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Cytogenetic relationships among *Rumex acetosa*, *Rumex arifolius* and *Rumex thyrsiflorus*

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INTRODUCTION

The cytogenetic investigation on the three *Rumex* species, *R acetosa*, *R. arifolius* and *R. thyrsiflorus*, was begun in 1955 with the aim to establish the mutual relations of these three taxa. Being morphologically and cytologically closely related the three taxa have sometimes been treated as subspecies of the species *R. acetosa* L. but this systematic approach has not found universal acceptance. In view of the different opinions a research based on cytogenetic techniques has been thought necessary to define what should be the correct classification of the three taxa.

All the three taxa of the investigation are common in Poland, *R. acetosa* and *R. thrysiflorus* occurring in the lowlands and *R. arifolius* on wet meadows in the mountains.

According to A. Löve's (1957) classification the three taxa belong to the subgenus *Acetosa*, section *Acetosa*, subsection *Acetosa*. The subsection *Acetosa* groups dioecious species characterized by rather large chromosomes usually with terminal or subterminal centromeres. The chromosome number is $2n = 14$ ♀ and 15 ♂. The mechanism of sex determination is based, similarly as in *Drosophila*, on the balance between the *X*-chromosomes and the autosomes.

R. acetosa, *R. arifolius* and *R. thyrsiflorus* are cytologically and in some regards taxonomically the best investigated species in the section *Acetosa*. Nevertheless, for all the interest that they have attracted, and this refers primarily to *R. acetosa* bacause of the natural polyploidy occurring in this dioecious species, the relation between them has not been fully explained. The first attempt to establish the relation between the forms growing in Scandinavia was made by Löve, who in the course of experiments lasting several years made many intra- and interspecific crosses between plants coming from different parts of the peninsula. Unfortunately the full report on these experiments was never published, but in the preliminary report Löve (1944) stated that he never had any difficulty in obtaining the F_1 progenies and that their fertility was not reduced. In view of these results he concluded that the taxa were not biologically isolated and that they should be treated as the subspecies of the Linnaean species *R. acetosa* L. He classified the three taxa of this investigation and the closely related species *Rumex ambiguus* as *R. acetosa* L. subsp. *pratensis* [= *acetosa*], subsp. *arifolius*, subsp. *thyrsiflorus*, and subsp. *ambiguus*. Löve's views on the classification within the group *Acetosa* was not shared by Rechinger (1949) who was of the opinion that these species would have to be investigated cytogenetically and that only then their proper classification would be possible.

In view of the discordant opinions this investigation has been devised as an attempt to explain in cytogenetic experiments the phylogenetic relation between the three taxa from the section *Acetosa*. In the course of this work the three taxa have been treated, conformably with formal systematic principles, as independent species. The correctness of this treatment will be discussed at the end of the report in the discussion of the experimental results.

THE MORPHOLOGY AND THE GEOGRAPHICAL DISTRIBUTION OF THE PARENTAL TAXA

R. acetosa is a perennial, dioecious species. The female plants are about 80 cm. tall and the male ones are much smaller and less numerous in populations. Basal leaves 2—6 times as long as they are broad. The basal lobes with moderately acute tips bent downwards. Ochrea laciniate. The branches of the inflorescence are single, directed upwards, branching only in the lower part of the inflorescence. The inner fruit valves 3—5 mm. long. Seeds dark brown, shiny. Flowering time: May to June. Root system branching, not very deep. The taxon is common in the lowlands, growing on meadows, along field roads, and in wayside ditches.

According to Löve (1944) *R. acetosa* has spread in many areas as a result of human activities. Within its distribution the species manifests a certain variability and the small morphological differences are sufficient to discriminate local varieties: e.g. in Scandinavia Löve distinguished and described variety *hirtulus* characterised by the presence of a gene determining hairiness on stems and leaves which gives the plants a grey colour.

The species is common throughout the lowlands of Europe, especially in North and Central Europe, in Subarctic and Central Asia, and in North America.

R. arifolius is a perennial, dioecious species. The female plants are up to 80 cm. tall and the male ones are much lower and less numerous. Basal leaves 1—6 times as long as they are broad, oval, seldom almost round: basal lobes usually obtuse, somewhat protruding outwards. Leaves light green, much thinner than in *R. acetosa*, with well marked nerves, petioles long. Ochrea entire or slightly laciniate at tops. The branches of inflorescence single, erect, arching away from main axis. The fruit valves 3—5 mm. long, usually with a reddish tint. Seeds usually larger than in *R. acetosa*, dark brown, beige, or yellowish. Flowering time: May to August. Roots branching. Grows in forests and on wet meadows in the mountains.

The species has been described under different names by various authors. Analysing the descriptions and herbarium specimens as well as the fresh plants Löve (1944) reached the conclusion that all these descriptions referred to the same group of plants, which he defined as *R. acetosa* subsp. *arifolius.*

R. arifolius is a mountain-arctic species occurring in the mountains of Europe, Central Asia, North Africa, West North America, and Alasca. It also grows in the Siberian tundra.

R. thyrsiflorus is a dioecious, perennial species. The female plants are up to 100 cm. tall and the male ones are much lower and less numerous. Basal leaves 4—14 times as long as they are broad, narrow lanceolate, often with crispate margines. Basal lobes large, acute, often protrude outward, thick, dark green. Inflorescence repeatedly branched and forms a dense tuft. Fruit valves 3—4 mm. long. Ochrea laciniate. Seeds small, shiny, dark brown. Long tap root. Flowering time: June to August. Grows in the lowlands on meadows, along dry field roads, waysides, rivers, and on railway banks.

The species has often been described in the literature either as an independent unit under different names, or as a variety of *R. acetosa.* Löve (1944) assumed that all these descriptions referred to the same taxon, which from his observations and researches he classified as a subspecies of *R. acetosa* L.

The distribution of *R. thyrsiflorus* extends in Asia and Europe: it is common in Siberia and in North-East, Central, and South-East Europe. According to Löve and Löve (1957) the species was carried by man to North America where it was reported from the neighbourhood of Quebec as early as 1922.

MATERIAL AND METHODS

The original plants for the experiments were collected from natural stands of *R. acetosa, R. arifolius,* and *R. thyrsiflorus* in Poland and in some cases in Czechoslovakia. In 1955 specimens of twenty two populations, a few plants in each case, were transferred to the experimental garden of the Department of Genetics of the Polish Academy of Sciences in Skierniewice where they were cultivated under, as far as possible, uniform conditions.

These plants were the parental generation in interspecific crosses.

A few intraspecific crosses between plants belonging to the same or different populations were also made. Altogether sixty seven interspecific and eleven intraspecific crosses were made. From these crosses twenty four F_1 populations, twelve F_2 populations, and nine F_3 populations were obtained.

The analysis of the parental plants and of the hybrids covers the morfology, the viability, the time of flowering, and pollen and seed fertility. The cytological investigations covered the number and the morphology of somatic chromosomes and the course of microsporogenesis.

The morphological descriptions referred to the height of the plants, the size of leaves, the shape of leaf blades, the type of inflorescence, and the colour of seeds. The shape of leaves was defined in terms of the ratio of the length to the width of the leaf blades: this ratio is here called the index of leaf shape. The indices for the particular plants were calculated from the average dimensions of five typical leaves.

The type of inflorescence was a trait difficult to define. Although the inflorescence of *R. thyrsiflorus* differed markedly from the inflorescence of *R. acetosa* and *R. arifolius*, it was difficult to find some simple definition characterizing the intermediate types. For the sake of simplicity only three classes of inflorescences were discriminated in the crosses: inflorescence with compound branching (type *thyrsiflorus*), inflorescence with simple branching (type *acetosa*), and inflorescence with intermediate branching.

Two classes of seeds were recognized according to their colour: dark brown and light coloured (beige). The brown colour was always uniform, but the light coloured seeds could be of different shades ranging from grey-green to yellowish. In the description of seeds these differences were disregarded and all the seeds that were not dark brown were classified as light coloured.

The time of flowering was counted from the moment the stigmata appeared in female plants and the discharge of pollen occured in male plants.

Fertility was determined separately for the male and the female plants. Pollen fertility counts were made on acetocarmine smears; the proportion of fertile pollen grains was determined in two buds from every plant by counting 100 to 200 grains in each bud. The fertility of the female plants was much more difficult to determine.

In a well developed inflorescence of *Rumex* the number of female flowers arranged in whorls on the main flower stem and its branches ranges from a few hundreds to a few thousands. The female flower consists of a monocarpous pistil containing a single ovule. After fertilization the ovule develops into an achene and the inner whorl of the perianth into the wind-dispersal organ. Under natural conditions the number of seeds produced by one floral stem ranges from a few hundred (*R. arifolius, R. acetosa*) to a few thousand (*R. thyrsiflorus*), depending on how strongly the inflorescence is branched and on the vigour of the plant. In view of these difficulties it is impossible to develop a practicable method of accurately determining the fertility of female *Rumex* plants.

