Further observations on spontaneous polyploidization in *Rumex* hybrids

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In previous publications a peculiar mechanism of polyploidization was described in hybrids between *R. thyrsiflorus* as one parental form and *R. acetosa* or *R. arifolius* as the other (Świetlińska 1960, 1963; Żuk 1963). In the cross *R. thyrsiflorus* (Puławy) $\times$ *R. acetosa* (Choroszcz) polyploid F_2 and F_3 generations were obtained. It was established that polyploid plants arose from the union of unreduced gametes produced by some F_1 and F_2 hybrids. The abolition of the second meiotic division was responsible for the formation of diploid gametes. As this phenomenon was only accidentally observed during the cytogenetic study of the *Rumex acetosa* group, the hybrid combination which gave the unexpected polyploids was only partially studied. It was therefore considered worthwhile to sow the rest of the hybrid seeds from the cross: ♀ 46 *R. thyrsiflorus* (Puławy) $\times$ ♂ *R. acetosa* (Choroszcz) and to raise further generations and backcrosses in order to follow more closely the inheritance of unreduced gametes formation.

The methods used were the same as described in previous publications.

CYTOLOGICAL EXAMINATION OF F_1 POPULATION

The F_1 population consisted of 99 plants — 11 male and 88 female. All plants were diploids: ♀ — $2X+12a$; ♂ — $X+2Y+12a$. Meiosis was investigated in male plants only. In two of the male plants (9 and 52) diads instead of tetrads were formed. Four plants (5, 12, 21, 24) produced only tetrads. In the remaining five (42, 65, 66, 80, 99) both diads and tetrads were formed.

In the course of microsporogenesis the picture of the first meiotic division was in general similar to that in parental plants. At diakinesis six bivalents and one trivalent Y-X-Y were observed. At MI univalents were sporadically visible. At AI in a small part of PMC chromosome bridges with acentric fragments, lagging chromosomes and bridges without

fragments could be seen. The disturbances observed did not interfere with normal partition of the chromosomes. At late AI the respective distribution of chromosomes was: $X+6a$ and $2Y+6a$.

In $F_1/9$ plant cytokinesis occurred immediately after the first division. The changes taking place in PMC's at this time are shown in Figs. 1—4. The cell plate was formed just after the completion of the first division (Fig. 1) or somewhat later (Fig. 4). Two daughter cells (diads) were formed. In the nuclei of diad chromosomes were visible as 7 or 8 contracted rods. In a later stage two chromatides of each chromosome were conjoined only by a common centric region (Fig. 5). Metacentric chromosomes X, Y and „v“ are visible as cross-like figures. The X chromosome in this stage is shown in Fig. 6. Nucleoli were still present and the nuclear membrane was preserved. As a consequence of some kind of endomitotic chromosome replication, the chromosome number in diads become doubled. Diads in resting stage after chromosome doubling are shown in Fig. 7. Sometimes two pollen grains held together until prophase of mitotic division (Fig. 8). Each PMC gave two microspores one with 14 ($2X+12a$) and another with 16 ($4Y+12a$) chromosomes. The metaphasal plate of pollen mitosis with 14 chromosomes is shown in Fig. 9. Pollen fertility in this plant was reduced to 62%.

In plant $F_1/65$ beside diads also tetrads were formed. Pollen grains derived from tetrads were normal with haploid chromosome number. Tetrads and diads were formed in the same anther more or less with the same frequency. It was observed that tetrads usually occupy the basal and diads the apical part of the anther. The just mentioned plant produced four types of gametes: haploid with chromosome number 7 or 8 and with doubled chromosome number 14 or 16. Pollen fertility was 67%.

In plant $F_1/5$ no disturbances in second meiotic division were observed and normal tetrads were formed. In spite of normal course of meiosis, the pollen fertility was highly reduced and reached only 52%.

Seed set in F_1 population was lower than in parental forms and relatively high proportion of seeds produced was malformed.

CYTOLOGICAL EXAMINATION OF F_2 POPULATIONS AND BACKCROSSES

In order to establish if unreduced gametes were formed also in megasporogenesis, many crosses were performed with different male and female plants. It was expected that cytological examination of the progeny (both F_2 and Bc) would show what types of gametes were formed in macrosporogenesis of a given female plant. The results of crossing are given in Table 1.

