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The Cytogenetic Structure of *Vicia sativa* Aggregate

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Summary. The cytogenetic structure of *Vicia sativa* aneuploid series was assessed by examination of the chromosome pairing in hybrids between types having 2n = 10, 2n = 12 and 2n = 14. Two different karyotypes were distinguished at both the 2n = 10 and 2n = 12 levels. Chromosome pairing in hybrids involved two 2n = 10 karyotypes, indicating that the parental lines differed by two translocations. A similar indication was obtained for the two 2n = 12 karyotypes employed. The meiotic behavior of the 2n = 10 × 2n = 12 hybrids indicated that the parental lines differed by up to three translocations, some of which involved unequal chromosome segments. It has been proposed that the 2n = 10 types were developed from the 2n = 12 via centric or tandem fusion and additional rearrangements further accelerated chromosome repatterning at the two 2n levels. Hybrids between the 2n = 14 *V. sativa* and the former 2n types had very irregular chromosome pairing and were highly sterile. It has been proposed that the 2n = 14 type is a relatively new evolvement in *V. sativa* because of its shorter complement in comparison with the other karyotypes. The subterraneous pods of the 2n = 14 type, a characteristic which is absent in other *V. sativa* types and in the entire genus *Vicia*, also supports an advanced, phylogenetic position. The 2n = 14 type probably arose from n = 7 gametes produced by the 2n = 12 × 2n = 10 hybrid and the establishment of the row 2n = 14 type was acquired through conspicuous chromosome deletions. In spite of its remarkable chromosomal variation, *V. sativa* can still be considered, for breeding purposes, as being one gene pool. The wild forms of *V. sativa* can thus be valuable sources for improving the cultivated vetch.

Key words: *Vicia sativa* – Cytogenetic structure

Introduction

The *Vicia sativa* aggregate represents a unique combination of remarkable morphological variation, adaptive radiation and aneuploid series, including several karyotypes in three 2n levels. Several taxa have been distinguished in *V. sativa*. These taxa were treated as different species by Mettin and Hanelt (1964) but as subspecies by Ball (1968) and Davis and Plitmann (1970). Members of the *V. sativa* aggregate occupy diverse ecological niches which include primary habitats in steppe and maquis vegetation and secondary, or man-made, habitats such as road sides and fallow fields. The cultivated derivatives of *V. sativa* can also be assigned to this latter class. Three different chromosome numbers – 2n = 10, 2n = 12 and 2n = 14 – were reported for this aggregate. It has been shown that conspicuous karyotype variation exists both in the 2n = 12 and 2n = 10 types (Mettin and Hanelt 1964, 1973; Yamamoto 1961; Hollings and Stace 1974; Ladizinsky in press). While Mettin and Hanelt related any karyotype to specific taxon, remarkable intrataxon karyotypic variation was described by Hollings and Stace. Furthermore, Ladizinsky found a given karyotype in several taxa and several karyotypes in the same taxon. The cytogenetic relationships between the 2n = 10 and 2n = 12 types were examined by several authors (Mettin and Hanelt 1964; Yamamoto 1959, 1961). Recently the performance of, and chromosome pairing in the 2n = 12 × 2n = 14 hybrid was reported (Yamamoto 1977). Although complete information on the cytogenetic relationships in *V. sativa* is not available, it has been proposed that the evolution in this aggregate was via decreasing of the chromosome number (Hanelt and Mettin 1966; Plitmann 1967; Hollings and Stace 1974).

In the present study a more comprehensive effort has been made to assess the cytogenetic affinities between the various karyotypes and to provide a new interpretation regarding the mode of evolution in the *V. sativa* aggregate.

Materials and Methods

The various lines of *V. sativa* examined in the present study were identified by their chromosome number and karyotype. The five karyotypes recognized and their complement length are shown in

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Fig. 1. The various lines employed and their chromosome number are listed in Table 1. For study of chromosome pairing in meiosis, buds were fixed in 3:1 absolute ethanol acetic acid and stored in 70% ethanol. Anthers at the appropriate stage were stained by aceto-carmine. Pollen fertility was determined by staining mature pollen grains by aceto-carmine. A pollen grain was considered normal if it had regular shape and darkly stained cytoplasm. Usually 500 pollen grains were scored in each parental line and hybrid. Seed fertility was determined by the proportion of flowers developed to seed-bearing pods and the number of ovules developed to seeds in these pods.

