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8. Inbreeding experiments

The *Cardamine pratensis* group manifests homomorphic self-incompatibility remaining under sporophytic control. Investigations on this problem have been carried out previously by numerous authors (HILDEBRAND 1896 cit. acc. to LÖVKVIST 1956, CORRENS 1912, BEATUS 1929, BATEMAN 1955, LÖVKVIST 1956). However, it should be emphasized that only LÖVKVIST performed his experiments on plants that were cytologically controlled.

Out of 355 plants used in LÖVKVIST's study, only 9 were diploid; no seed setting was observed after forced selfings. However, it is not quite sure which diploid taxon has been in fact represented in the material of the Swedish author .

In the course of the present study, forced selfings and control cross-pollinations were performed on 44 plants representing all the six diploid taxa. It should be mentioned that *C. udicola* from Ticino was used only in rather limited number of pollinations. In addition, some crosses were made within *C. Matthioli*.

Artificial pollinations were made in conditioned, insect-proof chambers. Four series of experiments were parallely carried out:

A - pollinations with the pollen of the same flower
B - pollinations with the pollen from other flower of the same individual
C - pollinations with the pollen from other individual of the same population
D - pollinations with the pollen from other population of the same taxon

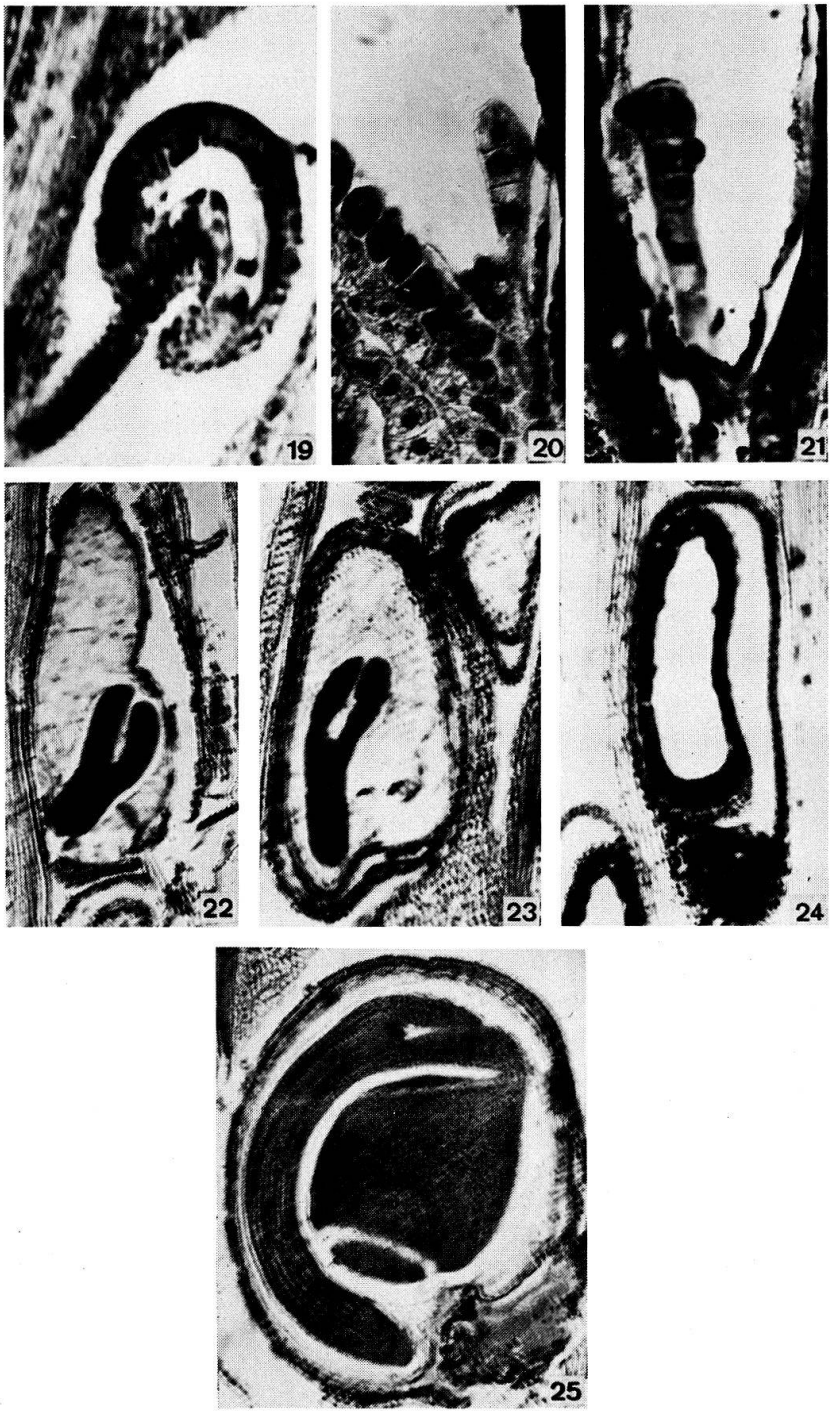
The pollinated flowers were respectively tagged; in about two and a half months the fruits were collected. Subsequently, the germination tests were made. The young plants obtained from selfings as well as some representative specimens raised from control have been kept in conditioned chambers.