In this investigation the difficulty was bypassed by estimating the relative ability of the hybrids to set seeds from free pollination as compared to the parental generation, the parental fertility being accepted as 100. This procedure will be fully explained together with the results of the observations on female fertility in the hybrids. In the case of controlled pollination the number of seeds was counted when it was not more than 500, but when there were more seeds the number of seeds in one cubic centimetre was counted and the approximate number of seeds in the whole sample was calculated.

The course of meiosis was examined only in microsporogenesis permanent preparations being used for the purpose. The buds of the male plants were fixed according to Navashin's method as modified by Müntzing (1932) after previous treatment during 5—10 minutes in 1:3 aceto-alcohol. The buds were always fixed in the afternoon since then the meiotic divisions were the most numerous. The microtome sections were 14—16 microns thick. Staining was in crystal violet according to Newton's method.

Mitotic chromosomes were observed either on permanent preparations or sometimes on smears. The root tips were fixed in Navashin fixative modified according to Müntzing. Sometimes fixation was preceded by immersion for four hours in 0.03 per cent solution of 8-oxyquinoline (Tjio & Levan 1950). The microtome sections were 12 microns thick and were stained with crystal violet. Root tips for smears were first kept for three to four hours in a solution of 8-oxyquinoline, according to the procedure developed by J. Żuk (1963) and then placed for 30 minutes to 48 hours in aceto-alcohol. The fixed root tips were macerated by heating lightly in 9:1 two per cent aceto-orcein with hydrochloric acid and then squashed in two per cent orcein.

EXPERIMENTAL RESULTS

1. Parental taxa

The origin of the parental plants

R. acetosa. The parental plants of this species were obtained from four stands: a meadow in the Kampinos Forest, a pasture by Jaktorów, a wayside ditch by Reguły near Warsaw, and a meadow by Choroszcz

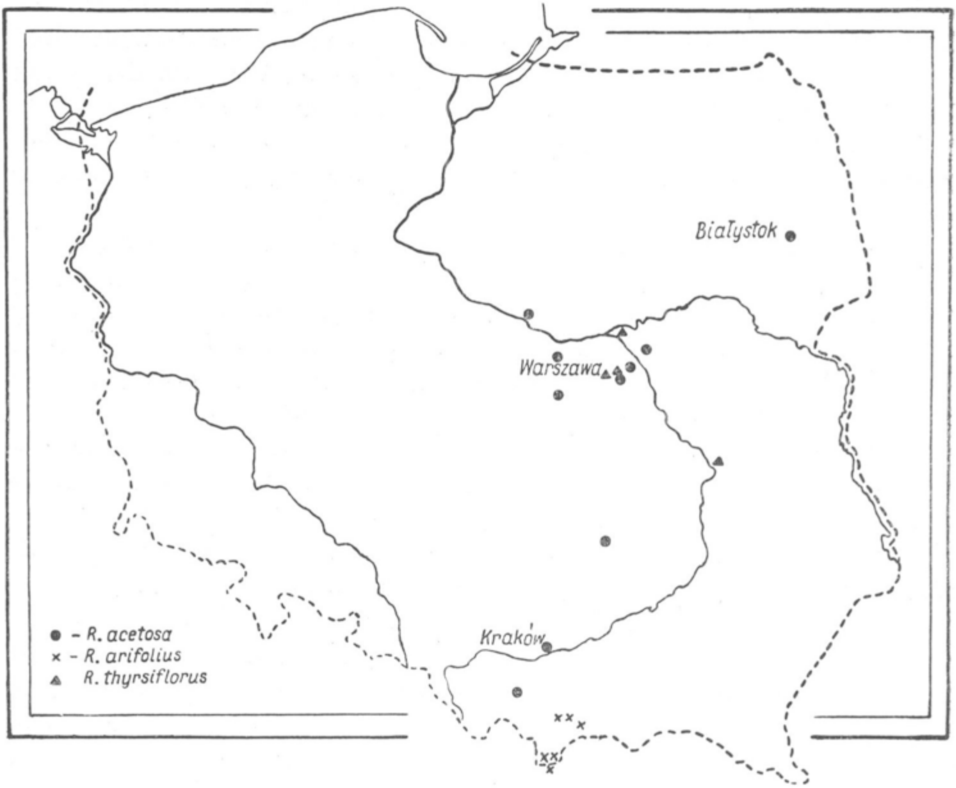


Fig. 1. Distribution of the studied natural populations *R. acetosa*, *R. arifolius* and *R. thyrsiflorus* in Poland

near Białystok. Specimens were also brought from six populations in the regions of Kielce, Kraków, Płock, Skierniewice, Sucha, and Ząbki near Warsaw for determinations of karyotypes in the different parts of the country.

R. arifolius. The parental plants came from fourteen stands in the Gorce Mts., the Pieniny Mts., and the Tatra Mts. In selecting the plants much attention was given to the natural stands in the Gorce and Pieniny Mts., since *R. arifolius* from those areas manifested the greatest variability.

R. thyrsiflorus. The parental plants came from four stands: a flood dike along the Vistula by Puławy, two pastures by Jaktorów and Brwinów, and a meadow on the banks of the Vistula by Nowy Dwór. All stands are marked on the map (Fig. 1).

The morphology of the plants

The morphological analysis of the initial populations showed a considerable variability in the shape of the basal leaves within the particular species. This was specially apparent in *R. arifolius* and *R. thyrsi-*

T a b l e 1

Height of plants, size and shape index of leaves in R. thyrsiflorus, R. acetosa and R. arifolius populations and in some intraspecific hybrids.

	Population	Altitude m a.s.l.	No. of plants	Mean in cm.		Leaves shape index		
				height of stems	length of leaves	width of leaves	Mean	Range
Lowland	R. thyrsiflorus							
	Nowy Dwór		28	92	12.50	4.40	2.84	2.10 - 3.48
	Puławy		8	114	10.30	3.50	2.98	2.34 - 4.35
	♀ Puławy × ♂ Puławy		20	126	10.54	3.46	3.04	1.87 - 4.58
	Jaktorów		5	85	8.13	1.90	4.27	2.40 - 5.00
	♀ Jaktorów × ♂ Jaktorów		25	117	9.96	2.24	4.40	3.60 - 5.80
	R. acetosa							
	Kampinos		10	62	7.05	2.89	2.43	1.39 - 3.04
	Jaktorów		5	61	6.25	2.74	2.28	1.76 - 2.65
	Choroszcz		20	70	7.24	3.40	2.12	1.62 - 2.96
	♀ Choroszcz × ♂ Choroszcz		20	93	7.89	3.65	2.16	1.92 - 2.36
	♀ Reguły × ♂ Choroszcz		20	93	8.80	3.89	2.26	1.58 - 3.65
Gorce	R. arifolius							
	Olszówka	600	9	70	8.25	4.12	2.00	1.40 - 3.21
	Knurów	600	8	-	9.76	4.34	2.24	1.57 - 3.34
	Hucisko	700	5	-	9.55	4.71	2.02	1.71 - 2.31
	Furcówka	850	9	-	8.74	4.94	1.74	1.64 - 2.64
	Szałasiska	900	10	54	8.88	5.17	1.71	1.39 - 3.68
	Rezerwat Orkana	1100	7	61	7.67	5.41	1.41	1.05 - 1.97
	Hala Długa	1250	20	61	8.18	5.50	1.48	1.09 - 2.02

cont. Table 1

Population		Altitude m a.s.l.	No. of plants	Mean in cm.		Leaves shape index		
				height of stems	length of leaves	width of leaves	Mean	Range
	R. arifolius							
Pieniny	Niedzica	500	13	-	11.73	4.68	2.48	1.39 - 3.44
Pieniny	Krościenko	600	6	-	9.63	4.99	1.91	1.30 - 2.60
Pieniny	♀ Krościenko × ♂ Krościenko	600	18	76	9.70	4.50	2.20	1.51 - 3.94
Pieniny	Trzy Korony	900	9	-	8.75	5.10	1.71	1.33 - 2.00
Pieniny	Kuźnice	1020	5	-	6.78	4.80	1.35	1.06 - 1.74
Tatry	Hala Kopienica	1240	20	79	9.01	5.77	1.56	1.25 - 2.10
Tatry	Kozi Grzbiet	1450	5	-	7.30	5.45	1.34	1.12 - 1.90
Tatry	Hala Gąsienicowa	1510	5	-	8.40	6.10	1.39	1.07 - 1.58

florus. The values of the leaf shape index for plants from the various stands and for the intraspecific crosses are listed in Table 1.

As is to be seen in Table 1 the variability of the leaf shape index in *R. acetosa* was relatively small: the average value of the index for the particular populations ranged 2.12 to 2.43. The characteristic shapes of the basal leaves in *R. acetosa* are shown in Fig. 2.