Results

All the parental lines used in the present study had regular meiosis. In two lines – No. 138 (2n = 10B) and No. 169 (2n = 12A) – two univalents were only rarely observed (Table 2). The conspicuous difference in the karyotype shape of 10A and 10B did not affect the shape of the bivalents. In both, rod and ring bivalents were observed in about similar proportions indicating quite regular chiasma formation in the short arms of the aerocentric chromosomes. Ring and rod bivalents were also common in the 2n = 12 and 2n = 14 parental lines. The fertility of the parental lines was high both in pollen stainability and seed set.

F_1 hybrids. The hybrids of the various combinations examined developed normally and produced many branches. Chromosome pairing in these hybrids was as follows:

2n = 10A × 2n = 10B: A chromosome configuration indicating a translocation difference between the two parental lines was observed in 14out of the 20 cells of this hybrid examined in MI (Table 4). At diakinesis, that ring of four chromosomes occasionally was attached to the nucleolus, indicating that the satellited chromosomes were involved in the rearrangement. In other cells chromosomes involved in the quadrivalent were not associated with the nucleolus. It therefore can be inferred that the parental lines of this hybrid differed in fact by two reciprocal translocations. In cells where no quadrivalent was formed, up to two heteromorphic bivalents were observed. The regular shape of the chiasma in these bivalents indicated that the two chromosomes were homologous in their distal segments. Pollen fertility of this hybrid was low and consistent with the chromosome association found in MI (Table 3). Although nearly 50% of the flowers were developed to seed bearing pods, no more than two seeds per pod were developed.

2n = 12A × 2n = 12B: The metaphase I chromosome association of this hybrid was very irregular with considerable proportions of univalents and quadrivalents (Table 3). Ring bivalents were rare and the mean of chiasmata per cell was greatly reduced in comparison to that of the parental lines. In the cells examined, the chromosomes were organized in 14 different combinations (Table 5). Multivalent associations detected in about 25% of the cells indicated that the parental lines differed by two translocations. One of these translocations was between chro-

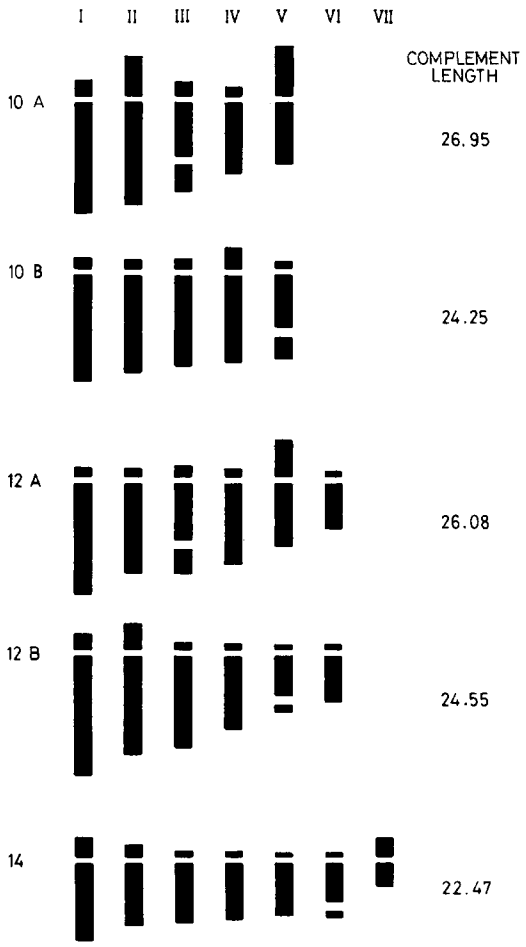

Fig. 1. Idiograms and complement length (according to Ladizinsky, in press) of the five karyotypes of *V. sativa* employed in the present study.

Table 1. Chromosome number, karyotype and taxanomy of the various lines of *V. sativa* employed in crosses

Line no.	2n	Karyotype	Taxon
134	10	A	var. *angustifolia*
135	10	A	var. *angustifolia*
159	10	A	var. *cordata*
136	10	B	var. *cordata*
138	10	B	var. *cordata*
154	12	A	var. *sativa*
167	12	A	var. *sativa*
169	12	A	var. *sativa*
153	12	B	var. *cordata*
161	14		var. *amphicarpa*

Table 2. Metaphase I chromosome pairing and fertility of the parental lines used in crosses

