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present experiments. It is interesting to note that the yield of seeds was very good yet the germination was nil (Table 14). The plants from Ticino have not produced any germinating seeds in all experimental series (selfings, cross-pollinations within the same population, inter-population crosses as well as interspecific crosses), if they were used as female parent. This particular behaviour requires further investigations, especially those on *C. udicola* originating from the second center of its disjunctive geographical range (the Lake of Thun).

The present results permit to characterize the diploid taxa of the *C. pratensis* group as predominantly self-incompatible. It seems probable that the incompatibility blocks remain under multi-allelic control. They operate most frequently at pre-mating stages and might cause an inhibition of the pollen tube growth; on the other hand, the seed incompatibility apparently plays a complementary role resulting in seed or germination failure. Negative response to selfings seem to appear sometimes at later developmental stages (break-down of the inbred plants); however, in most of the studied cases the self-incompatibility barrier does not seem to be complete.

## 9. Interspecific crosses

### 9.1. Seed output

Interspecific crosses between six diploid taxa belonging to the *Cardamine pratensis* group were performed in three consecutive years 1972-1974. Only the experiments from 1972 and 1973 were included into the present paper for the seeds obtained from the last series are actually being at their dormancy period.

Various strains were intercrossed on 30 combinations, 15 of which led to the production of  $F_1$  hybrids. The results are given in Table 20.

Artificial cross-pollinations were made in insect-proof conditioned chambers where the parent plants were transferred long before their flowering. The normal precautions were taken to prevent contamination of cultures through mixing of pollen or seeds. All plants were emasculated about 48 h. before the opening of the flowers. Each pollination was repeated in 24 h. interval in order to get the stigmas at their most receptive stage.

Two and a half months after the pollinations, the siliques were collected and a score of developed fruits was made in relation to the total

number of pollinated flowers. About three months later, the seeds were sown on moist blotting paper and the percentage of germinating ones was subsequently calculated. Young hybrid plants have been kept in cultivation partly in conditioned chambers, partly in a cold greenhouse. Plants obtained in 1972 were transferred into experimental field after having completed their first year of growth.

It was recently emphasized by BENTZER (1973) that an estimation of genomic relationships between taxa which is based on the ability of a particular cross to produce seeds that germinate, is only of a limited reliability. Numerous authors have shown that there was no apparent correlation between crossability and fertility (e.g. ORNDUFF 1969), nor was there any particular correlation between the germinating potential of hybrid seeds and their viability (STRID 1970). On the other hand, reciprocal differences in compatibility and pollen fertility, inversely correlated with one another, were found by GRANT (1952) in some crosses performed at homoploid level with the *Gilia capitata* group.

Not all strains of the diploid taxa within the *C. pratensis* group have been included into the present experiments. It should be also noted that the ratio of hybrid individuals to the flowers that were pollinated is not entirely reliable, for the germination of seeds was sometimes low, even in control. Another factor is that in some materials, hybrid or parental alike, seeds ranged in continuous series from obviously sound to obviously abortive and dividing line between viability and inviability, could not be traced without doubt. The result of these and other conditions is that minor differences in the degree of crossability might be obscured by incomplete data, or by experimental errors. Our experiments do, however, reveal marked differences in crossing behaviour of the respective diploid taxa and some general correlations are apparent.

The most pronounced crossability was found between *C. nemorosa* and *C. rivularis*. Both reciprocal crosses yielded a fair amount of rather well-developed seeds which manifested a definite ratio of germination (41.4%, 62.1% in the respective crosses). Plants of the first hybrid generation were growing vigorously and flowered during the first year of their growth.

