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Selffertilization in *Campanula rotundifolia* L. s. l. group

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Abstract

Artificial selfpollination of six taxa of *C. rotundifolia* L. group was perfomed. More than 60% of the tetraploid plants and diploid *C. rotundifolia* s. str. representatives set seeds which germinated in some 42—76%. The seed setting in *C. serrata* was a little lower and the germination was very poor (0.07%). Only 18% of *C. cochleariifolia* plants yielded seeds after selfpollination. These seeds failed to germinate.

The selfed offspring was viable only in part. Some developmental disturbances were observed. A general tendency to reduction of height of stems and of the number of flowers per stem was also noted in successive selfed generations. A gradual decrease of pollen fertility was also observed. No tendency to gradual decrease of selfed seed fertility and germination was demonstrated.

The factors preventing selffertilization proved to be efficient in *C. cochleariifolia* and *C. serrata*, but it seems that in nature they are strong enough even at a tetraploid level.

INTRODUCTION

In earlier studies of the *Campanula rotundifolia* L.s.l. group, the opinion prevailed that *Campanula* representatives are allogamous plants which can, however, set seeds after selfpollination (Brogniart, 1839; Hegi, 1913). This view was not supported by the observation of Witasek (1902), who found that some plants of the *C. rotundifolia* group failed to set fruits when flowering in an insectfree room. Also contemporary authors consider the *C. rotundifolia* representatives as obligatorily allogamous (Gadella 1963, 1964, Podlech 1965, Kovanda 1970). Experimental evidence was provided by Gadella and Kovanda.

Their observations, however, are not in agreement with the data of the present author who succeeded in obtaining selfed seeds even in several successive generations.

MATERIAL AND METHODS

The experimental plants belong to six taxa of the *C. rotundifolia* group and represent two ploidy levels. *C. rotundifolia* L.s.str. (4x), *C. polymorpha* Witasek (4x), *C. scheuchzeri* Vill. (4x), *C. serrata* (Kit.) Hendrych (2x) and *C. cochleariifolia* Lam. (2x) originated from Poland. The plants of *C. rotundifolia* L.s.str. (2x) and *C. xylocarpa* Kovanda (2x) were derived from Czechoslovakia as they have sofar not been found in Poland. All plants were cultivated on an experimental plot in possibly uniform conditions. The selfed seeds were sown in a greenhouse, repotted and then transplanted on the plot. Selfpollination was effected under cellophane bags without castration. The pollen grains were derived from the same flower or from the younger ones of the same plant. Pollination was started when the tripartite stigmas were opened. Pollination was repeated every day until the stigma wilted. If the fertilization failed, the stigmas enlarged continuously, bending backwards so that they could reach the style hairs. However, the hairs were usually wilted at that time and fertilization could not be accomplished. In such cases the corolla gradually withres beginning from the top of the lobes. Sometimes only the style with enormous stigma persists.

In each taxon single plants originating from various habitats were pollinated with their own pollen grains. As a result the following s_1 generation consisted of several plants (varying in number from 1 to 21). All individual s_1 plants were selfpollinated to get as many as possible offsprings of successive selfed generations. This procedure was repeated in each selfed generation. Individual selfed progenies consisted of 1 to 10 lines which, however, did not differ greatly with the range of variation of morphological traits or fertility. Therefore, the data concerning the characteristics of individual lines were summarized and mean values were calculated as shown in tables 3—5.

Several characters were taken into account in the analysis of the selfed offspring as described in the author's earlier papers (Bielawska 1964, 1968). Beside the usual methods of plant analysis, the coefficient "W" was introduced (ratio of the average number of flowers per stem to the modal value of plant height).

