The hybridization of some *Rosa* species of different levels of ploidy

Hybridizace některých druhů rodu *Rosa* s různou ploidií

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In the present paper 69 types of crossings of the species of the genus *Rosa* are described. The species differed in ploidy level and were of normal and irregular meiosis. The possibility of facile hybridization between dissimilar species belonging to different sections of the genus *Rosa* was tested. Viability of hybrids and, at the same time, genetical factors of considerable variability in the whole genus *Rosa* are discussed.

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Taxonomic relationships and probable evolutionary trends within the polymorphic genus *Rosa* cannot be adequately clarified by traditional morphological approaches. Facile crossing even between dissimilar species belonging to different sections of the genus appears as one of the most important factors in the variability of this group. Thus hybridization experiments are required in order to examine the genetic circumstances resulting in viable hybrids.

RATSEK, YARNELL et FLORY (1939, 1941) pioneered the study of crossing between diploid species and of diploid with polyploid species. They evaluated the results both according to their taxonomic position within various sections of the genus and according to the chromosome number of the participant parent shrubs. They concluded that intrasectional crossings were more successful than those between species of different sections. The *Caninae* and *Gallicanae* species were more productive as maternal plants, whilst the *Carolinae* and *Cinnamomeae* species served better as pollinators.

FAGERLIND's hybridization experiments (1944a, b; 1945a, b; 1946; 1948; 1951) included crossings not only of the *Caninae* species with species of normal meiosis from other sections, but even with the species from the same section. Generalizing his experience, after many years of work, he concluded that all crossings outside the *Caninae* section were possible when species of the same level of ploidy were used. Crossings with a *Caninae* species as one of the components was the most successful. The *Caninae* species, when used as pollinators, behaved as diploid species because their pollen possessed seven chromosomes (irregular meiosis or balanced heterogramy in the sense of TÄCKHOLM 1922) and thus could be readily crossed with diploid species of the other sections. Crossings with tetraploid species succeeded only when *Caninae* species served as the maternal plants. Crossings with species possessing a higher level of ploidy were only partly compatible. Individual selection played a more important role in the *Caninae* section than in other sections.

Tab. 1. — List of species used in the experiments

R. *andegavensis* BAST. — 2n = 35, *Caninae* DC.
    [= *R. canina* L. var. *andegavensis* (Bast.) DESP., var. *grandidentata* Desp., var. *glandulifera* WOODS.]
R. *agrestis* SAVI — 2n = 35, *Caninae* DC.
R. *arvensis* HUDS. — 2n = 14, *Syntylae* DC.
    (*R. repens* SCOP., R. *silvestris* HERRM.)
R. *canina* L. — 2n = 35, *Caninae* DC.
    [incl. var. *lutetiana* (LÉM.) BAK., var. *dumalis* BAKER non BECHSTEIN, *R. falens* DÉS.,
      cv. *inermis*,, etc.]
R. *corymbifera* BORKH. — 2n = 35, *Caninae* DC.
    (*R. dumetorum* THUILL., R. *platyphylla* RAU)
R. *elliptica* TAUSCH — 2n = 35, *Caninae* DC.
    (= *R. graveolens* GREN., R. *inodora* BOULANG. part. non FRIES)
R. *filipes* REHDER et WILSON — 2n = 14, *Synstylae* DC.
R. *gallica* L. — 2n = 28, *Gallicanae* DC.
R. *jundzillii* BESS — 2n = 42, *Jundzilliae* CRÉP.
    (*R. trachyphylla* RAU, *R.marginata* auct. non WALLR.)
R. *majalis* HERRM. — 2n = 28, 2n = 14, *Cinnamomeae* DC.
    (= *R. cinnamomea* L.)
R. *multiflora* THUNBG. — 2n = 14, *Synstylae* DC.
    (*R = thunbergii* TRATT.)
R. *pendulina* L. — 2n = 28, *Cinnamomeae* DC.
    (= *R. alpina* L.)
R. *pomifera* HERRM. — 2n = 28, *Caninae* DC.
    (= *R. villosa* L. part.)
R. *pimpinellifolia* L. — 2n = 28, *Pimpinellifoliae* DC.
    (= *R. spinosissima* L.)
R. *pycnacantha* BORB. — 2n = 35, *Caninae* DC.
R. × *reversa* WALDST. et KIT. — 2n = 28, *Cinnamomeae* DC.
R. *rubiginosa* L. — 2n = 35, *Caninae* DC.
    (= *R. eglanteria* L., nom. ambig.)
R. *rugosa* THUNBG. — 2n = 14, *Cinnamomeae* DC.
R. *sherardii* DAVIES — 2n = 35, *Caninae* DC.
    (= *R. omissa* DÉS., R. *submollis* LEG.)
R. *subcollina* (CHR.) DALLA TORRE et SAR. — 2n = 35, *Caninae* DC.
    (= *R. incana* KIT., certe part.)
R. *sweginzowii* KOEHNE — 2n = 42, *Cinnamomeae* DC.
R. *tomentosa* SM. — 2n = 35, *Caninae* DC.
    (= *R. eutomentosa* SCHALOW)
R. *vosagiaca* DESP. — 2n = 35, *Caninae* DC.
    (= *R. glauca* VILL. non POURR., R. *dumalis* BECHST. part.)
R. *zalana* VIESB. — 2n = 35, *Caninae* DC.