Table 20. *Cardamine pratensis* s.l.: interspecific crosses at diploid level

Cross (seed parent listed first)	N of pollin. flowers	N of sili- ques	Total N of seeds	N of sound seeds	Ger- mina- tion
<i>C. granulosa</i> x <i>C. Matthioli</i> (569)	12	10	30	4 (13.3%)	nil
<i>C. Matthioli</i> (569) x <i>C. granulosa</i>	18	16	170	164 (96.5%)	4.2%
<i>C. granulosa</i> x <i>C. Matthioli</i> (561)	12	10	60	14 (23.3%)	7.1%
<i>C. Matthioli</i> (561) x <i>C. granulosa</i>	15	12	71	29 (40.8%)	nil
<i>C. granulosa</i> x <i>C. rivularis</i>	12	10	24	3 (12.5%)	nil
<i>C. rivularis</i> x <i>C. granulosa</i>	12	9	84	66 (78.6%)*	nil
<i>C. granulosa</i> x <i>C. pratensis</i>	13	10	63	27 (42.8%)	nil
<i>C. pratensis</i> x <i>C. granulosa</i>	15	15	247	144 (58.3%)	2.1%
<i>C. granulosa</i> x <i>C. nemorosa</i>	15	14	48	36 (75.0%)	nil
<i>C. nemorosa</i> x <i>C. granulosa</i>	16	16	313	36 (11.5%)	nil
<i>C. Matthioli</i> C. <i>udicola</i> (56)	13	12	181	163 (90.0%)	nil
<i>C. udicola</i> (56) x <i>C. Matthioli</i>	12	12	46	21 (45.6%)	nil
<i>C. Matthioli</i> (561) x <i>C. rivularis</i>	11	9	144	26 (18.0%)	nil
<i>C. rivularis</i> x <i>C. Matthioli</i> (561)	13	11	117	84 (71.8%)	nil
<i>C. Matthioli</i> (569) x <i>C. rivularis</i>	12	10	272	60 (22.1%)	5.0%
<i>C. rivularis</i> x <i>C. Matthioli</i> (569)	11	11	256	80 (31.2%)	nil
<i>C. Matthioli</i> (569) x <i>C. pratensis</i>	16	14	164	80 (48.8%)	41.2%
<i>C. pratensis</i> x <i>C. Matthioli</i> (569)	16	14	136	120 (88.2%)	5.8%
<i>C. Matthioli</i> (561) x <i>C. pratensis</i>	9	7	74	31 (41.9%)	27.5%
<i>C. pratensis</i> x <i>C. Matthioli</i> (561)	8	6	53	29 (54.7%)	19.3%
<i>C. Matthioli</i> (561) x <i>C. nemorosa</i>	13	10	96	34 (35.3%)	nil
<i>C. nemorosa</i> x <i>C. Matthioli</i> (561)	16	13	151	51 (33.8%)	nil
<i>C. rivularis</i> x <i>C. pratensis</i>	15	14	76	36 (47.3%)	5.5%
<i>C. pratensis</i> x <i>C. rivularis</i>	14	13	138	90 (65.2%)	32.2%
<i>C. rivularis</i> x <i>C. nemorosa</i>	18	15	78	64 (82.0%)	62.1%
<i>C. nemorosa</i> x <i>C. rivularis</i>	20	18	291	291 (100%)	41.0%
<i>C. pratensis</i> x <i>C. nemorosa</i>	17	15	252	234 (92.8%)	33.3%
<i>C. nemorosa</i> x <i>C. pratensis</i>	18	15	248	246 (99.2%)	0.4%
<i>C. nemorosa</i> x <i>C. udicola</i> (56)	14	12	197	105 (53.3%)	2.9%
<i>C. udicola</i> (56) x <i>C. nemorosa</i>	20	18	214	55 (25.7%)	nil

\* seeds well-formed but empty under thick seed-coat.

Note. The numbers in brackets by *C. Matthioli* and *C. udicola* refer to the collections that were used in crosses (see Tables 2,3)

*C. pratensis* showed an interesting pattern of crossability towards *C. nemorosa* and *C. rivularis*. Both crosses with these taxa resulted in sound-looking seeds when *C. pratensis* was used as female parent. The germination ratio comported 33.3% and 32.2%, respectively (Table 20). Young hybrid plants were growing normally and no aberrations were found.

The opposite cross-direction i.e. when *C. pratensis* was used as male

parent, resulted in rather a good yield of seeds; by contrast, their germination proved to be extremely low. It comported 0.4% in cross *C. nemorosa*  $\times$  *C. pratensis* and 5.5% when *C. rivularis* was pollinated by *C. pratensis*. The viability of few obtained hybrid plants did not seem, however, to be affected in any visible way.

*C. Matthioli* and *C. pratensis* appeared to be partly intercompatible: two different races of *C. Matthioli* crossed reciprocally with *C. pratensis* produced variable amount of sound-looking seeds (Table 20). The percentage of young  $F_1$  plants ranged from 5.8% to 41.2% and it appeared to follow the cross-direction: germination of seeds was better when *C. Matthioli* represented female parent.