RESULTS

Selffertilization of the experimental parental forms

The number of selfpollinated plants varied from 7 to 22 and the number of flowers from several dozen to several hundreds for the individual taxon. *C. xylocarpa* was exceptional in this respect as only one plant was available for examination. Table 1 shows the number of

Table 1

Ability of selffertilization in the *Campanula rotundifolia* L. group taxa

Ploidy level	Taxon	Number of selffertilized plants				Plants with germinating seeds	
		total	which setting seeds	which not setting seeds	plants setting seeds, %	number	%
4x	*C. rotundifolia* s. str. lowland	9	8	1	88.8	5[1])	100.0
	montane	7	4	3	57.1	4	100.0
	C. polymorpha	22	21	1	95.2	19[2])	95.0
	C. scheuchzeri	12	8	4	66.6	5[2])	71.4
2x	*C. rotundifolia* s. str.	14	12	2	85.7	6[3])	100.0
	C. serrata	9	5	4	55.5	4	80.0
	C. cochleariifolia	11	2	9	18.1	0	0.0
	C. xylocarpa	1	1	0	100.0	1	100.0

[1]) seeds of three plants not sown
[2]) seeds of one plant not sown
[3]) seeds of six plants not sown

plants in each taxon which set seeds after artificial selfpollination and which failed to do so, as well as the percentage of plants whose seeds germinated. It can be seen that more than 60% of tetraploid plants and diploid *C. rotundifolia* s.str. representatives succeeded in seed setting. In other diploid forms the percentage of fertile plants after selfpollination was considerably lower.

The attempts of obtaining seeds were repeated many times both in successive years of vegetation and in different summer months. The plants were considered as selffertile, irrespective of how many fruits and seeds they set. The seeds were often shrunken or empty. As indicated in table 1, in as many as 95—100% *C. rotundifolia* s.str. (4x and 2x) as well as in *C. polymorpha* plants yielded seeds after selfpollination and the seeds were capable of germination. Germination of selfed seeds in *C. scheuchzeri* and diploid *C. serrata* was rather poor. The seeds of every plant of *C. cochleariifolia* deriving from artificial selfpollination completely failed to germinate.

As seen from table 2, the number of seeds set per capsule after selfpollination was lower than that obtained after free pollination.

In tetraploid taxa seeds resulting from selffertilization germinated in some 42—76%. The level of seed germination in the diploid *C. rotundifolia* s.str. was nearly the same. These results do not differ greatly from those obtained for two intercrossed lowland representatives of

Table 2

Pollen and seed fertility in the *Campanula rotundifolia* L. group taxa

Ploidy level	Taxon	Mean number of seeds set per capsule		Selfed seeds germination, %
		from free pollination	from selfpollination	
4x	*C. rotundifolia* s. str. lowland	112.0(64.1—186.8)	3.4(0.5 —11.0)	46.3 (30.0 — 68.6)
	montane	136.3		76.6 (20.0 —100.0)
	C. polymorpha	143.1(55.6—234.8)	10.0(0.5 —40.0)	42.8 (0.0 — 79.0)
	C. scheuchzeri	169.7(111.4—259.2)	2.7(0.7 — 4.7)	55.0 (20.0 —100.0)
2x	*C. rotundifolia* s. str.	149.2(113.0—186.0)	12.6(15.4 —33.0)	39.2 (23.8 —68.0)
	C. serrata	98.0(39.6—176.1)	13.8(0.07—39.7)	0.07(0.04—75.0)
	C. cochleariifolia	215.6	0.4(0.13— 0.6)	0.0
	C. xylocarpa	121.8	0.5	33.3

Table 3

Some characters, and pollen and seed fertility of parental forms and their selfed offsprings in lowland *Campanula rotundifolia* L. s. str. 4x