Line no.	2n	No. cells	I	Rod II	Ring II	Mean chiasmata	Pollen fertility %	Flowers turned to pods %	Ovules developed to seeds %
134	10	30		3.00 (1-5)	2.00 (1-4)	7.30 (5-9)	97.0	60.3	72.0
135	10	30		2.20 (1-5)	2.80 (1-5)	8.66 (6-11)	93.6	67.7	85.0
136	10	30		2.50 (0-5)	2.50 (0-5)	8.33 (5-10)	97.0	79.6	75.0
138	10	25	0.08 (0-2)	1.52 (0-4)	3.44 (1-5)	8.84 (7-11)	98.4	83.5	64.7
159	10	30		2.36 (0-5)	2.63 (0-5)	8.40 (6-11)	76.0	92.5	65.3
153	12	20		3.95 (2-5)	2.05 (0-4)	9.65 (8-12)	97.2	86.3	69.6
154	12	29		2.86 (1-6)	3.13 (1-5)	10.44 (6-13)	98.0	70.9	83.0
167	12	30		3.6 (1-5)	2.4 (1-5)	9.53 (7-12)	96.2	71.8	77.3
169	12	29	0.07 (0-2)	3.06 (1-5)	2.89 (1-5)	10.27 (8-14)	98.2	57.9	63.4
161	14	25		3.72 (2-6)	3.28 (1-5)	12.12 (10-17)	92.2	89.2	77.7

mosomes of different size, resulting in a heteromorphic quadrivalent or trivalent. In addition, heteromorphic bivalents were observed. The fertility of this hybrid was very low (Table 3) and of about 500 flowers produced by this hybrid not even a single pod developed. Similar sterility was found also in the reciprocal cross combination. This might indicate either that 12A and 12B differ by additional chromosome rearrangements, or that genetic factors are involved in this sterility. The meiotic behavior of this hybrid is similar to that reported by Yamamoto (1969) for the 2n = 12 × 2n = 12 hybrid, but in his case the karyotypes of the two parental lines were practically identical.

2n = 10A × 2n = 12A: Five different hybrids of this combination were examined cytologically (Table 3). The various hybrids differed from one another by the amount of univalents and multivalents. The most common chromosome association in this combination was 4II + III (Table 6). In about 15% of the cells, associations were observed indicating a difference of two translocations between the 2n = 10 and 2n = 12 lines. In one cell even a chain of seven chromosomes was observed. Heteromorphic bivalents were found in this combination. At diakinesis it could have been shown that the satellited chromosomes were involved in a quadrivalent (Fig. 2). Pollen fertility of this hybrid combination was low but about half the number of the flowers developed to seed bearing pods. However, a great variation in the number of seeds per pod was noticed between the various hybrids (Table 3).

2n = 10B × 2n = 12B: Chromosome association in MI was also irregular in this combination (Table 3). It differed, however, from the previous 2n = 11 combination by a higher number of univalents per cell and a higher number of chromosome association types. The most frequent configuration was 2I + 3II + III (TAble 7). Multivalent associations indicated that the parental line of this hybrid differed by up to three translocations. Some of the heteromorphic bivalents here had asymmetric chiasma (Fig. 2) which could be inferred as a considerable deletion in a chromosome of one of the parental lines, or translocation of unequal segments. Pollen fertility was very low in this hybrid and no viable seeds were produced.

2n = 10A × 2n = 12B: The meiotic behavior of this hybrid was similar to that of the 2n = 10A × 2n = 12A combination. The most frequent chromosome associated type was 4II + III and it could be concluded that the two parental lines differed by up to 3 translocations (Table 8).

2n = 10A × 2n = 14: The 2n = 12 hybrids of this combination were examined. Morphologically they were similar to the 2n = 14 parent by the reduced growth rate and similar to the 2n = 10 parent by not having stolons and underground fruits. The meiosis of these hybrids was characterized by a relatively great number of univalents and up to 4 heteromorphic bivalents, some with asymmetric chiasmata and multivalents indicating a difference of up to 3 translocations between the parental lines (Tables 3, 9). At diakinesis the two satellited chromosomes were left unpaired or formed two heteromorphic bivalents

Table 3. Metaphase I chromosome pairing and fertility of hybrids between various cytotypes of *Vicia sativa*