Limited reciprocal compatibility was observed in crosses between *C. Matthioli* and *C. granulosa*. As in the formerly described cases, a marked drop between amount of sound-looking seeds and their germination was observed. The highest germination ratio observed in these crosses was 7.1%, in other combination it comported 4.2%, otherwise the germination was nil.

Very weak interfertility was found between *C. Matthioli* and *C. rivularis* out of four different crosses only one yielded seeds and 5% of hybrid plants were obtained.

Similar results were brought about by crosses between *C. udicola* from Ticino and *C. nemorosa*: 2.9% of hybrids were obtained and that solely from the cross where *C. nemorosa* was pollinated by *C. udicola*; seeds yielded from the reciprocal cross direction did not germinate at all.

The last cross which yielded any hybrid plants was that of *C. pratensis* pollinated by *C. granulosa*: 2.1% of  $F_1$  plants obtained from this cross and nil germination found in the reciprocal one point to an extremely low intercompatibility occurring between the two taxa.

The results of the present study permit to estimate the nature of internal mechanisms preventing or limiting hybridization within the *C. pratensis* group. The number of developed siliques was most frequently slightly inferior to that of pollinated flowers. It seems probable that the incompatibility blocks limiting the formation of hybrids between the diploid taxa operate as very important sieves at later post-mating stages. In this respect the interspecific crosses bring about different results as compared to inbreeding experiments where rather a non-significant number of

seeds was developed after most of the selfings (see p.103-106). Accordingly one can assume that self-incompatibility mechanisms act essentially at pre-mating stages (pollen incompatibility) whereas those separating particular taxa appear at more advanced period of the seed development (seed incompatibility). The present results stay in agreement with previous data of LÖVKVIST (1956) who obtained seeds from crosses between various cytotypes of the *C. pratensis* group; the ratio of sound-looking seeds varied remarkably in the material of the Swedish author.

It seems probable that the barriers of interspecific incompatibility act in a similar way at various levels of polyploidy within the whole group.

The seed incompatibility is a very complex phenomenon and numerous attempts were made to give the most accurate explanation for seed failure. It should be pointed out that this sort of aberration is rather well-known in crosses representing different levels of polyploidy on the other hand, seed-incompatibility appearing in crosses at homoploid level is rather rare.

Four principal theories dealing with seed incompatibility are based on the assumption of "genomic strength" or "genetic values". These terms were introduced by HOWARD (1947) and have been since utilized by numerous students. The basic of genetic values is that the interaction of different parts of the seed is assumed to require an exact balance of unknown substances essential for the development; concentration of these substances depends on genetic strength of genomes and on the number of genomes present in the respective tissues of the seed.

The most popular theory is that based on the ratio of genetic values between endosperm and embryo (HOWARD 1947). The second one shows that the ratio: endosperm/maternal tissues holds sometimes balance of the seed development. This theory has been most thoroughly tested by VALENTINE (1951, 1954, 1955, 1956, 1963) and WOODCELL (1960, 1961). The importance of the relationship between maternal and paternal genomes in the endosperm nuclei was emphasized in particular by RUTISHAUSER (1969). The last theory, developed by WAGENHEIM (1962) assumed that the important ratio is between genetic values of the endosperm genomes and plasmon. Recent investigations of GYMER and WHITTINGTON (1973) point to importance of this

latter mechanism.

It seems probable that discrepancies found in the course of the present investigations are largely due to the incompatibility between endosperm and the maternal tissues. In this respect, diploid taxa of the *C. pratensis* group approach the *Primula* species investigated by VALENTINE and WOODSELL. Unpublished results of the present authors are in favour of this assumption: in experimental crosses between *C. rivularis* and *C. amara*, hybrid plants of the  $F_1$  generations were growing and developing normally only after having removed their apparently too thick seed-coat; no germination has been observed in normal conditions, in spite of the fact that the embryos were well-developed.

## 9.2 $F_1$ hybrids

### *Vegetative development*

The vegetative development proved to be quite normal in most of the obtained hybrids. Only a single plant born from cross: *C. nemorosa*  $\times$  *C. udiicola* was aberrant i.e. its leaves were malformed and its growth was very slow.