The plants identified as *R. arifolius* very visibly lacked uniformity. The observations made in the Gorce Mts. showed that in the foot hills (altitudes up to 600 metres above sea level) the plants with the growth habit resembling *R. acetosa* predominated. The basal leaves of these plants were not very wide and usually with acute tipped basal lobes (Fig. 3), their colour was somewhat deeper green and they were thicker than the typical *R. arifolius* leaves. The inflorescence was weakly branched, the seeds were mainly brown, plants with light coloured seeds being rare. In the lower mountain-forest zone (600—1000 metres above sea level) the proportion in the populations of plants approaching the growth habit of typical *R. arifolius* — i.e. wider, thin, light green leaves, rounded basal lobes, light coloured seeds — increased. The populations from this zone were not uniform since they also included individuals intermediate between *R. acetosa* and *R. arifolius* (Fig. 4). The stands from the highest altitudes (Mt. Lubań, the Hala Długa ridge on Mt. Turbacz) were occupied by typical *R. arifolius* (Fig. 5). A similar differentiation was observed in the *Rumex* populations from the Pieniny Mts. The populations reported from the Tatra Mts. at altitudes 1020 to 1510 metres above sea level were uniform, typical for *R. arifolius*. Fig. 6 shows the basal leaves of *R. arifolius* from the Kozi Grzbiet ridge in the Tatra Mts.

Measurements showed that the average value of the leaf shape index for the particular populations decreased with the increasing altitude above sea level (Table 1). The leaf shape index of the plants from stands below 1000 metres above sea level approached the values of this index in *R. acetosa* its average values ranging 1.71 to 2.48. The average values of the leaf shape index of *R. arifolius* from higher altitudes ranged 1.34 to 1.56; variability within these limits may be assumed as characteristic for typical *R. arifolius*. The results of these measurements confirmed the conclusions of the preliminary field observations that *R. acetosa* changed gradually through a series of intermediate forms into *R. arifolius*.

Appreciable differences in the shape of the basal leaves were also found in *R. thyrsiflorus*. Measurements of these leaves on plants from three different stands showed that in the population from Jaktorów the basal leaves were much narrower than in the populations from Puławy and Nowy Dwór. The average value of the leaf shape index in the population from Jaktorów was 4.27 and for the F_1 cross within

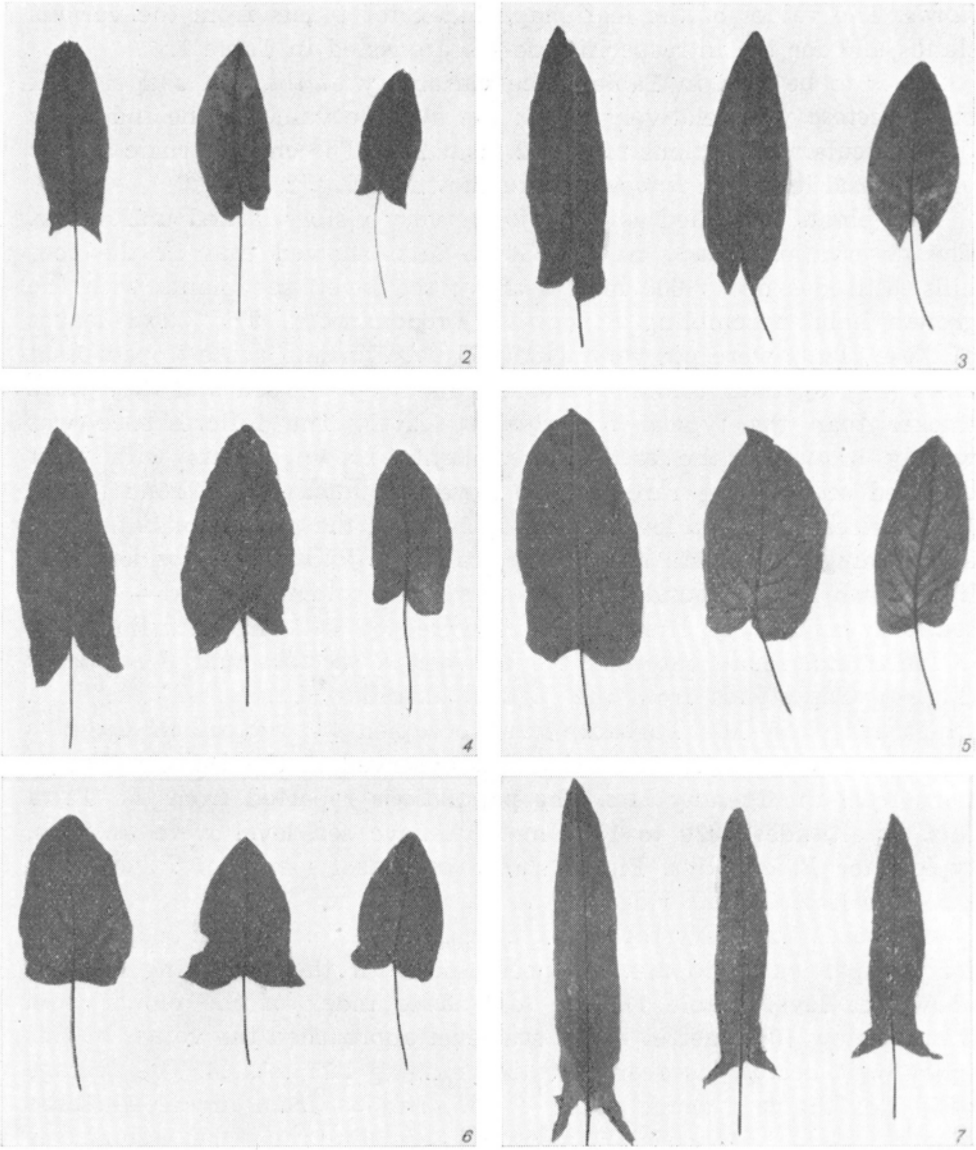


Fig. 2-7. Basal leaves. 2 — *R. acetosa* from Choroszcz: 3-6 — *R. arifolius* from: 3 — Knurów, 4 — Szałasiska, 5 — Hala Długa, 6 — Kozi Grzbiet, 7 — *R. thyrsiflorus* from Nowy Dwór

this population it was even higher, i.e. 4.40. In the populations from Nowy Dwór and Puławy the average value of the leaf shape index was only 2.84 and 3.04 respectively. The basal leaves of *R. thyrsiflorus* from Nowy Dwór are shown on Fig. 7.

On the other hand, the three taxa manifested no variability in the types of the inflorescences. The branches of the inflorescence in *R.*

acetosa and *R. arifolius* were single and in *R. thyrsiflorus* the inflorescence was repeteadly branched.

The seeds of *R. acetosa* and *R. thyrsiflorus* were all brown and in *R. arifolius* some plants had brown and others light coloured seeds.

In the natural populations of *R. acetosa* the proportion of male individuals ranged 15 to 20 per cent. In the case of *R. arifolius* the differences in the proportion of the male plants were much greater: e.g. on the Hala Długa ridge in the Gorce Mts. 115 female, one male, and four bisexual plants were found (0.85 per cent males), whereas at the foot of Mt. Babia Góra to 160 female plants there were 92 male plants (60.5 per cent males). In the populations of *R. thyrsiflorus* the proportion of male plants ranged 10 to 20 per cent, similarly as in *R. acetosa*.

All the populations of *R. acetosa* flowered simultaneously beginning in various years between the 5th and the 30th of May. *R. arifolius* in the lowlands flowered earlier than *R. acetosa*: most populations began flowering already in the first days of May, but the plants from some stands, e.g. from Kozi Grzbiet ridge in the Tatra Mts., flowered much later, not till late in May or even at the beginning of June. Among the *R. thyrsiflorus* populations, the one from Nowy Dwór was remarkable for its early flowering: it began to flower between May 20 and June 10 partly overlapping with the flowering of *R. acetosa*. The *R. thyrsiflorus* populations from Puławy and Jaktorów began to flower much later, i.e. between June 10 and 25; the differences in the flowering dates of these populations were repeatedly observed during several years.

Fertility

All the populations of the taxa manifested normal fertility both on their natural stands and on the experimental plots. The setting of seeds by free pollinated female plants was abundant. The numbers of seeds obtained from intraspecific crosses and the germination rates of these seeds are listed in Table 2. The germination rate was similar in all the three species ranging in most cases 40 to 80 per cent. The only exception was the much reduced seeding of *R. arifolius* from the pollinations made in 1955 and the lower germination rate of these seeds: however, it seems that the lower productivity in this case was associated with the reduced viability of the plants after they were transferred from their natural environment directly into lowland conditions: also the flowering of these plants was poor and few seeds were set even from free pollination.

Pollen fertility was high ranging 88 to 98.3 per cent (average 95.7 per cent) in *R. acetosa*, 83 to 99 per cent average 93.5 per cent

Table 2

Seed germination in F$_1$ of intraspecific hybrids among R. thyrsiflorus, R. acetosa and R. arifolius.