Hybrid combination	2n	no. cells	I	Rod II	Ring II	III	IV	V-VII	Mean chiasmata	Pollen fertility %	Flowers turned to pods %	Ovules developed to seeds %
2n = 10A × 2n = 10B	10											
159 × 136		20	0.45 (0-2)	2.40 (1-5)	0.90 (0-3)	0.15 (0-1)	0.55 (0-1)		6.45 (5-9)	9.8	46.3	13.5
2n = 12A × 2n = 12B	12											
154 × 153		43	1.97 (0-4)	2.64 (1-5)	0.90 (0-3)	0.46 (0-2)	0.32 (0-2)	0.02 (0-1)	6.60 (4-10)	0.7	0	0
2n = 10A × 2n = 12A	11											
135 × 154		24	0.30 (0-1)	2.33 (0-5)	1.87 (0-4)	0.62 (0-1)		0.08 (0-1)	7.75 (5-10)	12.2	34.0	15.2
134 × 169		18	0.11 (0-1)	1.78 (0-4)	1.62 (0-4)	0.72 (0-1)	0.22 (0-1)	0.11 (0-1)	8.83 (7-12)	4.3	57.8	33.5
134 × 167		24	0.12 (0-1)	1.57 (1-3)	1.80 (0-3)	0.54 (0-1)	0.08 (0-1)	0.33 (0-1)	8.25 (7-12)	8.7	44.7	16.0
159 × 154		36	0.36 (0-4)	1.68 (0-3)	1.60 (0-3)	0.70 (0-1)	0.22 (0-1)	0.22 (0-1)	8.55 (5-12)	13.8	59.0	17.6
159 × 169		20		1.85 (1-4)	1.65 (0-3)	0.75 (0-1)	0.15 (0-1)	0.20 (0-1)	7.60 (6-10)	15.8	41.3	14.2
2n = 10A × 2n = 12B	11											
134 × 153		52	0.82 (0-6)	2.32 (1-5)	1.41 (0-3)	0.54 (0-1)	0.06 (0-1)	0.17 (0-1)	6.75 (3-10)	12.0	49.0	13.2
2n = 10B × 2n = 12B	11											
128 × 153		33	1.63 (0-5)	2.00 (0-4)	1.24 (0-3)	0.51 (0-2)	0.14 (0-1)	0.12 (0-1)	7.03 (4-10)	2.1	21.2	0
2n = 10A × 2n = 14	12											
134 × 161		26	3.61 (1-6)	2.92 (0-5)	0.65 (0-2)	0.22 (0-1)	0.07 (0-1)	0.06 (0-1)	5.16 (4-9)	12.2	8.1	13.8
135 × 161		40	2.32 (0-6)	2.75 (0-5)	0.44 (0-2)	0.45 (0-2)	0.35 (0-1)	0.10 (0-1)	5.28 (4-9)	8.3	10.2	11.3
2n = 10B × 2n = 14	12											
136 × 161		72	3.40 (1-8)	2.98 (1-5)	0.14 (0-1)	0.43 (0-2)	0.12 (0-1)	0.05 (0-1)	5.00 (2-8)	5.5	5.9	21.5
2n = 12A × 2n = 14	13											
154 × 161		30	2.86 (0-5)	3.43 (2-6)	0.33 (0-2)	0.33 (0-2)	0.23 (0-1)		5.82	6.2	6.4	23.2
169 × 161		77	4.5 (1-9)	2.46 (0-6)	0.93 (0-2)	0.44 (0-2)	0.08 (0-1)		5.83	6.3	19.6	12.1