In about two months after germination, the young hybrid plants had already well-developed rosettes. Nearly all of them flowered in their first season. Only in the aberrant plant that was described above, no flowering shoots appeared. On the other hand, the two hybrids obtained from cross-direction: *C. rivularis*  $\times$  *C. pratensis*, produced some flowering shoots that developed up to a certain point yet eventually ceased to grow before flowering.

Vegetative propagation in hybrid plants began rather early; propagules on the rosette leaves occurred sometimes already in the third month after germination. They rooted easily and some of them produced later flowering shoots.

### *Meiosis in anthers*

The aim of the study on meiosis in anthers of the  $F_1$  hybrids has been to test further aspects of incompatibility between diploid taxa. On the whole, meiosis was investigated in 67 plants (Table 21). At later stages, all flowering hybrid plants were tested for percentage of good pollen.

The results of these investigations are presented in Table 24.

Table 21. Experimental  $F_1$  hybrids used for the study on meiosis in anthers

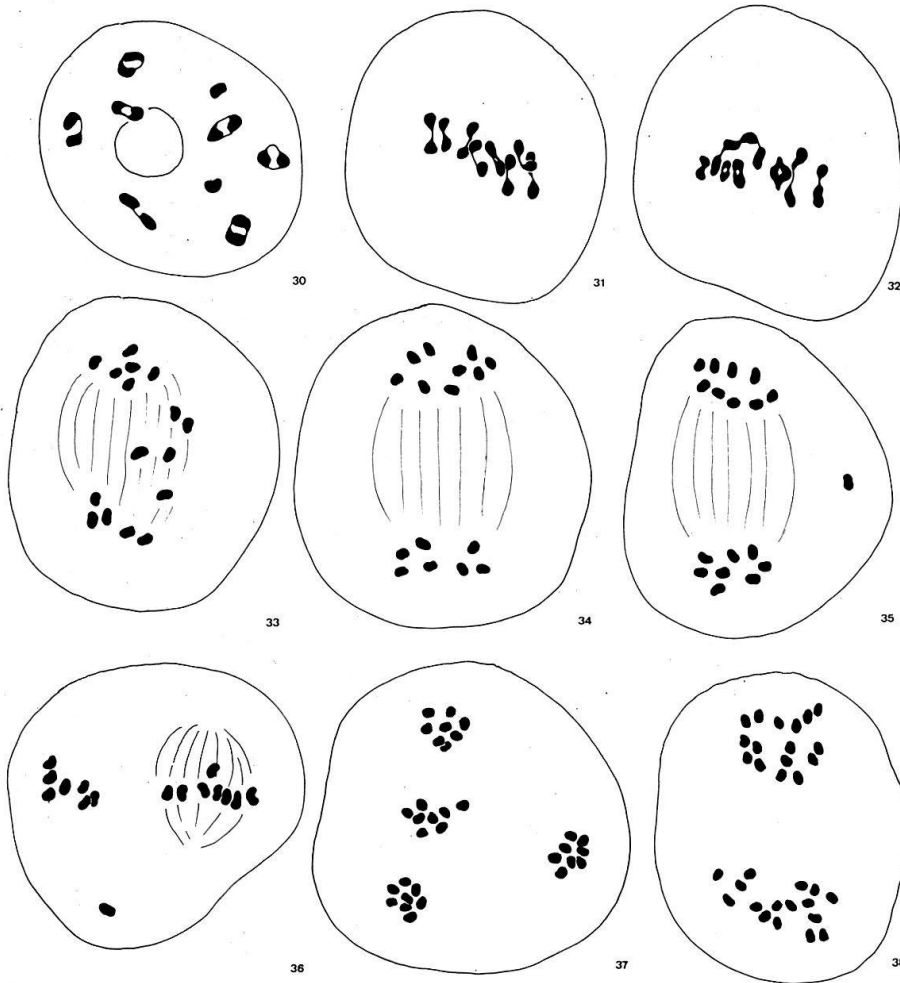
Cross type (female parent listed first)	number of studied plants
<i>C. granulosa</i> x <i>C. Matthioli</i> (561)	1
<i>C. Matthioli</i> (569) x <i>C. granulosa</i>	7
<i>C. pratensis</i> x <i>C. granulosa</i>	3
<i>C. nemorosa</i> x <i>C. granulosa</i>	2
<i>C. Matthioli</i> (569) x <i>C. rivularis</i>	3
<i>C. Matthioli</i> (569) x <i>C. pratensis</i>	5
<i>C. Matthioli</i> (569) x <i>C. pratensis</i> , 2n=18	1
<i>C. pratensis</i> x <i>C. Matthioli</i> (569)	7
<i>C. pratensis</i> x <i>C. Matthioli</i> (561)	8
<i>C. pratensis</i> x <i>C. rivularis</i>	6
<i>C. rivularis</i> x <i>C. nemorosa</i>	6
<i>C. nemorosa</i> x <i>C. rivularis</i>	7
<i>C. nemorosa</i> x <i>C. pratensis</i>	1
<i>C. pratensis</i> x <i>C. nemorosa</i>	7
<i>C. nemorosa</i> x <i>C. udicola</i>	3
Total	67
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Normal course of microsporogenesis was observed in most of the studied PMC s (Table 22). The chromosome pairing, although somewhat variable and incomplete, resulted mostly in eight bivalents (Fig. 31). Univalents occurred in rather a low number (Fig. 30). Polyvalents were found only exceptionally, in a single hybrid plant (Fig. 32, Table 22). The congression of chromosomes in I metaphase was regular.