Table 1

Chromosome number in F_2 and backcross progenies from different F_1 plants

Cross		No. of seeds obtained	No. of plants obtained	Diploids	Triploids	Tetraploids
♀	♂					
$F_1 10 \times$	$F_1 9$	151	16	4	4	4
	$F_1 21$	293	8	8		
	<i>R. thyrs.</i> 8	100*	10**	10		
	<i>R. acet.</i> 10	100*	7	7		
$F_1 14 \times$	$F_1 21$	15	5	5		
	$F_1 24$	2	2	2		
	$F_1 42$	237	14	12	2	
	<i>R. thyrs.</i> 8	55	10**	10		
	<i>R. acet.</i> 9	100*	9	9		
$F_1 40 \times$	$F_1 5$	72	9	8	1	
	$F_1 9$	310	60	5		55
	$F_1 66$	87	15	14	1	
	$F_1 99$	269	8	8		
	<i>R. thyrs.</i> 8	100*	10**	10		
	<i>R. acet.</i> 7	100*	7	7		
$F_1 47 \times$	$F_1 24$	10	5	5		
	$F_1 42$	3	2	2		
	$F_1 52$	2	1	1		
	$F_1 80$	57	6	6		
$F_1 27 \times$	$F_1 65$	127	11	10		1
<i>R. thyrs.</i> 1 $\times$	$F_1 9$	27	2	2		
<i>R. thyrs.</i> 2 $\times$	$F_1 9$	150*	11	1	2	6
	$F_1 66$	74	13	13		
	$F_1 99$	100*	10**	9		1
<i>R. acet.</i> 1 $\times$	$F_1 5$	18	8	8		
„ 2 $\times$	$F_1 9$	100*	3		3	
„ 3 $\times$	$F_1 9$	100*	10	9	1	

* No of seeds sown.

** No of plants examined.

Somatic chromosome numbers were counted in 266 plants of F_2 and Bc. Of these 185 were diploids, 67 tetraploids and 14 triploids. The list of 17 different karyotypes is given below:

F_2 1/5 — ♀ 14(2X+1j+11i)	F_2 13/1 — ♀ 28(4X+2j+2v+20i)
13/12 — ♂ 15(X+2Y+1j+2v+1T+8i)	13/4 — ♂ 30(2X+4Y+2j+2v+2T+18i)
8/4 — ♀ 21(3X+2j+3T+13i)	15/11 — ♂ 30(2X+4Y+2j+22i)
13/7 — ♀ 21(3X+1j+2v+2T+13i)	
9/4 — ♀ 28(4X+2j+2v+2T+18i)	Bc 26/5 — ♀ 21(3X+2v+2T+14i)
9/5 — ♀ 28(4X+2j+1v+21i)	29/9 — ♀ 21(3X+1j+1v+16i)
9/6 — ♀ 28(4X+1j+2v+21i)	31/2 — ♀ 21(3X+1v+17i)
9/17 — ♀ 28(4X+2j+2v+20i)	34/9 — ♀ 21(3X+2j+2v+1T+13i)
9/18 — ♀ 28(4X+1j+1v+22i)	34/6 — ♀ 28(4X+2j+2v+2T+18i)

A diploid karyotype of F_2 1/5 is presented in Fig. 13. In the established karyotypes chromosomes „v“, „j“ and „T“ occurred singly in twos or threes as it was to be expected from the asymmetrical karyotype of F_1 generation: $2X$ (or $X+2Y$) $+1j+1v+10i$ (Świetlińska 1960). Identification of the „T“ type chromosome was most difficult, especially in paraffin preparations which were used in the case of F_1 plants. This may be the reason why „T“ type chromosomes have not been found in F_1 though they occurred in the parental population of *R. acetosa* (Świetlińska 1963).

From Table 1 it is evident that some combinations of diploid F_1 plants gave high proportion of polyploids in generation F_2 . In the cross ♀ $40 \times \sigma 9$ there were 55 tetraploids and only 5 diploids. It was established that gametes of the male plant $F_1/9$ were unreduced. The high proportion of tetraploids obtained suggests that unreduced gametes were also produced by the female plant $F_1/40$. Several tri- and tetraploids also occurred in the cross ♀ $10 \times \sigma 9$. Triploids were not frequent in all combinations, their viability was probably much lower or fertilization was preferential. In each case, beside tri- and tetraploids, normal diploids occurred. It is thus evident that female F_1 hybrids similarly as male ones produced unreduced gametes in different proportions.