No. of plant or generation	Height of stems, cm	No. of flowers per stem	W	Corolla				Pollen fertility, %	Mean number of seeds set per capsule		Selfed seeds germination, %
				A	$\frac{A-B}{A}$	$\frac{A}{C}$	$\frac{K}{A}$		from free pollination	from self-pollination	
13	72(55—81)	47.2	0.65	18.1	0.36	1.69	0.34	98.3	138.8	1.88	68.5
S_1	42(33—55)	30.2	0.7	19.3	0.36	1.93	0.38	93.9	148.7	3.20	
S_2	23(10—32)	11.8	0.51	18.2	0.32	1.89	0.29	83.6	98.9	0.70	50.0
S_3	22	10.0	0.46	15.3	0.39	1.69	0.34	58.2	64.6	1.38	6.8
S_4	26(22—40)	14.2	0.53	17.4	0.34	1.77	0.38	80.5	111.0	2.87	50.0
S_5	28	3.0	0.1							1.50	33.0
14	40(35—50)	15.2	0.38	20.5	0.33	1.81	0.31	98.0	91.1	11.00	68.6
S_1	28(20—40)	12.2	0.43	19.5	0.35	1.92	0.36	81.1	58.0		
S_2	18(12—27)	6.5	0.36	19.3	0.32	1.85	0.35	83.8	105.7		40.4
S_3				19.9	0.32	1.93	0.32	86.6			
46	35(26—40)	13.1	0.37	20.3	0.33	1.75	0.27	98.9	78.1	1.40	38.6
S_1	28(21—38)	8.7	0.31	18.5	0.30	1.98	0.36	90.4	60.9	2.20	25.0
S_2	15	3.8	0.25	19.2	0.27	2.27	0.27	90.1	94.4		4.0
S_3	14	1.8	0.12	16.1	0.30	1.83	0.29	96.5			
16	60(50—70)	28.5	0.47	21.2	0.31	2.00	0.27	88.5	64.1		30.0
S_1	60(50—70)	33.2	0.55	18.0	0.37	1.67	0.25	63.5	63.6		84.6
S_2	48(40—54)	29.2	0.61	20.1	0.33	1.90	0.37	77.6	160.4	4.10	73.8
S_3	49(40—60)	28.0	0.56	19.6	0.36	1.88	0.32	82.6	98.1	2.90	46.6
S_4								56.1	67.0	1.50	52.3
S_5								46.3	62.6	0.40	
S_6								58.1[1])	70.4[1])		
17	44(29—63)	29.6	0.67	19.1	0.32	1.91	0.30	49.8	71.2		40.0
S_1	41(23—56)	31.7	0.75	19.4	0.32	1.95	0.28	71.9	129.7	3.56	32.0
S_2	29(23—35)	18.6	0.64	19.6	0.34	2.04	0.35	64.9	56.1	33.00	100.0

[1]) One plant was sterile

C. rotundifolia s.str. and other intercrossed tetraploid taxa (Bielawska 1968, 1969, 1972). *C. serrata* set relatively numerous seeds from selfpollination, but their germination was very poor (0.07%). In one case germination reached 75% but this refers to four seeds only and two of the three seedlings died in an early stage. In general, seed setting in this taxon was highly unbalanced and inhibited at various stages of development. *C. cochleariifolia* set seeds after selfpollination only occasionally and these did not germinate at all. From *C. xylocarpa* only nine seeds and three seedlings were obtained.

Selfed progeny

A considerable number of selfed progeny died in the early seedling stage. With some exceptions the growth of plants which survived was rather poor. Some of them suffered from chlorosis in the early stage of development or during longer time. Some plants were delayed in stem shooting. Plants which became strong enough, were planted out and cultivated on the experimental plot in possibly the same conditions as their parental forms. Analysis of morphological traits was performed only in the selfed progeny of *C. rotundifolia* s.str. (4x) and *C. polymorpha* as they were numerous enough to demonstrate a representative range of variation. The selfed offspring exhibits a general tendency to reduction of the height of stems and the number of flowers per stem in successive generations. The other tendency was to maintain a similar value of the "W" ratio in all selfed progenies bred. The ratio was reduced only infrequently, especially in the case of very weak plants. The flowers were, however, not observed to grow smaller. Tables 3—5 demonstrate some chosen examples of these regularities. Two s_1 representatives of tetraploid *C. rotundifolia* s.str. are shown in the preceeding paper (Bielawska 1964, figs 2 and 7).

Pollen fertility

In all diploid and tetraploid taxa under study the level of pollen fertility of s_1 was the same or approximated that of the parental plants. In successive selfed generations usually the tendency to a gradual decrease of pollen fertility was noted (tables 3—5). The most striking symptom of pollen sterility was the reduction in the number of pollen grains. Sometimes only five narrow bands of pollen grains could be observed on the style as they reflect five splittings of the stamina.