JIČÍNSKÁ (1977) dealt with similar problems; i.e. origin of natural hybrids, heredity of morphological features in F_1 generation, and hybridizability at different ploidy level. Hybridization experiments were carried out with roses possessing (1) both the same and different number of chromosomes, and

Tab. 2. — Scheme of crossings

	2n	4n	5n	6n
2n	×	×	×	—
4n	—	×	×	×
5n	×	×	×	×
6n	—	×	×	—

Crossings marked — were not performed

Tab. 3. — Crossings of species with normal meiosis 2n × 2n

No.	Species	C	B	H	%H/B	A	S	%S/A
1	R. arvensis × R. rugosa	3	82	1	1.2	8	0	0
2	R. arvensis × R. multiflora	1	24	0	0	0	0	0
3	R. arvensis × R. filipes	1	25	2	8.0	7	0	0
4	R. rugosa × R. arvensis	1	23	0	0	0	0	0

(2) both normal and caninae-type of meiosis; these experiments were also intended to investigate plants with chromosome numbers of $2n = 21$, $2n = 35$ and $2n = 49$ in the F_1 generation.

MATERIALS AND METHODS

Plants used for the experiments belonged to the collection of live *Rosa* species of the Botanical Institute, Czechoslovak Academy of Sciences, Průhonice near Prague. All experimental plants were identified by I. Klášterský, a distinguished expert on the genus *Rosa*, who established the collection in 1963.

Table 1 contains the list of species used in the experiments, together with their taxonomic evaluation, with synonyms, and respective chromosome numbers (after I. KLÁŠTERSKÁ and M. N. KONČALOVÁ in op. div.).

In eralier papers (JIČÍNSKÁ 1975; 1976a, b) the methods of emasculation and pollination have already been described.

Tab. 4. — Crossings of species with normal meiosis 2n × 4n

No.	Species	C	B	H	%H/B	A	S	%S/A
5	R. majalis × R. pimpinellifolia	2	60	33	55.0	667	38	5.6
6	R. arvensis × R. pimpinellifolia	1	27	0	0	0	0	0
7	R. arvensis × R. gallica	1	47	5	10.6	21	1	4.8
8	R. arvensis × R. reversa	1	29	0	0	0	0	0
9	R. arvensis × R. majalis	1	35	0	0	0	0	0
10	R. rugosa × R. pimpinellifolia	1	25	4	16.0	279	14	5.0
11	R. rugosa × R. majalis	1	29	0	0	0	0	0

RESULT AND DISCUSSION

Generalized schemes of crossings, arranged according to the ploidy of species, are given in Table 2 where diploid species have the symbol of 2n, tetraploid species 4n, etc. The basic chromosome number of the *Rosa* genus is of course x = 7.