The chromosome numbers found in backcrosses indicate that unreduced gametes were also produced by some female plants from parental population of *R. thyrsiflorus*. Cross ♀ *R. thyrsiflorus* $2 \times \sigma F_1/9$ yielded beside di- and triploids several tetraploids.

In F_2 generations there were 9 diploid and 8 tetraploid male plants. No intersexual plants were found. Among female plants, there were 7 triploids, 52 tetraploids and 133 diploids.

In two male diploids formation of diads was noted, in the remaining seven the course of meiosis was normal. Among tetraploids diads were found in two (9/15 and 9/13), and tetrads also in two (13/14 and 15/11) plants. In one plant (9/13) both diads and tetrads were formed. In two plants (9/1 and 9/32) there were serious disturbances in first and in second meiotic divisions and only abortive abnormal microspores were formed. In the latter, microsporogenesis was not studied.

In all tetraploids conjugation of chromosomes in first meiotic division was very hard to follow. Especially difficult was the observation of conjugation of sex chromosomes. Bi-, tri- and tetravalents were formed among autosomes. Also univalents were observed. The pictures of AI in most plants were regular.

In tetraploid 9/15 cytokinesis took place after first meiotic division and diads were formed. The behaviour of chromosomes in diads was like that in F_1 plants. Diads from this plant are shown in Fig. 10. Doubling of the chromosome number in diads led to the formation of

Fig. 1—8. Meiosis in PMC's of F_1 hybrid *R. thyrsoiflorus* $\times$ *R. acetosa* (plant No. 9). Fig. 1—4: PMC's after I meiotic division, note cell plate formation. Fig. 5: Two daughter cells (diads) with dividing chromosomes. Fig. 6: X chromosome in one of the daughter cells. Two chromatids are conjoined by a common centric region. Fig. 7: Diads in resting stage after doubling of chromosome number. Fig. 8: Prophase of pollen mitosis in unreduced pollen grains. Fig. 9: Metaphasal plate in unreduced pollen grain with 14 chromosomes. Approx. 2000 $\times$.

Fig. 10—12. Meiosis in PMC's of tetraploid F_2 hybrids *R. thyrsiflorus* $\times$ *R. acetosa*. Fig. 10: Diads in plant No. 9/15 with cytokinesis after I meiotic division. Fig. 11: Tetrads in plant No. 13/14 with normal meiosis. Fig. 12: PMC's of plant No. 9/1 with abnormalities in cell plate formation after I meiotic division (note the endomitotic duplication of chromosomes). Approx. 2000 $\times$.

Fig. 13—15. Root tips metaphases. Fig. 13: Diploid F_2 hybrid No. 1/5 — ♀ $2n=14$ ($2X+1j+11i$). Fig. 14: Aneuploid No. 18/9 from the progeny of triploid female plant — $2n=32(2X+4Y+2v+1T+23i)$. Fig. 15: Aneuploid No. 18/27 from the progeny of triploid female plant — ♀ $2n=37(3X+4Y+3j+26i)$. Approx. 2000 $\times$.

microspores with unreduced, tetraploid chromosome numbers. It was possible to establish the chromosome number in one plate of pollen mitosis as 28—30.

In tetraploid 13/14 regular stages of the second meiotic division were observed and tetrads were formed (Fig. 11). Chromosome number counted on two mitotic plates in pollen was 14 and 15.

Serious disturbances were observed in the course of meiosis of tetraploid 9/1. At A I numerous chromatin bridges, lagging bivalents and acentric fragments were present. Segregation of chromosomes was irregular and more than two nuclei were formed after A I. The telophase nuclei differed greatly in size and were frequently connected by chromatin bridges. After first division cytokinesis took place. Chromatin bridges connecting sister nuclei were visible also after cell walls formation. The behaviour of chromosomes in daughter cells was like that in diads nuclei. Typical pictures of chromatids conjoined only in centromeres were observed (Fig. 12). No typical second meiotic division was observed and microspores with varying number of chromosomes were produced.