Cross		Year	No. of seeds obtained	% germination
♀	♂			
R. thyrsiflorus				
Puławy	× Puławy	1955	500	86
Nowy Dwór	× Nowy Dwór		900	87
Jaktorów	× Jaktorów		530	54
Puławy	× Nowy Dwór		330	52
R. acetosa				
Choroszcz	× Choroszcz		460	70
Choroszcz	× Choroszcz		310	40
Reguły	× Choroszcz		131	75
R. arifolius				
Hala Długa	× Hala Długa		150	20
Szałasiska	× Szałasiska		170	25
Kopienica	× Kopienica	1957	1500	65
Krościenko	× Kopienica		ca 2000	51
Kopienica	× Krościenko		ca 1200	50

in *R. arifolius*, and 86 to 97.8 per cent (average 92 per cent) in *R. thyrsiflorus.*

In some buds the pollen did not stain well and its appearance resembled the early stages of degeneration. Such buds were, however, very few and were disregarded when calculating the pollen fertility rate.

Cytology

The cytology of *R. acetosa* has been studied more than of any other species of the subgenus *Acetosa*. According to Sinoto (1924) the first cytological investigation on *R. acetosa* was carried out in 1906 by Roth, but the chromosome number he reported (n = 8, 2n = 16) was not confirmed in later researches. The correct chromosome number of this species was given by Kihara and Ono (1925, 1926) who found that it was 2n = 14 in female plants and 2n = 15 in male plants. The same chromosome number for *R. acetosa* and related species was reported by many other workers: Sinoto (1924, 1929), Ono (1928, 1930, 1935), Kihara and Yamamoto (1931), Meurman (1927), Yamamoto (1938), and Löve (1940, 1944).

The sex chromosomes of *R. acetosa* were described by Kihara and Yamamoto (1931). The chromosome set of the female plants comprises twelve autosomes and two *X*-chromosomes. The *X*-chromosomes have a medial or submedial centromere and are the longest in the set (Fig. 8). The male individuals have twelve autosomes, one *X*-chromosome, and two *Y*-chromosomes. The *Y*-chromosomes are much shorter than the *X*-chromosomes; they also have two arms and their centromere only very exceptionally occupies the medial position (Fig. 9). Ono's (1935) studies indicate that the sex chromosomes display much variability in the position of the centromere and the total length of the two arms. Much differentiation is also apparent in the set of autosomes. Kihara and Yamamoto (1931) identified and described four main types of autosomes occurring in *R. acetosa* and the related taxa.

The most common is the rod-shaped autosome of type *i* with a terminal centromere; the part lying beyond the centromere forms a head (Fig. 8). The *i*-chromosomes differ greatly in their length. The chromosomes of type *T* differ from the *i*-chromosomes by that they have a trabant (Fig. 8). The chromosomes of type *v* have two arms and an almost medial centromere; they usually are much shorter than the *Y*-chromosomes (Fig. 11). The chromosomes of type *j* also have two arms, but they are much longer than the *v*-chromosomes; their centromeres being submedial the length of the arms is distinctly different (Fig. 11).

In the chromosome set of a plant the chromosomes of the various types may occur in different numbers, which may be either even or odd. Kihara and Yamamoto defines as asymmetrical the karyotypes that were heterozygous with regard to some types of autosomes (e.g. the karyotype $11i+1v$) contrasting them with symmetrical karyotypes where all the autosomes of each type occurred in pairs (e.g. $8i+2j+2v$). Table 3 lists the karyotypes found in the plants from the different stands of *R. acetosa*, *R. arifolius*, and *R. thyrsiflorus*.

In the case of *R. acetosa* the karyotypes were identified in 49 plants from ten different stands. The most frequent was the karyotype composed of the chromosomes of type *i*, but one or two of these autosomes had a trabant and, therefore, belonged to type *T*. The karyotype of a male and female plant from Choroszcz is shown in Figs 9, 23; the twenty examined plants of this population all had exactly the same karyotype $2X$ (or $X+2Y$)$+12i$. It seems, therefore, that this simple karyotype was typical for the whole of this population. The number of the examined plants in the other populations was much smaller and there could be no certainty that all the karyotypes in these populations

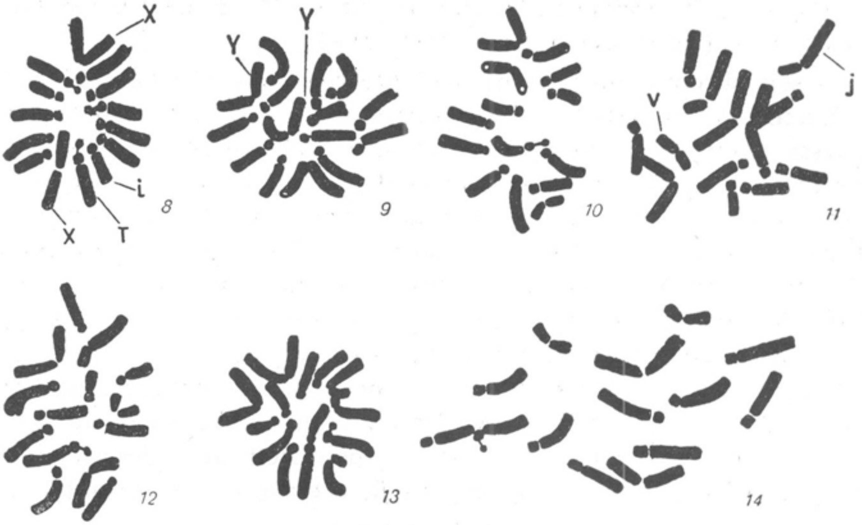


Fig. 8-14. Root tips metaphases. 8-11 — *R. acetosa* from: 8 — Płock ♀ 2n = 14 ($2X + 10i + 2T$), 9 — Choroszcz ♂ 2n = 15 ($X + 2Y + 12i$), 10 — Kielce ♀ 2n = 14 ($2X + 10i + T + v$), 11 — Sucha ♀ 2n = 14 ($2X + 10i + j + v$), 12-13 — *R. arifolius* from: 12 — Kuźnice ♀ 2n = 14 ($2X + 9i + j + v + T$), 13 — Kozi Grzbiet ♀ 2n = 14 ($2X + 8i + 3j + T$), 14 — *R. thyrsiflorus* from Jaktorów (smear) ♀ 2n = 14 ($2X + 9i + 2v + T$). × 1870

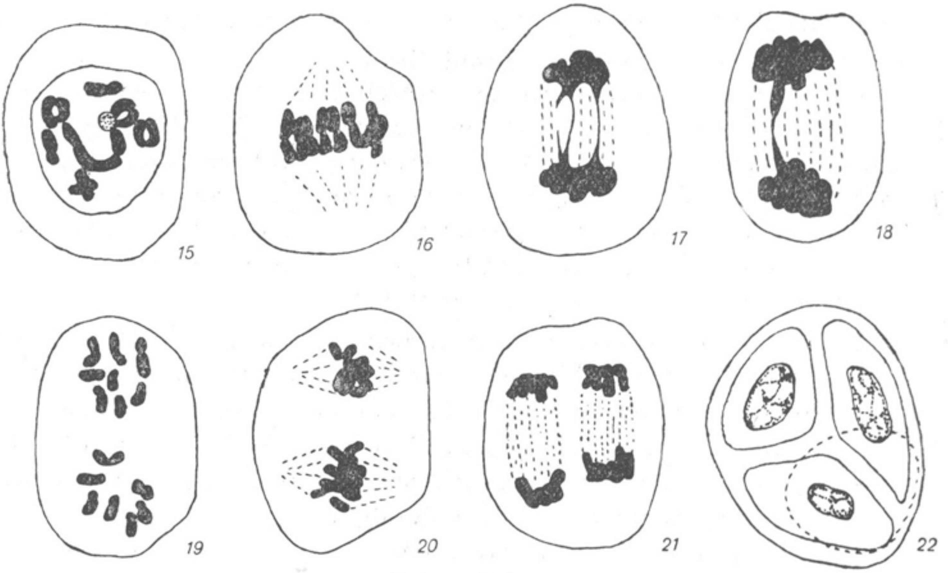
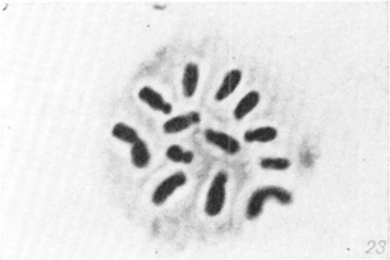
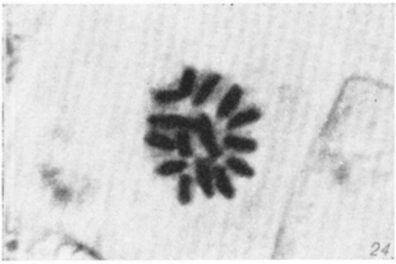
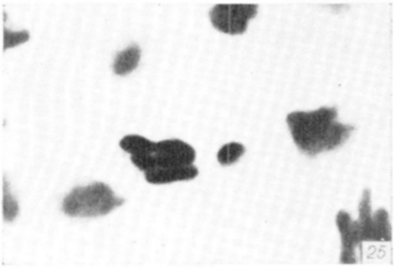
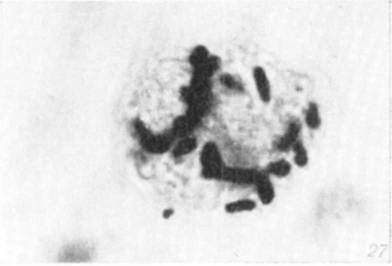