Detailed descriptions of crossings are presented in Tables 3—13. Types of crossings are listed according to the type of meiosis: species of normal

Tab. 5. — Crossings of species with normal meiosis 4n × 4n

No.	Species	C	B	H	%H/B	A	S	%S/A
12	R. gallica × R. pimpinellifolia	1	43	26	60.5	112	1	0.9
13	R. pendulina × R. pimpinellifolia	4	108	19	17.6	192	7	3.7
14	R. pendulina × R. reversa	1	26	8	30.8	133	19	14.3
15	R. pimpinellifolia × R. pendulina	4	80	35	43.8	318	18	5.7
16	R. pimpinellifolia × R. reversa	1	21	16	76.2	173	55	31.8
17	R. reversa × R. pendulina	3	65	22	33.9	127	6	4.7
18	R. reversa × R. pimpinellifolia	2	46	15	32.6	70	3	4.3

Tab. 6. — Crossings of species with irregular meiosis 5n × 4n (19), 5n × 5n (20, 21),
5n × 6n (22), 6n × 5n (23, 24, 25)

No.	Species	C	B	H	%H/B	A	S	%S/A
19	*R. zalana* × *R. pomifera*	1	15	7	46.7	85	58	68.2
20	*R. zalana* × *R. canina*	1	11	2	18.2	10	7	70.0
21	*R. corymbifera* × *R. agrestis*	1	21	12	57.1	26	17	65.4
22	*R. canina* × *R. jundzillii*	1	29	16	55.2	196	48	24.5
23	*R. jundzillii* × *R. canina*	1	20	0	0	0	0	0
24	*R. jundzillii* × *R. zalana*	1	25	20	80.0	409	53	13.0
25	*R. jundzillii* × *R. subcollina*	1	26	17	65.4	307	88	28.7

meiosis, as well as species of irregular meiosis, paternal plants of normal
meiosis and maternal plants of irregular meiosis, and vice versa. Each table
provides the following information: type of crossing (species), number of
maternal plants used for crossing (C), number of pollinated buds (B), num-
ber and percentage of ripened hips (H, %H/B), number of achenes (A),
number and percentage of grown seedlings (S, %S/A).

Tab. 7. — Crossings of species with normal meiosis with species with irregular meiosis 2n × 5n

No.	Species	C	B	H	%H/B	A	S	%S/A
26	*R. arvensis* × *R. canina*	1	35	1	2.9	10	2	20.0
27	*R. arvensis* × *R. corymbifera*	1	32	0	0	0	0	0
28	*R. arvensis* × *R. elliptica*	1	29	0	0	0	0	0
29	*R. arvensis* × *R. rubiginosa*	1	36	0	0	0	0	0
30	*R. arvensis* × *R. vosagiaca*	2	33	0	0	0	0	0
31	*R. arvensis* × *R. tomentosa*	1	27	0	0	0	0	0
32	*R. arvensis* × *R. zalana*	2	54	0	0	0	0	0
33	*R. rugosa* × *R. zalana*	1	14	0	0	0	0	0
34	*R. rugosa* × *R. canina*	1	13	0	0	0	0	0

a) Crossings of species of normal meiosis (Table 3—5)

Diploid and tetraploid species were crossed in combinations of the 2n × 2n,
2n × 4n and 4n × 4n types. Crossings of species of normal meiosis of the
2n × 2n and 2n × 4n types were, except in three 2n × 4n cases (*R. majalis*
× *R. pimpinellifolia*, *R. arvensis* × *R. gallica*, *R. rugosa* × *R. pimpinelli-
folia*), not successful — an unexpected result deserving further examination.
Nearly all of these crossings had *R. arvensis* and *R. rugosa* as the maternal
plant. However, in previous works (RATSEK, YARNELL et FLORY 1939, 1941;
FAGERLIND 1951) all crossings of the 2n × 4n type were described as viable