Seed fertility and germination

The number of seeds set per capsule after artificial selfpollination was as a rule much lower than after free pollination. In most cases the experimental plants develop only a low percentage of seeds as compared

Table 4

Some characters, and pollen and seed fertility of parental forms and their selfed offsprings in montane *Campanula rotundifolia* L. s. str. 4x

No. of plant or generation	Height of stems, cm	No. of flowers per stem	W	Corolla				Pollen fertility, %	Mean number of seeds set per capsule		Selfed seeds germination, %
				A	$\frac{A-B}{A}$	$\frac{A}{C}$	$\frac{K}{A}$		from free pollination	from self-pollination	
3	26(20—30)	12.8	0.49	18.8	0.34	1.90	0.33	100.0			100.0
S_1	25(15—38)	18.2	0.73	17.8	0.31	1.92	0.24	89.9	44.6		61.1
S_2	22(16—35)	12.8	0.59	17.8	0.35	1.95	0.35	80.0	75.1		12.4
S_3	15	6.6	0.42	16.8	0.36	1.93	0.37	86.0	51.1	4.5	
4	29(24—32)	8.8	0.35	22.7	0.33	1.73	0.43	97.7	136.3		90.0
S_1	20(10—35)	9.2	0.46	19.5	0.31	1.89	0.32	97.6	88.3		37.0
S_2	22(12—30)	10.9	0.49	17.9	0.33	1.78	0.35	88.7	118.5		37.0
S_3	25(18—32)	16.3	0.65	16.9	0.34	1.83	0.37	93.3	134.9		18.6
S_4	24(18—38)	6.2	0.25	17.6	0.36	2.01	0.41	84.2	81.9		
S_5								78.9	68.9		
22	40(33—46)	20.6	0.51	23.9	0.35	1.95	0.64	97.7			20.0
S_1	28(24—33)	12.4	0.44	19.2	0.33	1.92	0.32	96.8	128.2	3.6	24.7
S_2	15(12—20)	8.3	0.53	17.4	0.32	1.78	0.27	65.5	111.3		
26	10			17.1	0.34	1.63	0.47	98.5			
S_1											10.0

Table 5

Some characters, and pollen and seed fertility of parental forms and their selfed offsprings in *Campanula polymorpha* Witasek 4x

No. of plant or generation	Height of stems, cm	No. of flowers per stem	W	Corolla				Pollen fertility, %	Mean number of seeds set per capsule		Selfed seeds germination, %
				A	A-B / A	A / C	K / A		from frre pollination	from self-pollination	
2	17(12—19)	10.0	0.58	24.7	0.33	2.15	0.40	98.9	200.0	40.0	13.3
S_1	10(9—11)	3.5	0.35	20.5	0.28	2.14	0.34	99.0			
6	31	6.5	0.20	27.1	0.31	2.09	0.38	97.7	234.8		60.0
S_1	24(20—30)	7.6	0.31	23.0	0.30	2.21	0.32	94.1	21.6		30.7
S_2	23(17—28)	9.1	0.40	19.8	0.32	2.09	0.34	90.6	129.5		10.2
S_3	23(14—35)	12.0	0.52	19.2	0.35	1.84	0.35	83.9	95.6	12.0	40.6
S_4	25(18—35)	28.3	1.15	18.5	0.37	1.81	0.40	79.1	83.4	6.2	10.5
S_5								86.7	109.8		
27	23(19—27)	5.8	0.25	18.1	0.35	1.63	0.40				60.0
S_1	15(10—20)	8.7	0.58	16.7	0.34	1.77	0.31	66.1			46.8
S_2	17(12—26)	6.1	0.34	19.2	0.33	2.02	0.35	84.4	148.0		5.5
S_3	17	7.8	0.45	24.8	0.27	2.62	0.33	99.4	110.2	0.8	0.0
44	27(22—30)	7.5	0.27	18.3	0.35	1.77	0.34	89.6			53.3
S_1	40	28.2	0.70	19.1	0.33	1.80	0.32	97.2	93.8		100.0
S_2	16(10—21)	5.6	0.35	20.4	0.32	1.99	0.37	88.4	110.6		50.0
S_3	33	7.6	0.23	20.2	0.31	2.20	0.37	82.0			
50	29(26—35)	17.4	0.60	19.1	0.34	1.80	0.32	99.4			60.0
S_1	17(14—21)	13.1	0.75	16.6	0.30	1.94	0.43	99.0			0.0
59	19(16—21)	16.2	0.85	20.5	0.36	1.72	0.44	99.2			64.0
S_1	17(10—28)	7.7	0.45	18.0	0.29	1.69	0.45	98.8			50.0
S_2	17(15—20)	5.3	0.31								
114	22(18—25)	8.0	0.36	19.0	0.36	1.85	0.33	98.5	138.2	4.2	47.3
S_1	32(25—42)	12.4	0.38	20.1	0.34	2.00	0.34	90.7	100.4	5.9	37.0
S_2								83.0	123.8	9.5	
S_3								96.7	108.8		