For embryological investigations, materials were fixed in acetic alcohol (1:3), beginning from 48 h. after the pollination; fixations were carried on in 48 h. intervals, up to 42 days. It should be noted that some seeds maturated later i. e. in about 50 days.

Fixed flowers and siliques were dehydrated and embedded in paraffin in the usual way. Microtome sections, 10µ and 11µ thick were stained with Heidenhain's or Mayer's haematoxylin.

The structure of ovules and details of the seed development, including the observed aberrations, are alike in the whole investigated material. For that reason, descriptions given below would serve for any diploid taxon. (Figs. 19 - 25).

The ovules are campylotropous (Fig. 19). From an early developmental stage the young embryo sacs were in contact with the endothelium which consisted of a single layer of cells filled with a dense cytoplasm.



Figs.19-25. Diploid taxa of the *Cardamine pratensis* group: seed development after selfings and cross-pollinations. 19. Campylotropous ovule.c.225x. 20-21. Young embryos in endosperm.c. 720x. 22-23. Advanced development of embryo and endosperm. 24. Empty seed with developed seed-coat. 25. Normally developed seed.c.150x.

Mature ES was rather large, sometimes twisted and highly vacuolated. It contained three big, multinuclear and extremely long-persisting antipodals, a secondary nucleus and an egg-aparatus comprising egg-cell and two synergids.

The response to selfings proved to be somewhat ambiguous in the studied material. Individual as well as interpopulational variation was observed both in frequency of developed seeds as well as in their subsequent germination. The results which are presented here do no more than illustrate a general breeding behaviour of the diploid taxa within the *C. pratensis* group. For a more thorough analysis, it will be necessary not only to multiply the number of experiments but also to control them further, beyond the stage of young plants.

In most of the pollinated flowers the embryo sacs persisted for rather a long time, up to 18 to 20 days after pollination; however no observable changes in size and structure of the ovules and ovaries could be discerned. At later stages the degeneration of the ovules was observed.

In some flowers of *C. nemorosa*, siliques began to form in spite of fact that there was no seed development.

However, the seed failure after selfings was by no mean absolute. In some ovules, fixed by the 17th day after pollination, embryo sacs did not manifest any further developments, but the endothelium became hypertrophied, the whole ovule being larger than the other ones within the ovary. At later stages some empty seeds with nevertheless well developed seed-coat were found (Fig.24).