As it was to be expected from cytological examination, the F_2 generation was very heterogeneous in respect to the types of gametes produced. Diploids produced haploid (7 or 8 chromosomes) or unreduced microspores with 14 or 16 chromosomes. Tetraploids formed reduced microspores with chromosome number about 15 or unreduced ones with about 30 chromosomes. In tetraploids in which A I was disturbed, microspores differed greatly in chromosome number and were mostly unviable.

In backcrosses all male plants were diploid. In one individual, beside tetrads diads were found, in the remaining eight the course of microsporogenesis was normal and tetrads were formed.

The pollen fertility of F_2 hybrids differed greatly. In seven diploids producing tetrads pollen fertility was 28,6—84,5% (average 64,1) and in two diploids producing diads — 33,2 and 65,5%. In two tetraploids with normal meiosis pollen fertility was relatively high — 75,1 and 77,0% and similarly in two tetraploids producing diads — 72,2 and 73,1%, respectively. In tetraploid 9/1 with abnormal microspores, pollen fertility was reduced to 45,0%.

In backcrosses all male plants were diploid. In eight plants with normal meiosis pollen fertility was 30,0—89,9 (average 70,1%) and in the plant producing partly diads — 73,3%.

Seed setting in diploid F_2 hybrids was lower than in the F_1 generation. Especially low was seed setting in tri-, and tetraploids. Only few seeds were obtained from particular polyploid plants, and usually almost all were abortive. Relatively many normal seeds were obtained

from the tetraploid female plant 9/6 after pollination with pollen from the male tetraploid 15/11 with normal meiosis.

CYTOLOGICAL EXAMINATION OF F_3 GENERATIONS

The F_3 polyploid generation as described in the previous publication (Świetlińska 1963) consisted of abnormal seedlings with distinct anomalies in leaves development. All plants died within several weeks after planting on experimental field. Their somatic chromosome number was higher than 30, probably as a result of further duplication of the chromosome number in gametes produced by parental F_2 plants. Another set of 52 seedlings was planted in hot-bed. During the first year their growth was very poor and many plants died. In the next year the survivors grew much better and six plants flowered. Of these, two were male, two female and two were intersexes with male, female and intersexual flowers as well. All plants were completely sterile and produced no pollen grains and only few completely malformed seeds.

Another F_3 generation was obtained from the cross between tetraploid F_2 plants: ♀ 9/6 × ♂ 15/11. It consisted of 15 plants which grew well and were highly vigorous. The chromosome number established for 13 plants was as follows:

$F_3/1 - 30(3X+3Y+24a)$	$F_3/10 - 31(3X+2Y+2j+3T+4v+17i)$
2 — 30(5XY+25a)	11 — 28(4X+3Y+21a)
3 — 29(3X+2Y+24a)	12 — 28(2X+3Y+23a)
4 — 29(3X+2Y+2j+2T+2v+18i)	13 — 30(2X+4Y+24a)
5 — 30(3X+3Y+24a)	14 — 32(4X+3Y+25a)
6 — 29(3X+2Y+24a)	15 — 29(4X+3Y+22a)
8 — 30(2X+4Y+24a)	

The chromosome numbers in all plants listed above are tetraploid or very close to tetraploid. Deviations from tetraploid chromosome number observed in F_2 are caused by haphazard irregular segregation of chromosomes. Only two plants (8 and 13) had the same chromosome complement as the tetraploid parental forms. Instead of 24 most plants contained 21 to 26 autosomes. The complement of sex chromosomes instead of $2X+4Y$ or $4X$, consisted often of $3X+3Y$, $3X+2Y$ or $4X+3Y$ chromosomes. The sex of F_3 plants could not be established since they did not flower in the first year. But the composition of sex chromosomes and autosomes suggests that they were probably mainly intersexes. The results described indicate that it is very difficult to obtain a stable tetraploid line in *Rumex*.