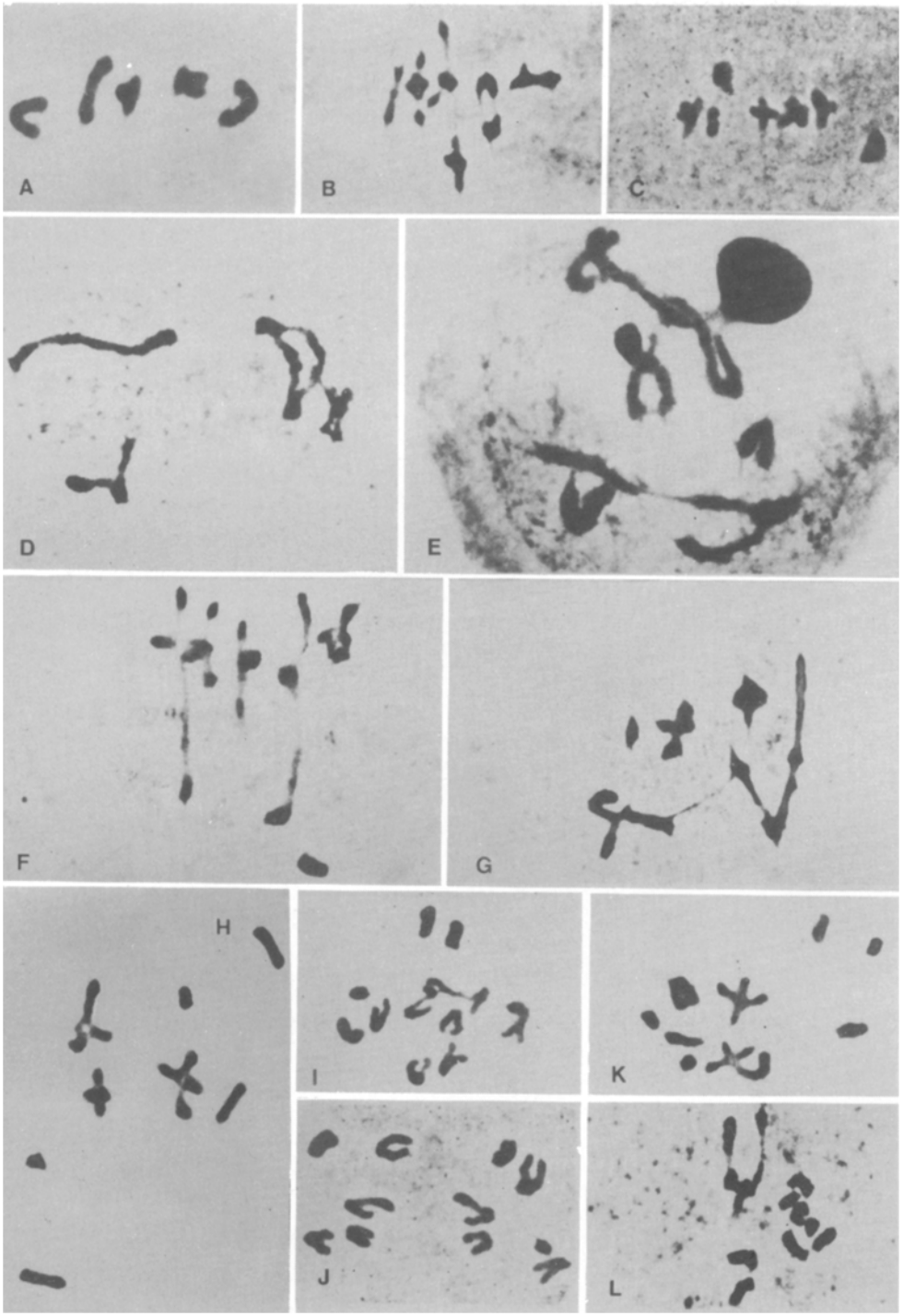

Fig. A-L. Meiosis in parental lines and hybrids of *V. sativa*

A 5II in 2n = 10A
B 6II in 2n = 12B
C 7II in 2n = 14
D 3II + IV in 2n = 10A × 2n = 10B
E 2I + II + III + IV in 2n = 10A × 2n = 12A. Note the attachment of the quadrivalent to the nucleolus
F I + 5II in 2n = 10A × 2n = 12A, note the two heteromorphic bivalents
G 3II + V in 2n = 10A × 2n = 12A
H 5I + 3II in 2n = 10B × 2n = 12B, note the heteromorphic bivalent with asymmetric chiasma
I-J AI of heteromorphic bivalent with asymmetric chiasma in 2n = 10B × 2n = 12B
K 6I + 2II + III in 2n = 12A × 2n = 14, note the heteromorphic trivalent
L 9I + 2II in 2n = 12A × 2n = 14

which attached to the nucleolus. This might indicate a conspicuous lack of homology between the satellited chromosomes of these parental lines. The fertility was low but in the range of the 2n = 11 hybrids.

2n = 10B × 2n = 14: Chromosome pairing of this hybrid was generally similar to that of the former 2n = 12 hybrid combination (Table 3). However, the two hybrids

Table 4. The frequency of the various chromosome association types in the 2n = 10A × 2n = 10B F_1 hybrid

Association	No. of cells
2I + 2II + IV	6
3II + IV	6
5II	5
I + 3II + III	2
2I + 4II	1
	20

Table 5. The frequency of the various chromosome association types in the 2n = 12A × 2n = 12B F_1 hybrid

Association	No. of cells
4I + 4II	7
6II	6
2I + 3II + IV	6
3I + 3II + III	4
2I + 2II + 2III	4
2I + 5II	4
3II + 2III	2
4II + IV	2
I + 4II + III	2
3I + II + III + IV	2
3II + VI	1
I + 2II + III + IV	1
2I + II + 2IV	1
4I + 2II + IV	1
	43

Table 6. The frequency of the various chromosome association types in the 2n = 10A × 2n = 12A F_1 hybrid

Associations	No. of cells
4II + III	51
3II + V	21
2II + III + IV	13
I + 5II	4
I + 3II + IV	4
4I + 2II + III	2
2I + 3II + III	1
2II + VII	1
I + 2II + VI	1
	98

Table 7. The frequency of the various chromosome association types in the 2n = 10B × 2n = 12B F_1 hybrid