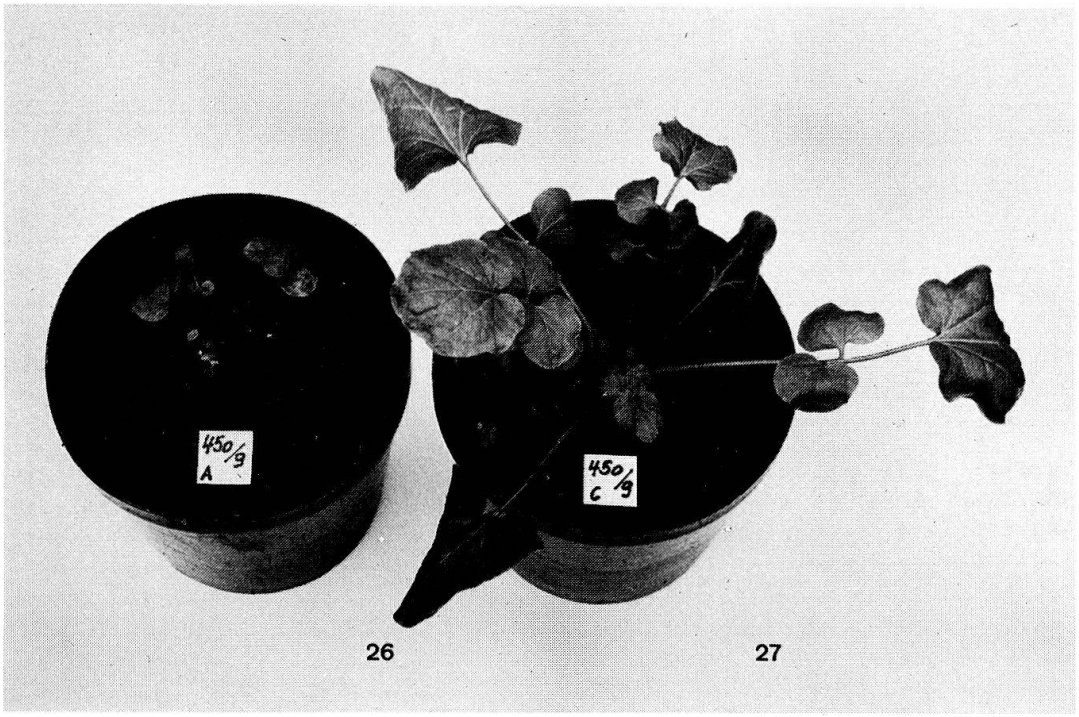
The development of embryo and endosperm presented sometimes aberrations. By 24 days after pollination, the zygote stayed undivided and only some few endosperm nuclei were visible. In some other materials fixed at the same time, a thin and elongated young embryo, most frequently two-celled, was observed. In one ovule from this series four-celled embryo was found (Fig. 20, Fig. 21). The cells of the embryo were strongely vacuolated. Endosperm nuclei in the above described ESs were few; they were rather evenly distributed within a thin layer of cytoplasm that lined the seed cavity. Only at the micropylar end was the endosperm a little better developed. In spite of apparently defective development of embryo and endosperm, the respective ovules were notably enlarged and the development of the seed-coat appeared to be rather advanced.

Normal seed development began about 7 - 9 days after pollination, both in selfings as well as in outcrosses. It was rather slow between 12 and 18 days: the embryo stayed small and spherical, its suspensor being distinctly elongated. Endosperm was multinuclear and it occurred in a larger amount at the micropylar end of the ES. Big antipodals reached deep into the seed cavity.

Between 18 and 26 days after pollination, the embryo and endosperm developed rather rapidly; by 28 days well-developed, elongated embryo surrounded by a dense endosperm was lying centrally within the seed cavity. The respective ovules were much enlarged and the seed-coat was advanced in its differentiation (Fig. 22, 23). By the 42nd day, some fully developed embryos were observed; endosperm was at that time mostly resorbed and the seed-coat presented no anomalies (Fig. 25).

Differences between selfings and control cross-pollinations occur mostly in the seed output (Tables 13 - 19). The seed setting proved to be invariably good in the latter experiments whereas the former ones yielded seeds in low and variable frequency. Only in two populations, one of *C. Matthioli* from fertilized meadow in the Piedmont, the other of *C. udicola* from Ticino, rather high percentage of apparently well-developed seeds was obtained from selfings. These results stay in agreement with embryological observations: various developmental stages of embryo and endosperm were most frequently observed in the selfed ovules of *C. Matthioli* and *C. udicola* from the stations mentioned above.