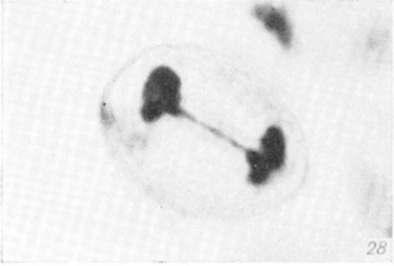
Fig. 15-22. Meiosis in PMCs of *R. acetosa*. 15 — diakinesis; 16 — MI; 17 — chromatine bridges in AI; 18 — lagging bivalent in AI; 19 — AI with 7 and 8 chromosomes; 20 — MII; 21 — AII; 22 — tetrad. × 1870

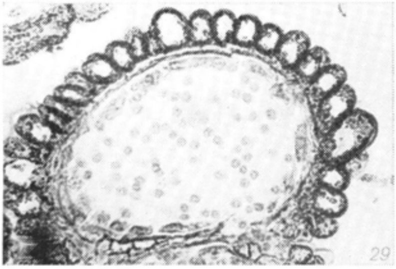












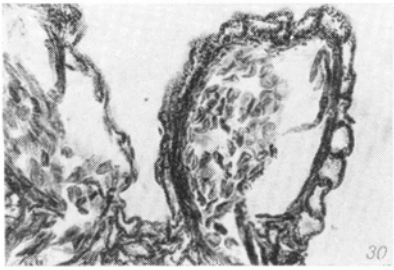


Fig. 23-24. Root tips metaphases. 23 — *R. acetosa* Choroszcz (smear) ♀ $2n = 14$ $(2X + 12i)$; 24 — F_1 *R. arifolius* Szałasiska × *R. acetosa* Choroszcz $2n = 14$ $(2X + 10i + j + T)$. × 1330

Fig. 25-28. Meiotic disturbances in PMCs in *Rumex* hybrids. 25-27 — F_2 *R. acetosa* Choroszcz × *R. thyrsiflorus* Jaktorów, 25 — univalent in MI, 26-27 — PMCs with spindle disturbances and abnormal chromosome separation; 28 — F_1 *R. arifolius* Niedzica × *R. thyrsiflorus* Nowy Dwór — chromatine bridge in AI. (Fig. 25-27 × 1660, Fig. 28 × 1330)

Fig. 29-30. Transversal sections of anthers of F_2 hybrid *R. thyrsiflorus* Nowy Dwór × *R. arifolius* Szałasiska. 29 — anther with normal developed pollen; 30 — degenerated anther. × 70 had been identified. The symmetrical karyotype $2X+10i+2T$, with two trabant chromosomes, of a female plant from Płock is shown in Fig. 8, whereas Fig. 10 shows the mitotic plate of a female plant from near Kielce with the asymmetrical karyotype $2X+10i+T+v$. A plant with the karyotype as the one last mentioned can produce gametes with either one v-chromosome or no v-chromosomes; if these gametes combine with similar gametes from other individuals, then plants having karyotypes symmetrical with regard to the v-chromosomes, i.e. comprising either two or no v-chromosomes, will appear in the population. The chromosomes of type v and j were found only in the population in Reguły, Kielce, and Sucha. As to the population of Sucha there was no certainty that the plants were typical *R. acetosa:* mention has already been made that in the foot-hills plants with intermediate traits between *R. arifolius* and *R. acetosa* are frequent. The mitotic plate of the female plant from Sucha with the karyotype $2X+10i+j+v$ is shown in Fig. 11. The most frequent karyotype in *R. acetosa* from the investigated stands is the one composed of i-autosomes. The variability of this karyotype consists mainly in the presence or the absence of the chromosomes with trabants. The karyotypes containing v- and j-chromosomes are very rare.

In the case of *R. arifolius* the karyotypes were established in 35 plants from 12 stands. As is to be seen (Table 3) the most frequent are the autosomes of type i and then the ones of type j. The T- and v-autosomes are less frequent. The karyotypes are often asymmetrical. No significant relationship was found between the composition of the chromosome set and the stands of the examined plants, but too few plants were examined to make any final conclusions. In the populations of *R. arifolius* from the Gorce Mts., the Pieniny Mts., and the Tatra Mts. the types of chromosomes are the same as in *R. acetosa*, but the autosomes of type j and v are much more frequent in *R. arifolius*. Fig. 12 shows the root tip metaphase of *R. arifolius* from Kuźnice ($2X+9i+j+v+T$). The karyotype of the male plant from the Kozi Grzbiet ridge ($2X+8i+3j+T$) (Fig. 13) is characteristic because it has three j-chromosomes, whereas the highest number of these chromosomes in the other karyotypes was two, similarly as of the v-chromosomes.

In *R. thyrsiflorus* the differentation of the autosomes is similiar as in *R. arifolius*. The karyotypes were established in 16 plants from four stands (Table 3). On all these four stands the autosomes of type j, v, and T are present together with the i-chromosomes. There are no significant differences between the karyotypes of the particular populations. A metaphase plate from the root tip cells of *R. thyrsiflorus* from Jaktorów with the karyotype $2X=14(2X+9i+2v+T)$ is shown in Fig. 14. *R. thyrsiflorus*, similarly as *R. acetosa* and *R. arifolius*, may have either symmetrical or asymmetrical karyotypes.

Table 3

Variation in autosomal sets in natural populations of R. thyrsiflorus, R. acetosa and R. arifolius.

Population	No. of plants examined	Autosomal set
R. thyrsiflorus		
Puławy	13	8i+2j+2v/4/[*]; 9i+j+v+T/1/; 7i+2v+2T+j/1/; 10i+j+T/1/; 8i+2j+2v/6/[**];
Jaktorów	3	9i+2v+T/1/; 8i+2j+v+T/1/; 10i+v+T/1/;
Reguły	1	8i+j+v+2T/1/;
Nowy Dwór	10	6i+2j+2v+2T/3/; 10i+v+T/2/; 8i+2v+j+T/1/[**]; 9i+j+2v/1/[**]; 10i+j+v/2/[**]; 9i+j+v+T/1/[**];
R. acetosa		
Choroszcz	20	12i/20/
Kampinos	2	12i/2/
Reguły	5	12i/1/; 10i+j+T/2/; 9i+2j+v/1/; 11i+j/1/;
Jaktorów	2	12i/2/
Ząbki	2	12i/2/
Skierniewice	2	11i+T/1/; 10i+2T/1/;
Płock	4	12i/3/; 10i+2T/1/
Kielce	5	12i/3/; 11i+T/1/; 10i+v+T/1/
Kraków	3	12i/3/
Sucha	4	11i+T/1/; 10i+2T/1/; 10i+j+v/2/
R. arifolius		
Ochotnica	1	10i+j+T/1/
Hucisko	2	10i+j+T/2/
Turbacz	4	10i+2j/2/; 9i+2j+T/1/; 11i+j/1/
Szałasiska	8	9i+2j+T/2/; 10i+j+v/1/; 10i+2j/2/; 8i+2j+2v/1/; 7i+2v+2j+T/1/; 9i+2j+v/1/
Hala Długa	2	11i+j/1/; 10i+2j/1/
Krościenko	3	12i/1/; 10i+2j/1/; 11i+T/1/;
Trzy Korony	1	10i+v+T/1/
Kuźnice	1	9i+v+j+T/1/
Hala Kopienica	5	11i+j/1/; 11i+T/2/; 10i+2j/1/; 10i+j+T/1/
Kozi Grzbiet	3	8i+3j+T/1/; 7i+3j+v+T/2/
Hala Gąsienicowa	3	10i+v+T/2/; 10i+j+T/1/
Dolina Ważecka	2	12i/1/; 11i+T/1/

[*] Number of plants with the same karyotype.

[**] Data from Żuk /1963/.