with the results of free pollination. This is true both for tetraploids and diploids. In successive selfed generations, however, a further decrease in seed number was not observed. Sometimes even a small increase of fertility was noted (tables 3—5, e.g. *C. rotundifolia* s.str. No. 17, *C. polymorpha* No. 114). Completely sterile plants were observed only sporadically.

As seen from tables 3—5, seed germination in successive selfed generation varied greatly, and in fact a clear tendency to its decrease was noted only in some progenies (*C. rotundifolia* s.str. Nos 16, 46, 3 and *C. polymorpha* No. 27). As a rule the seedlings in further selfed generations were much weaker and their viability was drastically reduced.

DISCUSSION

All the taxa of the *C. rotundifolia* L. group are allogamous. The flowers are markedly protandrous. Some hypotheses have been advanced concerning the mechanism of the postulated selfpollination process (H e g i 1913). However, as reported by some authors, the representatives of the *C. rotundifolia* group are considered to be uncapable of spontaneous selffertilization (W i t a s e k 1902; G a d e l l a 1963, 1964). This fact was confirmed also in the course of the present investigation.

Artificial selfpollination of the representatives of various taxa was attempted by G a d e l l a (1963, 1964) and K o v a n d a (1970). They did not, however, succeed in obtaining selfed seeds. These results are in contrast to the findings of the present author.

According to the present observations, the mean number of seeds set per capsule in selfpollination was as a rule much lower than that in free pollination. It is, therefore, possible that the discrepancy between these results and those reported by other authors are due to differences in the number of selfpollinated flowers. In the course of the present investigation, the number of flowers exposed to artificial selfpollination was as a rule several times higher than in the experiments of other authors. According to G a d e l l a (1964), in his study only several flowers were artificially selfpollinated in each taxon, e.g. *C. rotundifolia* s.str. 2x (19 flowers), 4x (13 flowers) and 6x (8 flowers). In the studies of K o v a n d a (1970) 6 flowers of *C. rotundifolia* s.str. and 10 flowers of *C. gentilis* Kovanda were the highest numbers. In the present study artificial selfpollination was repeated in some cases for many successive years. It seems that numerous pollinations highly increased the probability of obtaining seeds since with such a procedure flowers could be selected with some tendency to selfcompatibility. It cannot be excluded also that the ecotypes of Polish origin are not similar to the Czechoslovakian or other ones in respect to their selffertilization ability.

However, the representatives of diploid *C. rotundifolia* s.str. derived from Czechoslovakia were partly fertile in the present study but it is not known whether these plants were the same as those examined by Dr. K o v a n d a.

In the course of the present experiments two diploid taxa, *C. serrata* and *C. cochleariifolia*, turned out to be particularly selfsterile. Both are highly advanced in their evolution. On the other hand, the diploid *C. rotundifolia* s.str. and all the tetraploid taxa under investigation were reasonably selffertile. The majority of plants set a good amount of seeds after artificial selfpollination and the percentage of germination was rather high.

Tetraploid selfed plants after several generations of selffertilization developed some symptoms of weakness, their seed germination was reduced and a slight decrease of pollen fertility was observed. Only infrequent plants survived.

From the results of the present investigation conclusion can be drawn that diploid taxa are less capable of selffertilization than tetraploid ones. It, should, however, be borne in mind that the ability of tetraploid forms to selffertilization was only revealed in particular conditions.

There is no doubt that in natural habitats seed setting after selfpollination is hardly possible because of the free competition with foreign pollen. Moreover, even if such selfed progeny could be derived, these would be too weak to survive. Thus it seems that in nature the factors preventing selffertilization are strong enough even at a tetraploid level.