Association	No. of cells
2I + 3II + III	9
I + 5II	6
4II + III	4
2I + 2II + V	3
2I + 3III	2
I + 3II + IV	3
3I + 2II + IV	1
3I + II + 2III	1
4I + 2II + III	1
5I + 3II	1
II + IV + V	1
2II + III + IV	1
	33

Table 8. The frequency of the various chromosome association types in the 2n = 10A × 2n = 12B F_1 hybrid

Association	No. of cells
4II + III	24
I + 5II	8
2I + 3II + III	4
I + 3II + IV	2
3II + V	7
2I + 2II + V	3
3I + 4II	2
5I + 3II	1
6I + II + III	1
	52

Table 9. The frequency of the various chromosome association types in 2n = 10A × 2n = 14 F_1 hybrids

Association	No. of cells
2I + 5II	13
4I + 4II	12
I + 4II + III	8
6I + 3II	7
2I + 3II + IV	5
5I + 2II + III	4
4II + IV	4
3I + 3II + III	3
I + 2II + III + IV	3
2I + 3II + IV	2
2I + 2II + 2III	2
3I + 3II + III	1
3I + II + III + IV	1
3I + 2II + V	1
2I + II + III + V	1
4II + IV	1
	68

differed by the chromosome association type which was most frequent (Table 10). In the 2n = 10B × 2n = 14 hybrid, a difference of only two translocations between the parental lines could be concluded from the metaphase I chromosome association. The seed set was improved in comparison to the former combination (Table 3).

2n = 12A × 2n = 14: Two different hybrids of this 2n = 13 combination were examined. The F_1 hybrids were vegetatively similar to the 2n = 14 parent but they had no stolons or underground fruits. The meiosis of these hybrids were very irregular with numerous types of chromosome associations (Tables 3, 11). The two hybrids differed markedly from one another by the number of univalents and multivalents per cell. The most frequent chromosome association type was 3I + 5II, similar to that found by Yamamoto (1977), and configurations indicating that the parental lines differed by three translocations were observed. Heteromorphic bivalents with asymmetric chiasmata were common in this hybrid combination. The satellited chromosomes of the two parental lines either were left unpaired or formed two heteromorphic bivalents. The fertility was low and consistent with the irregular meiotic behavior.

Discussion

The complexity of the *V. sativa* aggregate as indicated by morphological plasticity, variation of chromosome number and chromosome shape, has further been emphasized by the very irregular cytogenetic affinities between the various karyotypes. Mettin and Hanelt (1973) have already reported two karyomorphological variants at the 2n = 10 level which differed from one another by a single reciprocal translocation. The two 2n = 10 karyotypes employed in the present study differed by two translocations, one of which involved the satellited chromosomes. However, these two rearrangements cannot fully explain the difference in the complement size and shape of the two karyotypes (Fig. 1). Since the karyotype of the taxon *V. cordata* (2n = 10) depicted by Mettin and Hanelt (1973) is very similar to our 10B type, it is obvious that the new 2n = 10 type described by them is not likely to be an intermediate link between our 10A and 10B types. It could be that pericentric inversion and deletions of small chromosome segments are partly responsible for the karyotypic differences between the two 2n = 10 karyotypes examined by us.

The situation in the 2n = 12 level is apparently even more complex. The two karyotypes employed, 12A and 12B, were quite similar in their complement size (Ladizinsky, in press) (Fig. 1) and their karyotypes were much closer in comparison with the 10A and 10B karyotypes. These 12A and 12B karyotypes, however, are conspicuously divergent from one another as indicated by the very irregular meiosis of their hybrid and particularly by the complete sterility of this hybrid. Yamamoto (1969) examined a hybrid between two karyotypically similar 2n = 12 lines. According to the chromosome association types in MI he concluded that his two lines differed by three translocations. Mettin and Hanelt (1964, 1973) mentioned four

Table 10. The frequency of the various chromosome association types in the 2n = 10B × 2n = 14 F_1 hybrids

Association	No. of cells
3I + 3II + III	13
4I + 4II	12
6I + 3II	11
2I + 5II	6
5I + 2II + III	6
2I + 3II + IV	5
I + 4II + III	3
4I + 2II + IV	3
8I + 2II	2
I + 3II + V	2
I + 2II + III + IV	1
2I + 2II + 2III	1
2I + 2II + VI	1
3I + II + III + IV	1
3I + 2II + V	1
4I + II + 2III	1
4I + II + VI	1
7I + II + III	1
	71

Table 11. The frequency of the various chromosome association types in the 2n = 12A × 2n = 14 F_1 hybrids