The course of microsporogenesis is the same in all three species. At diakinesis there are always six bivalents and one trivalent formed by the sex chromosomes (Fig. 15). In the trivalent the *X*-chromosome is in the middle and the *Y*-chromosomes are attached to the ends of its two arms. The same arrangement is also visible at metaphase I (Fig. 16). At anaphase I the X-chromosome moves to one pole and the Y-chromosomes to the opposite. The characteristic traits of anaphase I are chromatin bridges (Fig. 17) in numerous PMC's and lagging bivalents (Fig. 18). The bridges at anaphase I are of frequent occurrence: to 187 cells without bridges there were 37 showing this irregularity. At a later stage of anaphase the chromatin bridges break and the chromosomes separate to the poles. The number of chromosomes in the anaphase nuclei is seven or eight (Fig. 19). The metaphase of the second division is shown in Fig. 20 and the anaphase of the second division in Fig. 21. The second division leads to the formation of regular tetrads (Fig. 22).

2. Crossability

Crosses between *R. acetosa* and *R. thyrsiflorus*

Eighteen crosses were made between the biotypes belonging to three populations of *R. acetosa* and four populations of *R. thyrsiflorus*. The numbers of seeds obtained from these crosses and the germination

Table 4

Crossability of R. thyrsiflorus, R. acetosa and R. arifolius

Cross		Year	No. of seeds obtained	% germination
♀	♂			
R. acetosa × R. thyrsiflorus				
22 Choroszcz	× 61 Jaktorów	1955	67	46*
21 Choroszcz	× 69 Brwinów	1955	7	3*
38 Choroszcz	× 170 Nowy Dwór	1957	ca 1000	-
40 Choroszcz	× 170 Nowy Dwór	1957	ca 1000	-
R. thyrsiflorus × R. acetosa				
46 Puławy	× 3 Choroszcz	1955	600	79.3
59 Jaktorów	× 3 Choroszcz	1955	ca 1300	53.3
62 Jaktorów	× 3 Choroszcz	1955	67	-
180 Nowy Dwór	× 33 Choroszcz	1957	ca 900	-
172 Nowy Dwór	× 63 Jaktorów	1957	ca 4000	71.0
180 Nowy Dwór	× 54 Reguły	1957	ca 6000	-
R. arifolius × R. thyrsiflorus				
73 Olszówka	× 174 Nowy Dwór	1956	370	45.0
104 Niedzica	× 181 Nowy Dwór	1956	160	1.2
129 Niedzica	× 162 Nowy Dwór	1956	ca 1500	53.2
156 Trzy Korony	× 162 Nowy Dwór	1956	16	-
210 Kozi Grzbiet	× 162 Nowy Dwór	1956	320	32.7
205 Kuźnice	× 174 Nowy Dwór	1956	350	-

cont. Table 4

Cross		Year	No. of seeds obtained	% germination
♀	♂			
R. thyrsiflorus × R. arifolius				
176 Nowy Dwór	× 86 Szałasiska	1956	ca 4000	26.0
183 Nowy Dwór	× 211 Kozi Grzbiet	1956	ca 4500	51.5
180 Nowy Dwór	× 311 Hala Kopienica	1957	ca 1500	-
45 Puławy	× 149 Krościenko	1955	900	74.0
R. acetosa × R. arifolius				
8 Choroszcz	× 86 Szałasiska	1955	320	61.5
11 Choroszcz	× 86 Szałasiska	1955	17	0
23 Choroszcz	× 86 Szałasiska	1955	3	0
12 Choroszcz	× 149 Krościenko	1956	850	34.7
38 Choroszcz	× 7 Krościenko	1957	800	33.5
35 Choroszcz	× 7 Krościenko	1957	1200	-
34 Choroszcz	× 311 Kopienica	1957	300	31.0
R. arifolius × R. acetosa				
73 Rabka	× 3 Choroszcz	1955	30	0
117 Leśniczówka	× 63 Jaktorów	1955	21	14*
143 Furcówka	× 35 Kampinos	1955	24	16*
91 Szałasiska	× 3 Choroszcz	1955	73	65.7
89 Szałasiska	× 19 Choroszcz	1955	42	30*
97 Rez. Orkana	× 19 Choroszcz	1955	145	82.1
99 Rez. Orkana	× 24 Choroszcz	1955	216	56.9
123 Hala Długa	× 20 Choroszcz	1955	178	66.2
126 Hala Długa	× 3 Choroszcz	1955	110	6.4
127 Hala Długa	× 63 Jaktorów	1955	92	73.6
135 Niedzica	× 63 Jaktorów	1955	70	87.1
104 Niedzica	× 20 Choroszcz	1955	39	13*
145 Krościenko	× 3 Choroszcz	1955	29	6*
240 Niedzica	× 36 Choroszcz	1957	ca 900	55.0
1 Krościenko	× 33 Choroszcz	1957	ca 1200	-
154 Pustelnia	× 63 Jaktorów	1955	66	68.3
158 Trzy Korony	× 3 Choroszcz	1955	10	6*
19 Kopieniec	× 32 Choroszcz	1957	ca 1000	55.0
201 H. Gąsienicowa	× 20 Choroszcz	1956	120	9.9

* No. of seeds germinated.

rates of the seeds are listed in Table 4. The setting of seeds was the most abundant in the cross between *R. acetosa* and *R. thyrsiflorus* from Nowy Dwór regardless of the direction in which the cross was made.

This was obviously associated with the exceptionally early flowering date of this population of *R. thyrsiflorus*, since male and female plants in full bloom could be chosen for the crosses. In the case of the other *R. thyrsiflorus* populations the difference in the time of flowering of the parental plants was a serious obstacle: in eight attempted crosses no seeds were set. The failure to produce seeds in these crosses could have been caused not by the barriers preventing fertilization, but also to a large extent by the seasonal isolation of the parental species. The results of the crosses seem to indicate that the two species are not separated by distinct incompatibility barriers, since F_1 hybrids were obtained in virtually all the combinations of crosses between the various populations.

The germination rate of the seeds from the interspecific crosses did not differ significantly from the germination rate of the seeds from the crosses made within the parental species.

Crosses between *R. thyrsiflorus* and *R. arifolius*

The crosses in this case were between the biotypes of seven different populations of *R. arifolius* from the Gorce, Pieniny, and Tatra Mts. and *R. thyrsiflorus* from Nowy Dwór (Table 4). *R. thyrsiflorus* from Nowy Dwór was chosen because this population flowered early, which greatly facilitated the crosses with the early flowering *R. arifolius*.

The experiments showed that the two species intercrossed without any difficulty. The setting of seeds was particularly high when *R. thyrsiflorus* was the maternal plant, but this is comprehensible, since the female plants of this species always produce more seeds than *R. arifolius*. The germination rate was the same as or only a little lower than of the seeds from the intraspecific crosses of the parental species. The cross between *R. thrysiflorus* Puławy and *R. arifolius* Krościenko gave 405 seeds with a high germination rate, which indicates that the high crossability of the two species did not characterize only the *R. thyrsiflorus* population from Nowy Dwór but also the other populations of this species.

Crosses between *R. acetosa* and *R. arifolius*

Between *R. acetosa* and *R. arifolius* from the Gorce Mts., the Pieniny Mts., and Tatra Mts. 36 crosses were made. They were repeated during three consecutive years. The setting of seeds was weakest in the first year, i.e. in the year the parental plants of *R. arifolius* were transplanted from their natural stands. Ten of the 28 crosses made in the first year produced no seeds and the number of seeds from the remaining crosses ranged 3 to 320. The *R. arifolius* plants used for the crosses in the following years were grown from seeds sown out in the lowlands. In all the later crosses the setting of seeds was high ranging from 120 to 1200 seeds.

The seeds from the crosses were always well developed. When the maternal plant was *R. acetosa* all the seeds were brown and when *R. arifolius* was the maternal plant some were brown and some light coloured. The germination rate of the seeds from most of the crosses ranged 30 to 87 per cent (Table 4), i.e. it was at the same level as from crosses within the parental species. In some crosses however the germination of the seeds was appreciably weaker.

3. The morphology of the hybrids

F_1 Hybrids

From the crosses between the various biotypes of the three taxa 24 F_1 populations were obtained. In all instances the F_1 hybrids were fully vigorous and well developed manifesting no symptoms of malformation (Table 5). The hybrid populations differed, however, with regard to their environmental requirements. The F_1 hybrids, which had *R. tyhrsiflorus* as one of the parents, were more resistant to drought than the hybrids of *R. acetosa* with *R. arifolius*. Out of 16 F_1 populations of hybrids between different biotypes of *R. acetosa* and *R. arifolius* three perished entirely in the first year even before they flowered: the cause of this must have been the excessively dry soil since the same populations flourished on a moist soil for two years. The F_1 hybrids *R. thyrsiflorus* × *R. arifolius* were very resistant to drought; the only exception here was the cross *R. thyrsiflorus* Nowy Dwór × *R. arifolius* Szłasiska half of the F_1 progeny having perished before flowering in spite of the vigorous growth.