Seed germination after selfings proved to be rather erratic. In *C. pratensis* only two seeds developed in a single individual out of 13 tested ones. One seed germinated giving rise to a vigorous young plant. Selfings in *C. granulosa* yielded likewise two seeds from a single plant (10 individuals tested); however, the germination was nil (Table 13). Out of two studied populations of *C. rivularis*, only one produced seeds after selfings; three tested plants yielded no seeds at all, in one plant a single developed seed was found, in the last individual 13 seeds were collected. None of these seeds germinated. *C. nemorosa* manifested still some more variation: out of three studied populations, two yielded seeds in very variable frequency (Table 19). In addition, development of well-formed, yet empty siliques was observed. Two seeds germinated; however, the young plants were apparently affected in their development (Figs 26,27).



Figs 26,27. 14 days old plants of *Cardamine nemorosa:*
26. Plant obtained from selfings.
27. Plant obtained from cross-pollination, about ½ natural size.

Table 13. *Cardamine granulosa:* seed output after selfings and cross-pollinations

No.of plant	Total number of pollinated flowers - Series				Germination Series			
	A	B	C	D	A	B	C	D
560/2	10(-)	8(-)	16(132)	4(24)	-	-	12.1%	2.3%
560/4	11(-)	7(-)	9(40)	6(37)	-	-	11.1%	1.8%
560/5	9(2)	1(-)	8(68)	9(51)	-	-	9.8%	1.1%
560/10	9(-)	5(-)	10(97)	3(6)	-	-	14.8%	10.0%
560/14	15(-)	--	7(42)	- -	-	-	7.4%	-
567/1	17(-)	5(-)	4(13)	3(12)	-	-	5.5%	0.3%
567/4	8(-)	6(-)	4(18)	6(21)	-	-	32.2%	5.8%
567/5	2(-)	1(-)	17(67)	2(11)	-	-	28.3%	3.4%
567/7	16(-)	4(-)	1(6)	1(3)	-	-	30.0%	2.9%
567/8	7(-)	4(-)	9(57)	4(9)	-	-	8.8%	4-7%

Note. Number of sound-looking seeds is given in brackets

Table 14. *Cardamine Matthioli:* seed output after selfings and cross-pollinations

No.of plant	Total number of pollinated flowers - Series				Germination Series			
	A	B	C	D	A	B	C	D
561/1	5(32)	9(14)	6(10)	8(20)	14.2%	3.8%	23.2%	48.1%
561/3	13(116)	6(15)	14(38)	8(26)	22.4%	14.8%	31.2%	38.9%
561/4	7(36)	6(11)	7(13)	5(14)	18.6%	2.9%	41.3%	52.6%
561/5	6(18)	4(7)	8(52)	7(23)	11.1%	8.2%	12.3%	38.1%
561/8	11(56)	3(4)	8(16)	9(31)	18.1%	5.8%	33.2%	38.1%
568/9	12(-)	8(-)	8(71)	3(6)	-	-	46.3%	32.7%
568/11	10(-)	5(-)	13(126)	2(7)	-	-	52.3%	42.2%
568/12	8(-)	6(-)	7(79)	4(21)	-	-	49.8%	44.4%
569/3	13(-)	8(-)	11(116)	2(12)	-	-	29.6%	31.2%
569/7	9(-)	7(-)	7(164)	4(-)	-	-	56.3%	-
569/9	14(-)	6(-)	12(103)	6(31)	-	-	51.1%	22.8%
570/1	9(-)	6(-)	9(78)	4(30)	-	-	47.9%	36.5%
570/3	11(-)	3(-)	8(54)	5(44)	-	-	12.8%	11.3%
570/6	14(-)	7(-)	7(49)	4(38)	-	-	39.4%	41.6%

Note- Number of sound-looking seeds is given in brackets

Table 15. *Cardamine Matthioli:* crosses between two ecological races

Cross (seed parent listed first)	N of pollinated flowers	N of siliques	Total N of seeds	N of sound seeds	Germination
561 x 569	12	12	396	388	76.2%
569 x 561	11	10	389	382	82.8%

Average N of ovules in seed plants: 561 x 569 38.1
569 x 561 42.1

Table 16. *Cardamine udicola* from Ticino: seed output after selfings and cross-pollinations