Association	No. of cells
3I + 5II	19
7I + 3II	13
2I + 4II + III	11
4I + 3II + III	11
I + 6II	10
5I + 4II	9
6I + 2II + III	9
3I + 3II + IV	7
9I + 2II	5
I + 3II + 2III	2
2I + 2II + III + IV	2
5I + 2II + IV	2
I + 4II + IV	1
3I + 2III + IV	1
4I + II + III + IV	1
5I + II + 2III	1
7I + II + IV	1
8I + II + III	1
5II + III	1
	107

different karyotypes at the 2n = 12 level. While they related every karyotype to different taxon, Hollings and Stace (1974) found remarkable karyotypic variation within a single taxon. Similar results were obtained by Ladizinsky, (in press).

The meiotic behavior of the 2n = 11 hybrids in the three combinations examined between the various 2n = 10 and 2n = 12 lines clearly indicate that the differentiation between the 2n = 10 and 2n = 12 in *V. sativa* was not a simple process. In aneuploid series, reduction of the chromosome number is generally assumed to have been the main trend of evolution (Stebbins 1971). If this occurred via centric fusion, two acrocentric chromosomes merged to form one metacentric chromosome. Tandem fusion (White 1973) will cause a greater asymmetry by forming a large acrocentric chromosome from two small acrocentrics. While centric fusion cannot be ruled out in the evolution of 10A, the formation of the 10B type apparently occurred through tandem fusion. The heteromorphic bivalents and trivalents with asymmetric chiasma observed in the 10B × 12B hybrid also support this idea (Figs. 2, 3). Nevertheless, the meiotic behavior of the 2n = 11 hybrids could not be explained solely by a single event of centric or tandem fusion. It might be that the translocations indicated by multivalent associations in these hybrids are, at least in part, a much later evolvement of chromosome rearrangements accumulated independently in the 2n = 10 and 2n = 12 levels. Alternatively, it is possible that each of the various 2n = 10 karyotypes evolved from different 2n = 12 type and in the present study we did not match appropriate pairs. The greater complement length of 10A in comparison to those of 12A and 12B is compatible with such a possibility.

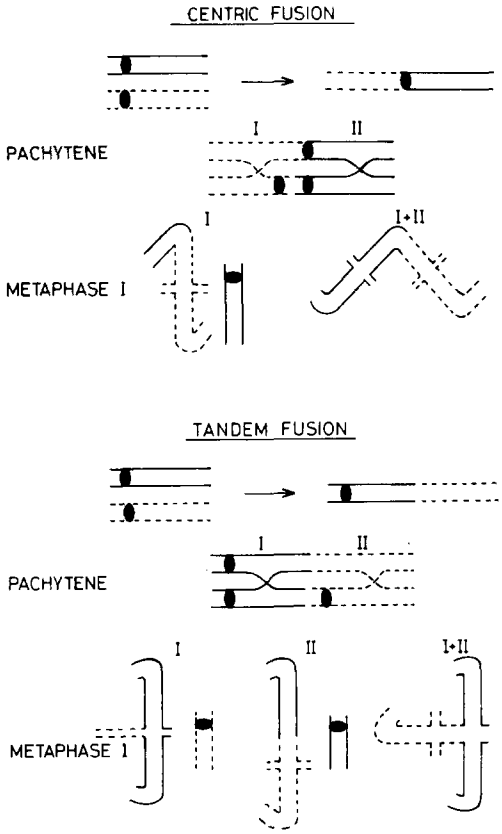

Fig. 3. Pachytene and metaphase I chromosome association in heterozygous to centric and tandem fusion. I and II represent the sites of crossing over and hte resultant chromosome configuration in MI.

According to Ladizinsky (in press), the 2n = 14 karyotype has the shortest complement length in *V. sativa*. One can conclude from the meiotic behavior of the 2n = 12 and 2n = 13 hybrids between 2n = 14 and 2n = 10 and 2n = 12, respectively, that the differentiation between the three chromosome levels was achieved through chromosome rearrangements and conspicuous deletion of chromosome segments. The lack of homology between the chromosomes of these parental lines was particularly noticed in the satellited chromosomes.