Tab. 8. — Crossings of species with normal meiosis with species with irregular meiosis
4n × 4n (35), 4n × 5n (36), 4n × 6n (37, 38)

No.	Species	C	B	H	%H/B	A	S	%S/A
35	*R. pendulina* × *R. pomifera*	1	16	0	0	0	0	0
36	*R. gallica* × *R. canina*	2	33	0	0	0	0	0
37	*R. gallica* × *R. jundzillii*	1	34	0	0	0	0	0
38	*R. gallica* × *R. zalana*	1	24	0	0	0	0	0

Tab. 9. — Crossings of species with irregular meiosis with species with normal meiosis 5n × 2n

No.	Species	C	B	H	%H/B	A	S	%S/A
39	R. rubiginosa × R. arvensis	1	23	11	47.8	81	36	44.4
40	R. canina × R. rugosa	1	28	8	28.6	127	19	15.0
41	R. pycnacantha × R. rugosa	1	17	5	29.4	254	30	11.8
42	R. rubiginosa × R. rugosa	1	27	14	51.9	221	62	28.0
43	R. sherardii × R. rugosa	1	17	7	41.2	65	4	6.2
44	R. zalana × R. rugosa	1	20	12	60.0	255	31	12.2

in this type of experiment. However, *R. arvensis* was not taken into account. Two species from the *Cinnamomeae* were crossed with *R. pimpinellifolia*, giving 55 and 16 % success. Crossings between the two *Cinnamomeae* species were not successful. In all positive cases seed viability was about 5 %, which might have been influenced by their proposed triploid character. All 4n × 4n crossings were successful — from nearly 18 to 76 %; viability of seeds varied from 4 to 32 %; in the case of *R. gallica* × *R. pimpinellifolia* seed viability was only 1 %.

FAGERLIND (1951), however, stated that all crossings of the 2n × 2n, 4n × 4n and 6n × 6n types outside the *Caninae* section were possible, and all 2n × 4n combinations gave mature plants. Seed viability varied from 0 to 100 %, with differences in individual plants.

b) Crossings of species of irregular meiosis (Table 6)

All crossings of the species of irregular meiosis within the *Caninae* section succeeded, as well as crossings of the *Caninae* species with *R. jundzillii* (sect. *Jundzilliae*), except that of *R. jundzillii* × *R. canina*. Percentages of successful crossings varied from 20 % for *R. zalana* × *R. canina* to 80 % for *R. jundzillii* × *R. zalana*. Seed viability was between 65–70 % for crossings within the *Caninae* section, and 13–29 % for crossings involving *R. jundzillii*. FAGERLIND (1951) obtained similar results showing that crossings with the participation of *Caninae* species (4n, 5n, 6n) gave the most successful results. The reason for this compatibility can be explained in terms of variability of individual plants in the *Caninae* species.

c) Crossings of species of normal meiosis with species of irregular meiosis (Tables 7—8)

Crossings of the 2n × 5n type totally failed except that of *R. arvensis* × *R. canina* with only 3 % success, but giving seeds of relatively high viability (20 %). Crossing of the 4n × 4n, 4n × 5n and 4n × 6n types were also not successful. Most of the crossings were performed with *R. gallica*

Tab. 10. — Crossings of species with irregular meiosis with species with normal meiosis 4n × 4n (45, 46), 4n × 2n (47)

No.	Species	C	B	H	%H/B	A	S	%S/A
45	R. pomifera × R. pimpinellifolia	1	19	0	0	0	0	0
46	R. pomifera × R. pendulina	3	65	23	35.4	429	44	10.3
47	R. pomifera × R. majalis	1	32	0	0	0	0	0

Tab. 11. — Crossings of species with irregular meiosis with species with normal meiosis 5n × 4n