Measurements of the F_1 populations (Table 6) showed that in many instances the growth of the hybrids was more vigorous than of the parental generation (Table 1). This was specially apparent in the crosses *R. thyrsiflorus* × *R. arifolius* and in one of the crosses *R. thyrsiflorus* × ×*R. acetosa* (♀ 46 Puławy × ♂ 3 Choroszcz).

Morphologically the F_1 progeny was intermediate between the parental species. The F_1 hybrids *R. thyrsiflorus* × *R. acetosa* and *R. thyrsiflorus* × *R. arifolius* had inflorescences with compound branching but since the inflorescences were less compact than in the typical *R. thyrsiflorus* plants they were also classified as intermediate.

The shape of the leaves of the hybrids was intermediate between the parental populations (Table 6). The leaf shape index of the particular F_1 populations in the various groups of crosses differed considerably according to how this trait was developed in the parental biotypes.

Table 5

Growth, viability and sex of F_1 and F_2 hybrids and some backcrosses among R. thyrsiflorus, R. acetosa and R. arifolius.

Cross		Hybrids generation	Growth of plants	No. of plants	% of viable plants	% of male plants	No. of bisexual plants
♀	♂						
R. acetosa × R. thyrsiflorus							
22 Choroszcz	× 61 Jaktorów	F_1	normal	47	93.5	18.6	-
		F_2	disturbed	284	88.6	3.4	-
18 F_1	× 61 Jaktorów	B	disturbed	38	87.5	12.1	-
21 F_1	× 31 Choroszcz	B	normal	185	88.5	10.3	-
R. thyrsiflorus × R. acetosa							
57 Jaktorów	× 3 Choroszcz	F_1	normal	124	98.4	20.4	-
		F_2	disturbed	208	89.5	15.5	-
56 Puławy	× 3 Choroszcz	F_1	normal	179	98.4	15.9	-
		F_2 /12×8/	normal	150	82.0	18.0	-
		F_2 /12×15/	normal	124	93.6	5.1	-
		F_2 /12×16/	disturbed	104	58.6	6.5	1
46 Puławy	× 8 F_1	B	normal	200	97.0	20.0	1
46 Puławy	× 15 F_1	B	normal	122	86.0	5.7	-
163 Nowy Dwór	× 63 Jaktorów	F_1	normal	104	97.2	4.3	-
		F_2 /36×61/	disturbed	131	94.7	6.0	1
		F_2 /13×77/	disturbed	128	99.3	19.3	-

cont. Table 5

Cross		Hybrids generation	Growth of plants	No. of plants	% of viable plants	% of male plants	No. of bisexual plants
♀	♂						
R. thyrsiflorus × R. arifolius							
183 Nowy Dwór	× 211 Kozi Grzbiet	F_1	normal	104	97.2	31.6	-
		F_2 /20×34/	disturbed	88	87.5	16.9	-
		F_2 /38×41/	disturbed	115	91.4	5.7	-
176 Nowy Dwór	× 86 Szałasiska	F_1	normal	52	69.7	61.0	-
		F_2	disturbed	210	55.3	9.2	1
R. arifolius × R. thyrsiflorus							
210 Kozi Grzbiet	× 162 Nowy Dwór	F_1	normal	104	96.2	6.0	-
		F_2	normal	340	68.3	5.6	-
129 Niedzica	× 162 Nowy Dwór	F_1	normal	104	98.1	5.8	-
		F_2 /24×62/	normal	193	95.9	0	1
		F_2 /73×51/	normal	35	71.5	12.0	-
R. arifolius × R. acetosa							
104 Czorsztyn	× 20 Choroszcz	F_1	normal	13	12.0	1.0	-
		F_2	normal	50	28.0	10.2	-
197 Ręz. Orkana	× 20 Choroszcz	F_1	normal	119	95.0	16.8	-
		F_2	normal	63	98.5	10.2	-
127 Turbacz	× 63 Jaktorów	F_1	normal	68	91.2	9.4	-
		F_2	normal	126	73.1	18.4	-
R. acetosa × R. arifolius							
12 Choroszcz	× 149 Krościenko	F_1	normal	104	100.0	3.3	-
		F_2	normal	370	16.3	23.3	-

In F_1 104 Czorsztyn × 20 Choroszcz absolute numbers of plants instead of per cent are given

T a b l e 6

Height of plants, size and shape index of leaves in F_1 hybrids among R. thyrsiflorus, R. acetosa and R. arifolius.

Cross		No. of plants	Mean in cm.			Leaves shape index	
♀	♂		Height of stems	Length of leaves	Width of leaves	Mean	Range
R. acetosa × R. thyrsiflorus							
22 Choroszcz	× 61 Jaktorów	8	91.2	9.90	4.20	2.47	1.56 - 3.36
R. thyrsiflorus × R. acetosa							
59 Jaktorów	× 3 Choroszcz	20	121.0	8.90	3.03	2.96	2.31 - 4.54
46 Puławy	× 3 Choroszcz	18	146.0	12.30	4.80	2.60	2.07 - 3.55
163 Nowy Dwór	× 63 Jaktorów	30	100.1	13.00	6.00	2.13	1.80 - 2.67
R. thyrsiflorus × R. arifolius							
183 Nowy Dwór	× 211 Kozi Grzbiet	30	118.8	14.03	6.24	2.28	1.73 - 2.78
176 Nowy Dwór	× 86 Szałasiska	30	95.4	14.60	5.44	2.77	1.78 - 4.02
R. arifolius × R. thyrsiflorus							
210 Kozi Grzbiet	× 162 Nowy Dwór	30	132.0	11.73	6.10	2.00	1.20 - 2.40
129 Niedzica	× 162 Nowy Dwór	30	114.4	11.57	4.80	2.42	1.90 - 3.24
R. acetosa × R. arifolius							
1 Choroszcz	× 149 Krościenko	30	91.0	12.6	5.50	2.27	1.83 - 2.98
8 Choroszcz	× 86 Szałasiska	19	99.0	10.3	4.80	2.19	1.57 - 3.02
10 Choroszcz	× 33 Hala Kopieniec	8	-	10.7	5.90	1.83	1.45 - 1.95

cont. Table 6

Cross		No. of plants	Mean in cm.			Leaves shape index	
♀	♂		Height of stems	Length of leaves	Width of leaves	Mean	Range
R. arifolius x R. acetosa							
135 Niedzica	x 63 Jaktorów	17	85.4	10.90	3.80	2.94	2.06 - 5.00
104 Niedzica	x 20 Choroszcz	13	-	9.80	4.10	2.39	1.97 - 3.36
154 Pustelnia	x 63 Jaktorów	22	62.1	9.90	4.90	2.05	1.57 - 3.02
117 Leśniczówka	x 63 Jaktorów	11	-	8.80	4.90	1.74	1.46 - 2.18
89 Szałasiska	x 19 Choroszcz	18	-	11.55	4.60	2.52	1.99 - 3.69
91 Szałasiska	x 3 Choroszcz	18	101.8	9.10	4.90	1.89	1.52 - 2.55
99 Rezerw. Orkana	x 24 Choroszcz	20	94.5	10.40	5.10	2.03	1.48 - 2.62
97 Rezerw. Orkana	x 19 Choroszcz	21	94.7	12.00	4.90	2.59	1.61 - 3.58
123 Hala Długa	x 20 Choroszcz	20	109.5	11.80	5.20	2.33	1.60 - 2.79
126 Hala Długa	x 3 Choroszcz	7	-	9.70	5.90	1.84	1.33 - 2.50
127 Hala Długa	x 63 Jaktorów	20	96.0	11.10	5.20	2.17	1.57 - 3.11
19 Hala Kopienica	x 32 Choroszcz	10	-	10.90	7.00	1.56	1.37 - 1.83
201 Hala Gąsienicowa	x 20 Choroszcz	9	92.5	10.10	5.60	1.77	1.33 - 2.20

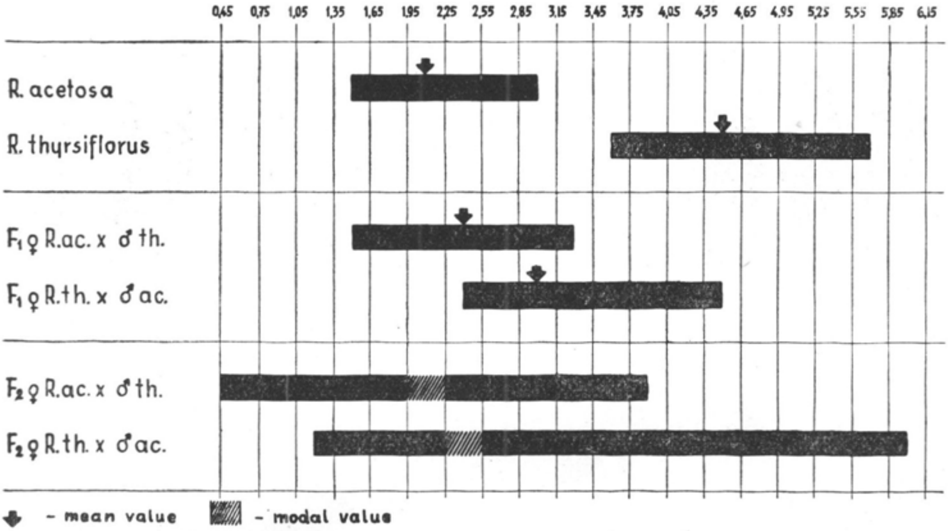


Fig. 31. Range of variation of leaves shape indexes in reciprocal hybrids between *R. acetosa* Choroszcz and *R. thyrsiflorus* Jaktorów