In I anaphase the chromosomes were most frequently distributed in a normal way towards the poles. In some PMC s, however, several chromosomes were either lagging in the equatorial plate, or remained scattered along the spindle (Fig. 33). It can be assumed that restitution nuclei might sometimes be formed as a result of such disturbances, for some unreduced PMC s were found at the second division (Fig. 38). Another aberration observed



in the studied material consisted in elimination of some chromosomes, both during the first as well as the second division in the PMC s (Figs 35,36).



Figs 30-38. Experimental  $F_1$  hybrids: meiosis in anthers.

30. *C. rivularis* x *C. nemorosa*: diakinesis with 7 bivalents and 2 unival.
31. *C. pratensis* x *C. nemorosa*: I metaphase with 8 bivalents.
32. *C. granulosa* x *C. Matthioli*(561): I metaphase with 1 quadrivalent and 6 bivalents.
33. *C. pratensis* x *C. rivularis*: I anaphase with some chromosomes scattered along the spindle
34. *C. nemorosa* x *C. pratensis*: unequal distribution (7 versus 9 chromosomes) at I anaphase.
35. *C. Matthioli*(569)x *C. pratensis*,  $2n=18$ : unequal distribution at I anaphase accompanied by elimination of a single chromosome.
36. *C. Matthioli*(569)x *C. rivularis*: II metaphase with a single eliminated chromosome.
37. *C. nemorosa* x *C. udicola*: normal II telophase.
38. *C. granulosa* x *C. Matthioli*(561):II telophase in an unreduced PMC c.2100x.

Table 22. Experimental  $F_1$  hybrids between diploid taxa of the *C. pratensis* group: meiosis in anthers

Diakinesis-Metaphase I		Anaphase I - Telophase I			Anaphase II - Telophase II			
Chromosome pairing	Normal	Bridges	Laggards	Elimination	Normal	Bridges	Laggards	Elimination
<i>C. granulosa</i> x <i>C. Matthioli</i> (561):								
8 <sub>II</sub> <sup>1</sup> , 1 <sub>III</sub> <sup>2</sup> , 9 <sub>II</sub> <sup>1</sup> , 1 <sub>IV</sub> <sup>6</sup> , 1 <sub>VI</sub> <sup>5</sup> , 1 <sub>II</sub> <sup>5</sup>	16	2	8	-	27*	4	2	-
<i>C. Matthioli</i> (569) x <i>C. granulosa</i> :								
8 <sub>II</sub> <sup>7</sup> , 2 <sub>II</sub> <sup>2</sup>	33	-	2	1	34	-	1	-
<i>C. pratensis</i> x <i>C. granulosa</i> :								
8 <sub>II</sub> <sup>5</sup> , 5 <sub>II</sub> <sup>6</sup> , 4 <sub>II</sub> <sup>8</sup>	21	1	5	2	17	-	4	-
<i>C. nemorosa</i> x <i>C. granulosa</i> :								
7 <sub>II</sub> <sup>2</sup> , 4 <sub>II</sub> <sup>8</sup>	9	-	8	4	12	1	6	2
<i>C. Matthioli</i> (569) x <i>C. rivularis</i> :								
8 <sub>II</sub> <sup>7</sup> , 2 <sub>II</sub> <sup>5</sup> , 6 <sub>II</sub> <sup>6</sup>	18	-	11	-	34	-	7	1
<i>C. Matthioli</i> (569) x <i>C. pratensis</i> :								
8 <sub>II</sub> <sup>6</sup> , 4 <sub>II</sub> <sup>4</sup>	26	2	2	1	14	1	2	-
<i>C. Matthioli</i> (569) x <i>C. pratensis</i> , 2n=18:								
9 <sub>II</sub> <sup>8</sup> , 2 <sub>II</sub> <sup>2</sup>	11**	-	4	3	6	7	4	3
<i>C. pratensis</i> x <i>C. Matthioli</i> (569):								
8 <sub>II</sub> <sup>7</sup> , 2 <sub>II</sub> <sup>2</sup>	39	-	2	-	54	1	2	2
<i>C. pratensis</i> x <i>C. Matthioli</i> (561):								
8 <sub>II</sub> <sup>6</sup> , 4 <sub>II</sub> <sup>4</sup>	42	3	4	-	21	1	4	2