No.	Species	C	B	H	%H/B	A	S	%S/A
48	*R. canina* × *R. gallica*	1	15	0	0	0	0	0
49	*R. canina* × *R. pimpinellifolia*	1	69	45	65.2	677	9	1.3
50	*R. corymbifera* × *R. pimpinellifolia*	1	31	30	96.8	460	61	13.3
51	*R. elliptica* × *R. pimpinellifolia*	1	30	23	76.7	242	10	0.4
52	*R. rubiginosa* × *R. pimpinellifolia*	1	43	20	46.5	337	27	8.0
53	*R. tomentosa* × *R. pimpinellifolia*	1	22	18	81.8	78	4	5.1
54	*R. zalana* × *R. pimpinellifolia*	1	52	30	57.7	532	43	8.1
55	*R. canina* × *R. pendulina*	2	35	24	68.6	520	43	8.3
56	*R. corymbifera* × *R. pendulina*	2	47	27	57.5	352	96	27.3
57	*R. elliptica* × *R. pendulina*	1	17	12	70.6	163	6	3.7
58	*R. rubiginosa* × *R. pendulina*	1	13	4	30.8	59	15	25.4
59	*R. subcollina* × *R. pendulina*	1	19	16	84.2	158	8	5.1
60	*R. tomentosa* × *R. pendulina*	2	42	27	64.3	190	12	6.3
61	*R. zalana* × *R. pendulina*	3	60	33	55.0	813	63	7.8
62	*R. canina* × *R. majalis*	3	76	48	63.2	627	66	10.5
63	*R. elliptica* × *R. majalis*	1	38	28	73.7	304	37	12.2
64	*R. rubiginosa* × *R. majalis*	2	58	28	48.3	576	55	9.6
65	*R. zalana* × *R. majalis*	2	54	27	50.0	489	62	12.7

and *R. arvensis*, both species being inferior maternal plants in all crossings. The same went for both *R. rugosa* and *R. pendulina* which were, on the other hand, excellent pollinators in reciprocal crossings.

FAGERLIND (1951) stated that the *Caninae* species could be successfully crossed in both directions with diploid species, due to seven chromosomes in their pollen and thus acting as diploid species. Again, in these experiments Fagerlind did not use *R. arvensis*. Of course, selection of individual plants may additionally influence the results.

d) Crossings of species of irregular meiosis with species of normal meiosis (Table 9—13)

Crossings of the 5n × 2n type were successful in all cases. The percentage of successful crossings varied from 30 to 60 %, the viability of seeds being from 6 to 44 %. In one crossing *R. arvensis* was used as a pollinator, in the other five crossings *R. rugosa* was the paternal plant. Both species are highly fertile as pollinating plants: similar fertility was not found in the case of maternal plants, which confirmed the earlier results of RATSEK, YARNELL et FLORY (1941). These authors stated that the *Cinnamomeae* species performed better as paternal plants, while pentaploid species from the *Caninae* section were better as maternal plants.

Crossings of the 4n × 4n type were not successful, except in the case of *R. pomifera* × *R. pendulina*, where the success of the crossing was 35 %.

Tab. 12. — Crossings of species with irregular meiosis with species with normal meiosis 5n × 6n

No.	Species	C	B	H	%H/B	A	S	%S/A
66	*R. andegavensis* × *R. sweginzowii*	1	23	21	91.3	150	3	2.0
67	*R. pycnacantha* × *R. sweginzowii*	1	20	5	25.0	27	1	3.7
68	*R. rubiginosa* × *R. sweginzowii*	1	11	10	90.9	42	7	16.7

No.	Species	C	B	H	%H/B	A	S	%S/A
69	*R. jundzillii* × *R. gallica*	1	20	0	0	0	0	0

the viability of the seeds was 10 %. The main reason for failure of these crossings could be attributed to the relatively small number of buds treated in the first case, and dependence on individual selection of a particular specimen plant in the second case; in two failed cases, the same individual was used but the crossing of another individual of the same species with *R. pendulina* succeeded. Nevertheless, incompatible reaction might have appeared as well. Values of successful crossings varied from 25 to nearly 97 %; those of viability of seeds ranged between 2 and 44 %. *R. rugosa* and *R. arvensis* were successful as paternal plants to the extent of 30 to 60 %.