The complex cytogenetic affinities between the various entities of *V. sativa* naturally raises the question of the possible mode of evolution in this aggregate. Reduction of chromosome number in aneuploid series has been suggested in *Crepis* (Tobgy 1943) and *Haplopapus* (Jackson 1962). A similar model, namely 2n = 14 → 2n = 12 → 2n = 10 has also been proposed for the *V. sativa* aggregate (Hanelt and Mettin 1966; Plitmann 1967; Hollings and Stace 1974). As already pointed out, the cytogenetic information is compatible with the 2n = 12 → 2n = 10 evolution. This conclusion is supported further by ecological data. In wild populations of *V. sativa* in Israel, the 2n = 12 types are mainly confined to primary habitats, while the 2n = 10 types display strong weedy tendencies and are particularly common in relatively recent, man-made habitats (Ladizinsky, in press). The major difficulty in accepting the other part of the declined aneuploidy in *V. sativa* aggregate, namely 2n = 14 → 2n = 12 is that the 2n = 14 type has a shorter chromosome complement in comparison to the other karyotypes. This implies that if the 2n = 14 is indeed the most primitive type in that aggregate, the evolvement of the 2n = 12 level had to be accompanied by a major gain of chromatin. This gain had to be particularly extensive since aneuploidy via reduction of the chromosome number is coupled with a loss of chromosome segments adjacent to the centromere. Another point which is incompatible with 2n = 14 → 2n = 12 evolution is the amphicarpy of the 2n = 14 type. This characteristic is absent in other forms of the *V. sativa* aggregate and in the entire genus *Vicia*. This characteristic is highly advantageous in dry habitats where the 2n = 14 use to grow (Plitmann 1973) and it most probably represents an advanced stage in *V. sativa* aggregate.

The major difficulty in accepting the opposite mode of evolution, namely, 2n = 12 → 2n = 14, is the need for acquiring a novel centromere. The mechanism proposed for this purpose, by centric fission (John and Lewis 1968) has been seriously questioned by White (1973). In addition, it has been shown in maize (Rhodes 1940) and in wheat (Sears 1952) that telocentric chromosomes originating by centromere misdivision are highly unstable. The evolution of the 2n = 14 forms of *V. sativa* can alternatively be explained through hybridization between 2n = 12 and 2n = 10. As shown by Yamamoto (1961), Mettin and Hanelt (1964) and the present study, chromosome pairing in MI and chromosome segregation in AI of the 2n = 10 × 2n = 12 hybrids is highly irregular. Consequently the formation of n = 7 gametes is not unexpected in these hybrids. Such gametes might contain a lot of duplications which do not necessarily interfere with their survival. A union between two such gametes will give raise to a 2n = 14 plant. Such a possibility is not totally speculative. Nerson (1970) examined the chromosome number in a 2n = 10 × 2n = 12 F_2 population. Of 15 plants examined by him, a 2n = 13 and a 2n = 14 plants were found; both were partially fertile.

According to the evidence presented so far the evolution of the *V. sativa* aggregate can be depicted as follows: The 2n = 12 is apparently the genuine type of *V. sativa*. At this level conspicuous morphological variation, chromosome repatterning and adapative radiation had occurred. Hybridization between various 2n = 12 types probably further increased the variation at this level. While there is apparently no correlation between morphological characteristics and karyotypes at this level, it is not yet known the exact affinity of the various karyotypes to specific habitats. Following centric or tandem fusion in the 2n = 12 types, the 2n = 10 level was originated. Since the 2n = 10 types display significant weedy tendency, it could be that they were evolved from weedy 2n = 12 types. On the other hand, the reduced genetic flexibility in the 2n = 10 resulting from the reduced chromosome number, could also play some role in the weediness of these types. It can be assumed that the evolution of the 2n = 10 was accelerated further by chromosome repatterning. The 2n = 14 level is apparently a relatively recent evolvement in the *V. sativa* aggregate and most probably a result of n = 7 gametes produced by 2n = 10 × 2n = 12 hybrid. The improved meiotic regularity and restoration of fertility of the row 2n = 14 hybrid derivative was probably achieved by deletion of duplicated and heterochromatic segments throughout the genome. It could thus be inferred that the 2n = 14 form originated in places of contact between the 2n = 12 and 2n = 10. Such mixed populations were detected in nature (Ladizinsky, in press) and in two wild populations even 2n = 12, 2n = 10 and 2n = 14 types were found side by side.

The *Vicia sativa* aggregate, thus, represents a unique case of rapid evolution and incipient speciation. Reproductive barriers have not yet been fully established and most of the types can still exchange genes with one another. The confused taxonomic status of *V. sativa* aggregate is apparently due to such hybridization. The partial fertility of interkaryotype hybrids and preservation of new suitable combinations by autogamy have further accelerated the evolution of this aggregate.

The remarkable cytogenetic affinities between the various karyotypes of *V. sativa* are of economic importance. For practical and breeding purposes they still can be considered as one gene pool. Consequently it is advisable to search for suitable characteristics in the wild forms of *V. sativa* and to transfer them to the cultivated lines.

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