromosome breakage in interspecific hybrids of *Bromus*. *Univ. Calif. Pub. Bot.* **28**: 335–447.
- Yasui, K. 1940. On the bivalents associations in the meiosis of the PMC of *Papaver somniferum*. *Cytologia* **10**: 551–557.
- 1941. F_1 plants of *P. bracteata* $\times$ *P. lateriatum*. *Cytologia* **11**: 452–463.
- 1943. On the chromosome pairing in the PMC of a triploid F_1 plant between *Papaver* No. 41, 8 and *P. bracteata*. *Cytologia* **13**: 126–138.