<i>C. pratensis</i> x <i>C. rivularis</i> : 8 <sub>II</sub>	48	-	6	-	29	1	12	-
<i>C. rivularis</i> x <i>C. nemorosa</i> : 8 <sub>II</sub> , 7 <sub>II</sub> , 2 <sub>I</sub> , 6 <sub>II</sub> , 4 <sub>I</sub>	37	-	3	1	42	-	-	-
<i>C. nemorosa</i> x <i>C. rivularis</i> : 8 <sub>II</sub> , 7 <sub>II</sub> , 2 <sub>I</sub>	67	-	4	-	43	1	2	-
<i>C. nemorosa</i> x <i>C. pratensis</i> : 8 <sub>II</sub>	22***	-	-	-	18	-	1	-
<i>C. pratensis</i> x <i>C. nemorosa</i> : 8 <sub>II</sub> , 7 <sub>II</sub> , 2 <sub>I</sub> , 6 <sub>II</sub> , 4 <sub>I</sub>	51	1	2	1	19	-	-	-
<i>C. nemorosa</i> x <i>C. udicola</i> : 8 <sub>II</sub> , 7 <sub>II</sub> , 2 <sub>I</sub> , 5 <sub>II</sub> , 6 <sub>I</sub>	34	-	4	1	14	-	3	-

\* in three PMCs unreduced chromosome number 2n=16 was observed (Fig. 30)

\*\* in some PMCs unequal distribution (10/8, 9/8 + 1 elimin.) was found

\*\*\* unequal distribution (7/9) was found in four PMCs (Fig. 34)

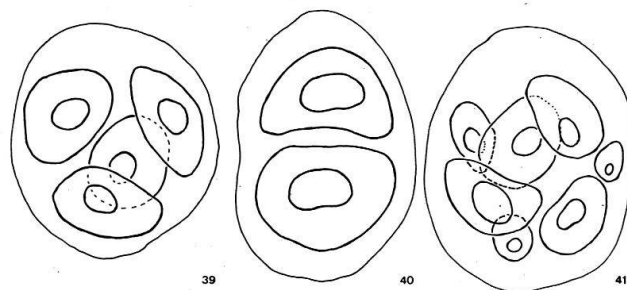
A particular distribution of chromosomes in I anaphase was sometimes observed. Instead of two groups, each containing eight chromosomes, nine chromosomes gathered at one pole whereas the other group comprised only seven chromosomes (Fig. 34). Such aneuploid distribution might subsequently contribute to the formation of aneusomatic plants; it should be recalled that hyperdiploid, aneusomatic plants were found in some diploid taxa studied in the course of the present work (see p. 82-86).