PROGENY OF A TRIPLOID FEMALE PLANT ($2n = 21$)

A triploid female plant from the backcross *R. thyrsoiflorus* × F_1 was pollinated by two diploid male plants, one producing normal and second

Table 2

Karyotypes, sex index, sex and pollen fertility in progeny of triploid female plant $2n = 21$ ($3X+18a$)

Plant	Karyotypes	Ratio X chromosomes: sets of autosomes	Sex	Pollen fertility
16/1	27 ($3X+1j+2v+21i$)	0.66	♂	0%
16/2	15 ($X+2Y+2v+10i$)	0.50	♂	93.6%
17/3	30 ($2X+4Y+24a$)	0.50	♂	42.9%
18/1	28 ($4X+24a$)	1.00	♀	
18/4	33 ($4X+2j+3v+24i$)	0.83	♀	
18/5	28 ($4X+24a$)	1.00	♀	
18/9	32 ($3X+2j+2v+25i$)	0.62	♀	
18/10	28 ($4X+1j+1v+22i$)	1.00	♀	
18/11	30 ($2X+4Y+24a$)	0.50	♂	87.4%
18/12	27 ($4X+4v+2i+2T+15i$)	1.04	♀	
18/13	30 ($4X+2Y+2j+2v+2T+18i$)	1.00	♀	
18/14	37 ($3X+4Y+30a$)	0.60	—	no flower shoots
18/16	28 ($4X+2j+2v+20i$)	1.00	♀	
18/18	24 ($4X+2j+1v+17i$)	1.20	♀	
18/19	32 ($2X+4Y+2j+2v+22i$)	0.46	—	no flower shoots
18/25	26 ($4X+2j+2v+18i$)	1.09	♀	
18/27	37 ($3X+4Y+3j+1v+26i$)	0.60	♂	0%
19/1	28 ($4X+1j+4v+19i$)	1.00	♀	
20/1	15 ($X+2Y+2j+2v+8i$)	0.50	♂	93.0%
20/7	15 ($2X+2v+2T+9i$)	0.92	♀	
21/2	22 ($2X+2Y+2v+16i$)	0.67	♂	0%

unreduced pollen grains. When normal pollen was used, only few fertile seeds were obtained and in progeny di- and aneuploids were found. In the case when unreduced pollen was used, many fertile seeds were obtained and progeny consisted of di-, tetra- and aneuploids. The whole cultivated progeny consisted of 20 ♀, 13 ♂, 8 ♀ and 7 plants which did not produce flower shoots at all. Chromosome numbers were established for 21 plants (Table 2). The karyotypes of the nonflowering plant 18/19— $2n = 32$ ($2X+4Y+2j+2v+22i$) and intersexual plant 18/27— $2n = 37$ ($3X+4Y+3j+1v+26i$) are shown in Figs 14 and 15 respectively. From the chromosome numbers established in the progeny, it is obvious that segregation of sex chromosomes and autosomes of the triploid female plant was not regular and resulted in production of gametes with wide

variation in chromosome number. The relatively high proportion of di- and tetraploids in the progeny was caused both by the preferential fertilization of gametes with a similar chromosome set and low viability of aneuploid zygotes. As seen from table 2 the sex expression of the plants listed is in accordance with their sex index. One exception was plant 16/1 which as regards to chromosome constitution should have been intersexual, and in spite of this produced only male flowers.

Variation of pollen fertility in male plants was wide ranging. In di- and tetraploids pollen fertility was from 42.9 to 93.6%. In male and intersexual aneuploids and one male triploid, degeneration of anthers or whole flowers was observed. Sometimes in anthers only a few sterile pollen grains were found. Fertility of female plants was usually very low but it was possible to obtain from some plants several seeds both from free and from controlled pollination.

DISCUSSION

The study of polyploidy in *Rumex* hybrids revealed the mechanism of unreduced gametes formation through abolition of the second meiotic division. As a result of this abnormality diads instead of tetrads were formed in hybrids.