On the other hand, 5n × 4n crossings succeeded in all cases, except *R. canina* × *R. gallica*, which was probably caused by a low quality of pollen in *R. gallica* in the year of crossings. Values of successful crossings varied from 50 to 97 %, those of viability of seeds were rather low — 0.5 to 13 %; exceptionally *R. corymbifera* × *R. pendulina* and *R. rubiginosa* × *R. pendulina* showed higher viability of seeds, 27 and 25 %, respectively. Similarly, AGERLIND (1951) found that the *Caninae*, when used as maternal plants, could successfully be crossed with tetraploid species.

All crossings of the 5n × 6n type were successful. Values of the successful crossings varied from 25 to more than 90 %, those of viability of seeds varied from 2 to 17 %. The highest values were found when *R. rubiginosa* was used as the maternal plant, which was successful in crossings of the 5n × 2n and also with 5n × 4n types.

The last type of crossing, of the 6n × 4n type, was not successful. This may be attributed either to unfortunate individual selection and/or to lack of pollination. The hypothetical hybrid should posses 2n = 49 which suggests a lower viability. FAGERLIND (1951) considered all combinations with maternal plants posessing higher chromosome number than paternal plants as incompatible ones.

SUMMARY

Crossings of species of normal meiosis were less successful when *R. arvensis* and *R. rugosa* were used as maternal plants. Both species served much better as paternal plants. All 4n × 4n crossings succeeded but the viability of seeds was low. All crossings of the species of irregular meiosis were demonstratable; values of successful crossings were mostly high as well as values of viability of seeds. In crossings of these species, individual selection of plants plays an important role. Crossings of species of normal meiosis with species of irregular meiosis failed; in most of these negative cases *R. rugosa* or *R. arvensis* served as maternal plants, in the rest *R. gallica* and *R. pendulina* also participated as maternal plants. Crossings of species of irregular meiosis with species of normal meiosis succeeded, except in four cases. Percentage of hips obtained was mostly high, viability of seeds varied significantly. The *Caninae* and *Jundzilliae* species are in most cases better as seed producers, whilst the *Pimpinellifoliae*, *Cinnamomeae* and *Synstylae* species are preferred as pollinators. In certain types of combination it may be either due to incompatibility or due to lower fertility of the pollen of the paternal plants.

SOUHRN

Křížení druhů rodu *Rosa* s normální meiozí byla méně úspěšná při použití druhů *R. arvensis* a *R. rugosa* jako mateřských rostlin. Oba druhy však sloužily mnohem lépe jako otcovské rostliny. Všechna křížení typu 4n × 4n byla úspěšná, ale vitalita semen byla nízká. Všechna křížení

druhů s nepravidelnou meiozí byla proveditelná; procento úspěšných křížení bylo většinou vysoké, stejně jako vitalita semen. Při křížení těchto druhů hraje velkou roli individuální výběr jedinců. Křížení druhů s normální meiozí s druhy s nepravidelnou meiozí se nepodařila. Ve většině těchto případů byly jako mateřské rostliny použity *R. rugosa* nebo *R. arvensis*, ve zbývajících pak *R. gallica* a *R. pendulina*. Křížení druhů s nepravidelnou meiozí s druhy s pravidelnou meiozí byla úspěšná kromě čtyř případů. Procento získaných šípků bylo vysoké, vitalita semen značně kolísala. Ve většině případů můžeme druhy ze sekcí *Caninae* a *Jundzilliae* považovat za lepší jako semenné rostliny, zatímco druhům ze sekcí *Pimpinellifoliae*, *Cinnamomeae* a *Synstylae* by měla být dána přednost jako rostlinám otcovským, což může také být v některých případech způsobeno jak inkompatibilitní reakcí, tak nižší fertilitou pylu otcovských druhů.

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