No.of plant	Total number of pollinated flowers - Series				Germination Series			
	A	B	C	D	A	B	C	D
56/1	14(40)	8(18)	10(6)	3(16)	-	-	-	-
56/2	8(38)	3(6)	8(7)	6(18)	-	-	-	-
56/3	7(43)	4(8)	9(11)	- -	-	-	-	-
56/4	12(130)	4(9)	8(16)	8(47)	-	-	-	-
56/5	9(51)	8(28)	10(6)	7(21)	-	-	-	-

Note. Number of sound-looking seeds is given in brackets

Table 17. *Cardamine rivularis:* seed output after selfings and cross-pollinations

No.of plant	Total number of pollinated flowers - Series				Germination Series			
	A	B	C	D	A	B	C	D
624/2	15(13)	6(-)	9(41)	4(2)	-	-	28.1%	3.2%
624/3	10(1)	4(-)	5(38)	- -	-	-	14.6%	-
624/5	14(-)	5(-)	8(72)	4(17)	-	-	43.2%	11.1%
624/8	11(-)	5(-)	9(69)	1(3)	-	-	21.3%	4.4%
624/10	12(-)	4(-)	8(64)	4(11)	-	-	12.8%	10.2%
168/9	9(-)	6(-)	7(68)	- -	-	-	38.2%	-
169/2	11(-)	5(-)	12(97)	6(26)	-	-	48.5%	16.2%
169/3	10(-)	- -	8(32)	4(9)	-	-	41.7%	9.9%
169/5	12(-)	6(-)	11(86)	2(6)	-	-	28.3%	2.7%
169/8	10(-)	7(-)	7(41)	4(12)	-	-	51.3%	18.7%

Note. Number of sound-looking seeds is given in brackets

Table 18. *Cardamine pratensis:* seed output after selfings and cross-pollinations

No.of plant	Total number of pollinated flowers - Series				Germination Series			
	A	B	C	D	A	B	C	D
75/1	5(-)	3(-)	6(32)	6(58)	-	-	56.6%	51.3%
75/3	4(-)	2(-)	8(38)	2(21)	-	-	49.8%	36.6%
75/6	9(-)	1(-)	4(14)	2(9)	-	-	44.9%	28.1%
75/7	8(1)	2(-)	9(61)	4(20)	-	-	52.7%	55.4%
464/1	12(-)	4(-)	8(59)	6(31)	-	-	44.7%	28.1%
464/7	9(-)	5(-)	11(78)	4(20)	-	-	62.1%	44.5%
464/8	11(-)	6(-)	10(72)	2(13)	-	-	54.4%	50.0%
464/10	10(-)	4(-)	8(80)	3(18)	-	-	51.9%	35.4%
464/13	12(-)	8(-)	6(49)	2(9)	-	-	18.3%	11.2%
720/2	8(-)	2(-)	9(73)	5(41)	-	-	69.9%	51.4%
720/6	6(2)	3(-)	11(81)	2(16)	1 seed	-	54.8%	33.5%
720/8	12(-)	4(-)	10(78)	6(37)	-	-	31.2%	28.4%
720/11	13(-)	2(-)	12(90)	- -	-	-	47.7%	-