The results from the previous and present publications concerning diads formation in *Rumex* hybrids are summarized in Table 3. The results obtained confirm our supposition that diads formation and abolishment of second meiotic division is genically determined. From Table 3 it is evident that this supposed factor (or factors) occurred in some natural populations of *R. thyrsiflorus*. The following facts lead to this conclusion. Plants forming diads were found only in hybrid involving *R. thyrsiflorus* as one of the parental forms. In hybrids between *R. acetosa* and *R. arifolius* this was never observed in the numerous crosses performed. The backcrosses with *R. thyrsiflorus* gave plants both forming diads and tetrads, whereas backcrosses with *R. acetosa* gave plants with tetrads only. One of the backcrosses *R. thyrsiflorus* ♀ × *F*₁ ♂ producing diads gave several tetraploids thus indicating that also female plants of *R. thyrsiflorus* produced unreduced gametes as it was observed in *F*₁ and *F*₂ hybrids.

In the cross *R. thyrsiflorus* (Puławy) × *R. acetosa* (Choroszcz) diads formation was observed in *F*₁, *F*₂ and backcrosses and in the cross *R. arifolius* (Krościenko) × *R. thyrsiflorus* (Nowy Dwór) only in the *F*₂ generation. The penetration of the abolition of second meiotic division varied greatly not only between crosses but also in successive hybrid generations. In *F*₁, *F*₂, *F*₃ and backcrosses some male plants produced almost

exclusively diads, some diads and tetrads and some only tetrads. Factors determining diads formation were transmitted to successive hybrid generations both by plants producing diads and those producing tetrads. It was also found that some F_2 tetraploids that arose from parental F_1 hybrids with only diads produced again normal tetrads. This suggests that abolition of the second meiotic division is determined by special combinations of the sets of genes. It seems also that external factors play some role in diads formation. Observations that diads are usually formed on the top, and tetrads at the bottom of the anther support this supposition.

Table 3

Diads and tetrads formation in *Rumex hybrids*

Generation Cross	F_1	F_2	F_3
<i>R. arifolius</i> (Krościenko) × <i>R. thyrsiflorus</i> (Nowy Dwór)	$2n = 14.15$ tetrads	$2n = 14.15$ { diads → tetrads →	$2n = 28.30$ $2n = 21.22$ $2n = 14.15$ -tetrads
<i>R. thyrsiflorus</i> (Puławy) ×	$2n = 14.15$ { diads → tetrads →	$2n = 14.15$ { diads → tetrads → $2n = 21$?	? $2n = 14.15$
<i>R. acetosa</i> (Choroszcz)		$2n = 28.30$ { diads → tetrads →	$2n < 30$ $2n < 30$ $2n = 28.30$

Backcrosses from the cross *R. thyrsiflorus* (Puławy) × *R. acetosa* (Choroszcz)

<i>R. thyrsiflorus</i> × F_1	$2n = 14.15$ { diads tetrads $2n = 21$? $2n = 28$?		
F_1 × <i>R. thyrsiflorus</i>	$2n = 14.15$ { diads tetrads		
<i>R. acetosa</i> × F_1	$2n = 14.15$ tetrads $2n = 21$?		
$(F_1 \times R. acetosa)$	$2n = 14.15$ tetrads		

There is no direct evidence that abolition of second meiotic division takes place in female plants but it may be deduced from the results of crossings. Cross $F_1 \text{ ♀ } 40 \times F_1 \text{ ♂ } 9$ yielded 50 tetraploids and only five diploids. This result suggests that in female plant $F_1/40$ a high proportion of unreduced gametes were produced and the second meiotic division was probably abortive.

Another mechanism of unreduced gametes formation in *Rumex* hybrids has been described by Żuk (1963), namely abortion of the first meiotic division and formation of restitution nucleus. Such a mechanism often induces polyploidization in many plant groups. Failure of first meiotic division in *Rumex* hybrids was observed as an exceptional event and in the neighbouring PMC's meiosis followed its regular course.

The mechanism of polyploidization through abolition of the second meiotic division and unreduced gametes formation is very rare in plants. This mechanism is of special interest because it results in polyploidization of almost the whole progeny from some specific combinations of parental plants. It is also interesting in connection with the mechanism of sex determination in *Rumex*. In tetraploid F_2 lines all plants were normal male or female and no intersexes occurred. This was not the case when unreduced gametes were formed as the result of abortion of the first meiotic division. In such instances, all gametes produced by male plants had the combination of autosomes and sex chromosomes $X+2Y+12a$ and in the progeny the polyploids were intersexual.