Table 23. Artificial  $F_1$  Hybrids between diploid taxa of the *Cardamine pratensis* group: tetrad stage in PMCs

Type of cross (female parent listed first)	Tetrads	Dyads	Triads	Polyads
<i>C. granulosa</i> x <i>C. Matthioli</i> (561)	32	8	-	12
<i>C. Matthioli</i> (569) x <i>C. granulosa</i>	43	2	1	3
<i>C. pratensis</i> x <i>C. granulosa</i>	16	1	-	2
<i>C. nemorosa</i> x <i>C. granulosa</i>	22	-	2	6
<i>C. Matthioli</i> (569) x <i>C. rivularis</i>	41	3	1	9
<i>C. Matthioli</i> (569) x <i>C. pratensis</i>	33	-	-	2
<i>C. Matthioli</i> (569) x <i>C. pratensis</i> , $2n=18$	18	-	1	6
<i>C. pratensis</i> x <i>C. Matthioli</i> (569)	28	1	-	3
<i>C. pratensis</i> x <i>C. Matthioli</i> (561)	39	1	1	1
<i>C. pratensis</i> x <i>C. rivularis</i>	72	4	-	-
<i>C. rivularis</i> x <i>C. nemorosa</i>	81	-	-	6
<i>C. nemorosa</i> x <i>C. rivularis</i>	112	6	-	1
<i>C. nemorosa</i> x <i>C. pratensis</i>	61	-	-	-
<i>C. pratensis</i> x <i>C. nemorosa</i>	49	1	-	1
<i>C. nemorosa</i> x <i>C. udicola</i>	52	-	-	4

The tetrad stage was most frequently normal (Table 23). However, in some hybrid plants, dyads of apparently unreduced microspores occurred in a variable frequency (Fig. 40). Some polyads were also observed in the studied

material (Fig. 41). The observations on the tetrad stage corroborate with the results obtained from investigations on microsporogenesis.



Figs 39-41. Experimental- $F_1$  hybrids: tetrad stage  
 39. Tetrad.  
 40. Dyad.  
 41. Polyad. c.1000 x.

The 18 chromosomic hybrid, born from cross *C. Matthioli* (569)  $\times$  *C. pratensis*, deserves a special mention. The plant was rather vigorous and flowered earlier than its siblings. The chromosome pairing in its PMCs was rather normal, yet in I anaphase uneven distribution of chromosomes was sometimes observed. As a result, gametes with 8 and 10 chromosomes, respectively, were sometimes formed. In some other PMCs, the anaphase groups comprised 8 and 9 chromosomes whereas a single chromosome was eliminated outside the spindle (Fig. 35). Tetrad stage was observed only in a limited material; normal tetrads were most frequently observed; in addition, a single triad, some dyads and several polyads occurred in the studied sample. The percentage of a good pollen was low (23%).

All flowering hybrid plants were tested for percentage of good pollen. The results are given in Table 24. It should be noted that only a general evaluation is possible, for the number of the obtained hybrids is extremely variable, ranging from a single plant up to 82 individuals. The lowest percentage of a good pollen comported 23%, the highest one 98%. The modal values corresponded to 70 - 90%.

In general, one could estimate the pollen fertility in artificial  $F_1$  hybrids as being rather reduced; however, it should be kept in mind that the diploid taxa of the *Cardamine pratensis* group represent themselves

Table 24. Percentage of good pollen in experimental  $F_1$  hybrids

Cross combination (female parent listed first)	number of plants										Total number	
	20%	30%	40%	50%	60%	70%	80%	90%	100%		of plants	
<i>C. granulosa</i> x <i>C. Matthioli</i> (561)	-	-	-	1	-	-	-	-	-	-	1	
<i>C. Matthioli</i> (569) x <i>C. granulosa</i>	-	-	3	2	1	1	1	-	-	-	7	
<i>C. pratensis</i> x <i>C. granulosa</i>	-	-	-	1	2	-	-	-	-	-	3	
<i>C. nemorosa</i> x <i>C. granulosa</i>	-	2	-	-	-	-	-	-	-	-	2	
<i>C. Matthioli</i> (569) x <i>C. rivularis</i>	-	1	2	-	-	-	-	-	-	-	3	
<i>C. Matthioli</i> (569) x <i>C. pratensis</i>	1	-	5	-	3	5	19	-	-	-	33	
<i>C. Matthioli</i> (569) x <i>C. pratensis</i> (2n=18)	1	-	-	-	-	-	-	-	-	-	1	
<i>C. pratensis</i> x <i>C. Matthioli</i> (569)	-	-	-	3	2	1	1	1	-	-	7	
<i>C. pratensis</i> x <i>C. Matthioli</i> (561)	-	-	-	-	1	1	1	3	2	-	8	
<i>C. pratensis</i> x <i>C. rivularis</i>	-	-	7	3	3	1	14	1	1	1	29	
<i>C. rivularis</i> x <i>C. nemorosa</i>	-	2	-	1	-	4	27	2	-	-	36	
<i>C. nemorosa</i> x <i>C. rivularis</i>	-	4	5	1	3	47	17	5	-	-	82	
<i>C. nemorosa</i> x <i>C. pratensis</i>	-	-	-	-	-	-	1	-	-	-	1	
<i>C. pratensis</i> x <i>C. nemorosa</i>	-	1	3	3	4	43	16	7	-	-	77	
<i>C. nemorosa</i> x <i>C. udicola</i>	-	-	-	1	1	1	-	-	-	-	3	