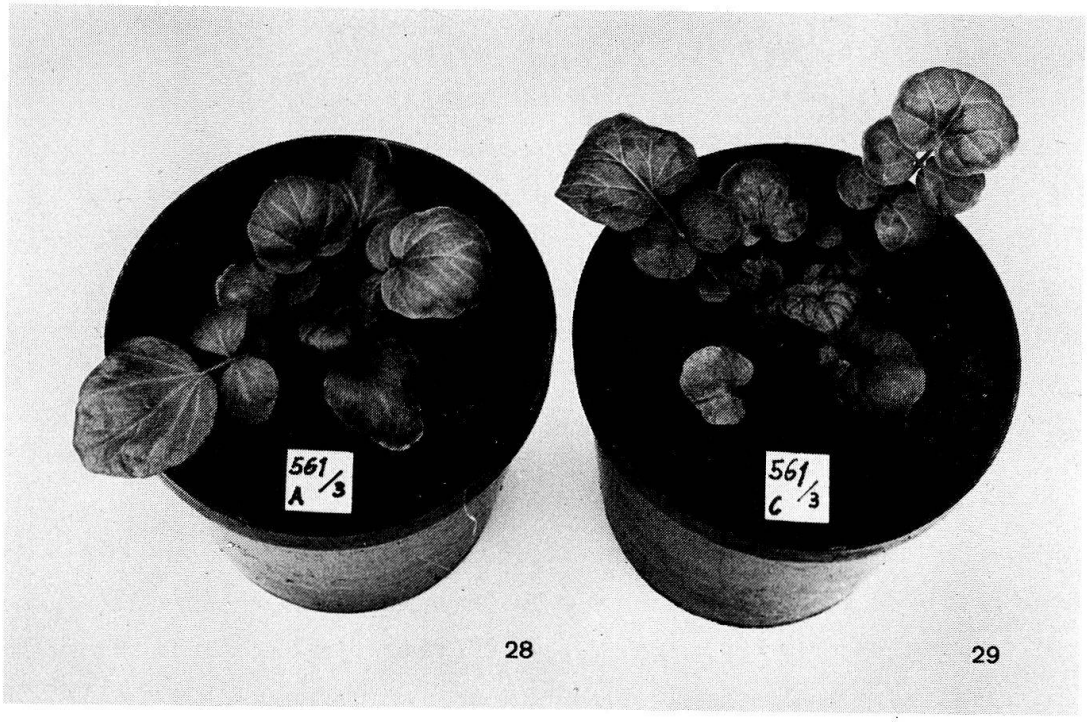
Note. Number of sound-looking seeds is given in brackets.

Table 19. *Cardamine nemorosa:* seed output after selfings and cross-pollinations

No.of plant	Total number of pollinated flowers - Series				Germination Series			
	A	B	C	D	A	B	C	D
70/2	8(-)	6(-)	6(31)	2(12)	-	-	41.2%	48.1%
70/8	12(-)	5(-)	9(21)	6(7)	-	-	54.0%	18.2%
70/13	9(-)	4(-)	12(47)	4(18)	-	-	38.6%	50.9%
440/1	11(-)**	4(-)	12(180)	3(40)	-	-	52.3%	51.7%
440/3	8(-)	2(-)	6(71)	4(36)	-	-	32.2%	30.1%
440/4	9(-)**	4(-)	18(216)	6(47)	-	-	54.4%	36.2%
440/5	14(6)	5(-)	9(104)	4(36)	-	-	30.6%	42.1%
440/9	12(21)	3(-)	8(47)	4(51)	-	-	28.3%	31.8%
450/9	8(6)	3(-)	4(36)	4(26)	1 seed	-	49.9%	38.4%
450/10	13(-)	8(1)	14(92)	10(79)	-	1 seed	48.6%	52.2%
450/11	22(-)	4(-)	9(59)	1(8)	-	-	56.4%	48.2%

** well-developed siliques containing no seeds
Note. Number of sound-looking seeds is given in brackets

C. Matthioli deserves a special mention. On the whole, 14 plants belonging to two ecological races were tested (Table 14). No seeds at all were developed from selfings in the plants originating from wet stations in northern Italy. On the other hand, the race growing in fertilized meadows in the Piedmont proved to be partly self-fertile. The five tested plants yielded seeds; however, their germination was highly variable(2.9% to 22.4% ,Table 14). The young plants raised from selfings were somewhat inferior towards the control material at very early stages of their deve - lopment, but in rather a short time no difference could be discerned (Figs 28, 29).



Figs 28, 29. 14 days old plants of *Cardamine Matthioli*.
28. Plant obtained from selfings
29. Plant obtained from cross-pollination, ca. 3/4 natural size.

The control cross-pollinations resulted in rather a good seed output. However, the germination was rather low, its average value being about 54%. It should be noted that the highest germination ratio was revealed in the interracial crosses within *C. Matthioli* (82.2%, Table 15).

The evaluation of results obtained on *C. udicola* is rather difficult for only the plants from a single population in Ticino were used in the

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, interpopulational 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