In the tetraploid F_2 population, the segregation of male plants with normal meiosis and with abolition of the II meiotic division was observed. By crossing tetraploid F_2 plants with normal meiosis it was possible to obtain a successive tetraploid generation (F_3). It is however, still doubtful whether there are any chances to obtain a true breeding tetraploid line because of the type of sex determination in *Rumex*. Segregation of chromosomes in tetraploids gave gametes with various combinations of autosomes and sex chromosomes, and the zygotes obtained had in many instances an intersexual sex index.

Many authors have found single tri- and tetraploid plants in natural populations of *R. acetosa* (Ono 1935; Yamamoto 1938; Löve 1942) but not one polyploid population was found in the *R. acetosa* group. The polyploid plants described in natural populations were probably formed as the result of abolition of the first meiotic division and were mostly sterile intersexes with karyotypes:

$$\begin{array}{l} \sigma^{\circ} \quad 3n = 22(2X+2Y+18a) \\ + \\ \sigma^{\circ} \quad 4n = 29(3X+2Y+24a) \\ + \\ \varphi \quad 3n = 21(3X+18a) \end{array}$$

It is obvious that such plants are eliminated in the competition with normal diploids.

The progeny of the triploid female plant from the backcross *R. thyrsiflorus* $\times F_1$ consisted mostly of aneuploid highly sterile plants. Many of them were intersexes or did not form flower shoots at all. So it seems that the only possibility (if any) to obtain a true breeding polyploid

line in *Rumex* is by crossing ♀ 28(4X+24a) × ♂ 30(2X+4Y+24a) tetraploid plants with normal meiosis. From the progeny, plants with the following segregation of sex chromosomes: ♀ 2X—2X and ♂ 2X—4Y should be selected for the subsequent crosses. Also plants that have lost some sex chromosomes or plants with new compound sex chromosomes would be suitable for the next crossing.

The mechanism of chromosome number doubling in gametes through abolition of the second meiotic division is interesting from the cytological point of view. The first meiotic division was quite regular but cytokinesis took place after A I like in *Monocotyledones*. Another interesting feature of the meiosis described was a kind of endomitotic duplication of the chromosome number in the nuclei of the diads. A similar mechanism of unreduced gametes formation in *Allium* was described by Levan (1936, 1937) where neither spindle formation in diads nor cytokinesis was observed. Gametes with unreduced chromosome number were formed and in the progeny polyploids were obtained. According to Levan the mechanism of "monokinetic meiosis" is not influenced by the structural properties of chromosomes but is genically controlled. The experimental data seems to indicate that the same type of mechanism of unreduced gametes formation operates in *Rumex* hybrids.

SUMMARY

The mechanism of unreduced gametes formation through abolition of the II meiotic division in *Rumex* hybrids is described. In F₁, F₂ and backcrosses of the hybrids *R. thyrsiflorus* × *R. acetosa*, almost exclusively unreduced gametes were produced by some male plants. Combinations of unreduced pollen and eggs gave tetraploid F₂ lines. In tetraploid F₂ generation, plants with normal meiosis and producing diads were found. Crossing of tetraploid F₂ plants with normal meiosis gave a tetraploid F₃ progeny. When F₂ plants producing diads were crossed in F₃ hypertetraploids were obtained. Evidence is presented that the mechanism of unreduced gametes formation through abolition of the second meiotic division is genically determined. The possibility of obtaining a true breeding tetraploid line in dioecious *Rumex* hybrids is discussed.

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*Dalsze obserwacje nad samorzutną poliploidalnością
u mieszańców Rumex*

Streszczenie

Opisano mechanizm powstawania niezredukowanych gamet u mieszańców między *Rumex thyrsiflorus* i *R. acetosa*. W mikrosporogenezie po pierwszym podziale mejotycznym powstawały diady. W jądrach diad obserwowano swego rodzaju endomitotyczny podział chromosomów. Z każdej diady powstawały dwa ziarna pyłku o niezredukowanej liczbie chromosomów. Potomstwo mieszańców wytwarzających niezredukowane gamety składało się z roślin poliploidalnych. Czynniki warunkujące powstawanie niezredukowanych gamet poprzez zniesienie drugiego podziału mejotycznego przekazywane były do kolejnych pokoleń mieszańców i krzyżówek wstecznych.