as a notably variable material in this respect, the frequency of a good pollen being sometimes very low. This particular phenomenon seems to be related, at least partly, to an extensive vegetative propagation within the complex. More detailed investigations on this subject are continued.

### 9.3 Isolation barriers between diploid taxa of the

#### *Cardamine pratensis* group

The factors that are relevant to the isolation of particular diploid taxa may be now summed up.

*C. nemorosa* and *C. rivularis* seem to keep their genetic affinities rather well. It should be noted, however, that hybridization between these taxa is actually rather impossible for they are separated by definite geographical, ecological and seasonal barriers.

Apparently unilateral crossability found between *C. pratensis* and *C. nemorosa*/*C. rivularis* seems to represent a factor that notably limits the possibilities for natural hybridization between these taxa. *C. pratensis* comes sometimes into contact with *C. nemorosa* and, in another part of its range, with *C. rivularis*. However, it is possible that some hybrids might be formed solely when *C. pratensis* is the recipient population.

*C. Matthioli* showed some intercompatibility with *C. pratensis*. However, the two taxa are separated from each other by a wide gap in their geographical distribution: the former one occurs in the Eastern Alps and south of the Alpine ridge, the latter one has its area just north of the Alps. This pattern seems to be rather sufficient for isolation.

Some limited crossability occurred between *C. Matthioli* and *C. granulosa*. These two taxa occur in the same region and were seen flowering at the same time. It appears possible that ecological differentiation might decide about a mutual isolation of these species. On the other hand, seed incompatibility could be an important factor contributing to elimination of some hybrid zygotes.

Crossing behaviour of *C. Matthioli* in relation to *C. rivularis* is apparently conditioned within the studied area by geographical, ecological and

seasonal barriers; seed incompatibility seems to be as well a rather important mechanism preventing spontaneous hybridization. Similar patterns appeared in relation between *C. Matthioli* and *C. nemorosa* as well as *C. udicola* and *C. nemorosa*. However, the crossing behaviour of *C. udicola* remains still to be investigated in detail.

It can be concluded that isolation barriers occurring between diploid taxa of the *C. pratensis* group are very variable in their nature and strength. They apparently act in cooperation: the most of diploid taxa remain distinct over their range partly because of differences in geographical distribution, partly because where they occur together their habitats differ and they have different times of flowering. But in some places they meet and flower together; given that the pollen is carried by insect vectors from one species to another, seed incompatibility is likely to represent a further barrier to successful hybridization. This internal mechanism acts at various post-mating stages, not only affecting development of embryo and endosperm, but also seems to influence the strongly reduced potential of germination of the hybrid seeds.

## 10. Discussion

The results of the present investigations contribute to the knowledge of evolutionary mechanisms that have played rôle in the speciation at homoploid level within the *Cardamine pratensis* group.

Some aspects of the problem i.e. types of variation and isolation barriers should be characterized in a general way. One might say that interpopulational variation within the *C. pratensis* complex is to a large extent camouflaged by the intrapopulational one. Alloamy that is a predominating type of the breeding system in all studied diploid taxa, undoubtedly represents an important factor in the creation of new genotypes. On the other hand, vegetative reproduction, strongly marked within the group of *C. pratensis*, seems to neutralize in some part the effects of selection; this means that the plants which have a characteristic genotype can be preserved in population even if they are sometimes unbalanced.

Isolation barriers occurring within the *C. pratensis* group are strongly diversified. The particular taxa are not separated by a single mechanism,