CONCLUSIONS

1. Artificial selfpollination of the representatives of six taxa of the *C. rotundifolia* L. group (*C. rotundifolia* L.s.str. 4x and 2x, *C. polymorpha* Witasek 4x, *C. scheuchzeri* Vill. 4x, *C. serrata* (Kit.) Hendrych 2x, *C. cochleariifolia* Lam. 2x and *C. xylocarpa* Kovanda 2x) was performed. The number of selfpollinated plants deriving from different habitats varied from 7 to 22 and the number of flowers from several dozen to several hundred for the individual taxon.

2. More than 60% of tetraploid plants and diploid *C. rotundifolia* s. str. representatives set selfed seeds, the percentage of selffertile plants in other diploid forms beeing lower.

3. The germination of the selfed seeds of some 95—100% selfpollinated plants in *C. rotundifolia* s.str. and *C. polymorpha* was noted. The percentage of plants in *C. scheuchzeri* and *C. serrata* with germinating seeds was a little lower.

4. The selfed seeds of tetraploid taxa and of diploid *C. rotundifolia*

s.str. germinated in some 42—76%. Germination was very poor in the case of *C. serrata* (0.07%) and failed completely in *C. cochleariifolia*.

5. The selfed progeny survived in part only. Some disturbances of growth and development were observed.

6. Analysis of successive selfed generations of *C. rotundifolia* s.str. (4x) and *C. polymorpha* demonstrated a general tendency to a reduction in the height of stems and in the number of flowers per stem and to the maintaining of a similar value of the "W" ratio.

7. The general tendency to a gradual decrease of pollen fertility was also noted. The reduction in the number of pollen grains was the most striking symptom of pollen sterility.

8. Though the amount of selfed seeds was much lower than after free pollination, the decrease in seed number was not observed in successive selfed generations. No clear tendency to decrease in seed germination was shown in successive selfed generations.

9. The two diploid taxa, *C. serrata* and *C. cochleariifolia*, proved to be particularly selfsterile. The diploid *C. rotundifolia* s.str. and all the tetraploid taxa were reasonably selffertile when artificially selfpollinated.

10. Selfed seed setting, however, and production of selfed plants is hardly possible in natural conditions.

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Samozapłodnienie w grupie Campanula rotundifolia L. s. l.

Streszczenie

Przeprowadzono sztuczne samozapylenie przedstawicieli sześciu taksonów grupy *C. rotundifolia* L.s.l.: *C. rotundifolia* L.s.str. (4x i 2x), *C. polymorpha* Witasek (4x), *C. scheuchzeri* Vill. (4x) *C. serrata* (Kit.) Hendrych (2x), *C. cochleariifolia* Lam (2x) i *C. xylocarpa* Kovanda (2x).

Otrzymano nasiona w przypadku 60% roślin tetraploidalnych i *C. rotundifolia* s.str. 2x, a rzadziej w przypadku *C. serrata* i *C. cochleariifolia*. Nasiona form tetraploidalnych i *C. rotundifolia* s.str. 2x kiełkowały w 42—76%, natomiast w przypadku diploidalnej *C. serrata* w 0,07%, a *C. cochleariifolia* nie wykiełkowały wcale.

Znaczna część potomstwa z samozapylenia ginęła we wczesnych stadiach rozwoju. Obserwowano zaburzenia rozwojowe. W kolejnych pokoleniach często malała żywotność roślin. Wystąpiła tendencja do zmniejszania się wysokości roślin i liczby kwiatów na pędzie przy zachowaniu zbliżonych wartości wzajemnego stosunku tych dwóch wielkości (W). Nie obserwowano zmniejszania się rozmiarów kwiatów. W kolejnych pokoleniach zwykle spadała płodność pyłku, a w pierwszym rzędzie zmniejszała się jego ilość. Nie obserwowano zmniejszania się liczby nasion na torebkę zawiązywanych po sztucznym samozapyleniu.

Uzyskanie nasion z samozapylenia w grupie powszechnie uważanej za obligatorycznie obcopylną zostało prawdopodobnie umożliwione dzięki przeprowadzeniu licznych zapyleń. W większym stopniu samosterylne okazały się taksony diploidalne (*C. serrata* i *C. cochleariifolia*), jednakże w naturze czynniki zapobiegające samozapłodnieniu działają skutecznie również na poziomie tetraploidalnym.