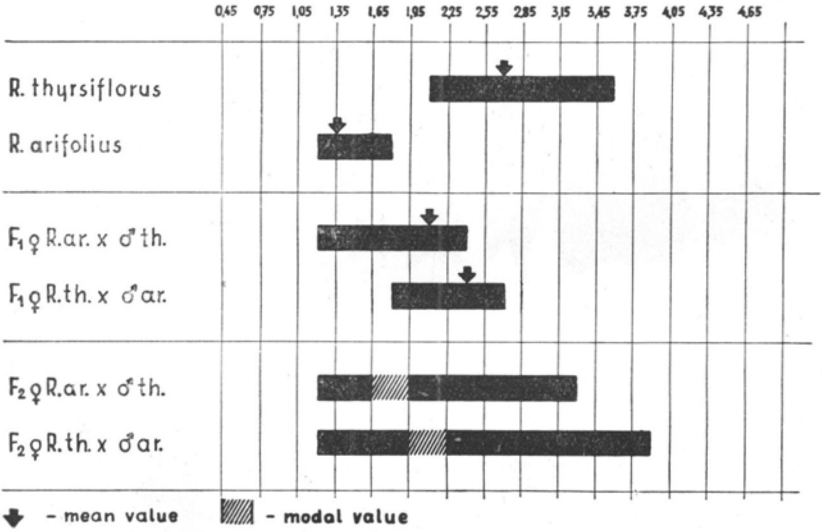
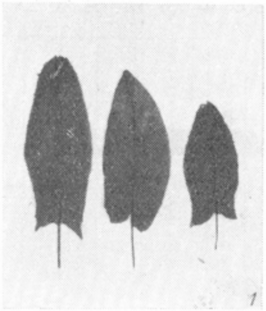
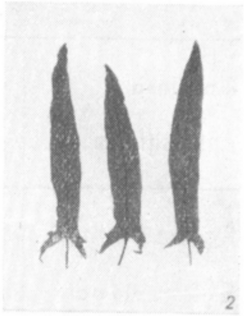
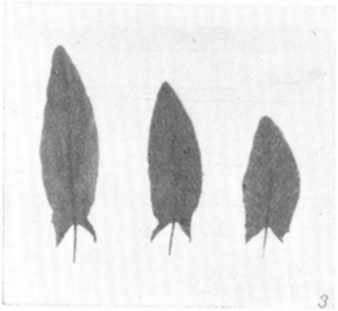
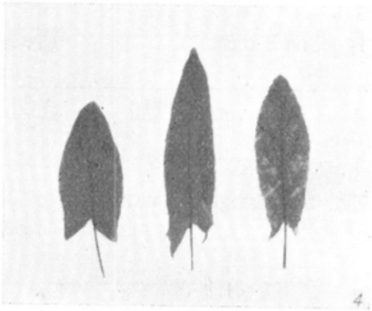


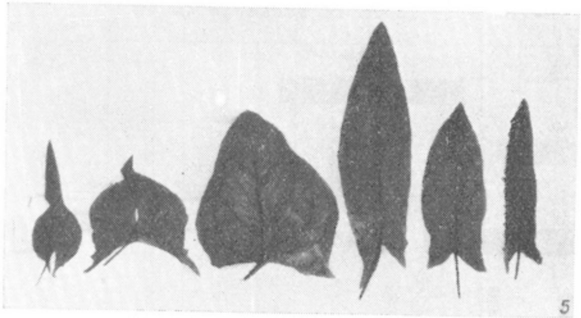
Fig. 32. Range of variation of leaves shape indexes in reciprocal hybrids between *R. arifolius* Kozi Grzbiet and *R. thyrsiflorus* Nowy Dwór











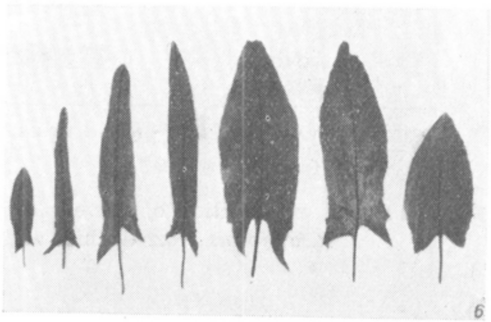
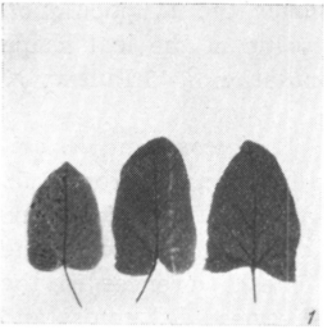
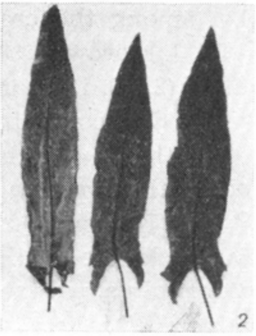
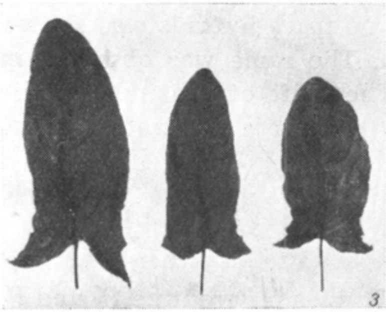


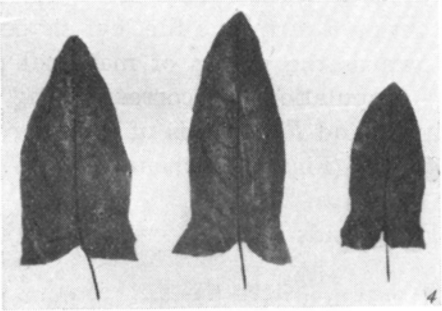
Fig. 33. Basal leaves of *R. acetosa* from Choroszcz, *R. thyrsiflorus* from Jaktorów and F_1 and F_2 of their reciprocal hybrids

1 — R. acetosa, 2 — R. thyrsiflorus, 3 — F_1 *R. acetosa × R. thyrsiflorus, 4 —* F_1 *R. thyrsiflorus × R. acetosa, 5 —* F_2 *R. acetosa × R. thyrsiflorus, 6 —* F_2 *R. thyrsiflorus × R. acetosa*









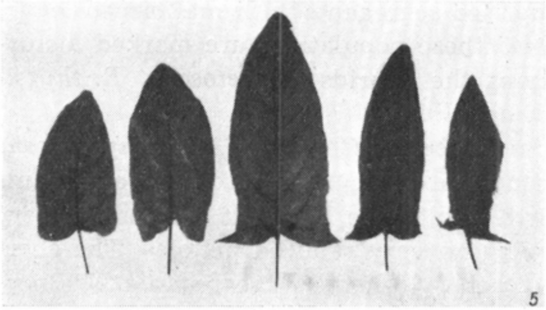
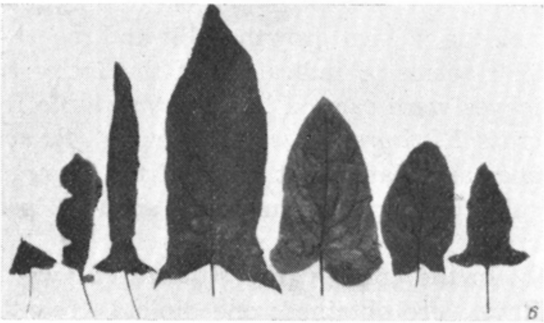


Fig. 34. Basal leaves of *R. arifolius* from Kozi Grzbiet, *R. thyrsiflorus* from Nowy Dwór and F_1 and F_2 of their reciprocal hybrids

1 — R. arifolius, 2 — R. thyrsiflorus,
3 — F_1 *R. arifolius × R. thyrsiflorus,*
4 — F_1 *R. thyrsiflorus × R. arifolius,*
5 — F_2 *R. arifolius × R. thyrsiflorus,*
6 — F_2 *R. thyrsiflorus × R. arifolius*



E.g. among the crosses *R. acetosa* × *R. thyrsiflorus* the F_1 population ♀ 59 Jaktorów × ♂ 3 Choroszcz had a higher value of the leaf shape index (2.96), i.e. narrower leaves, than the F_1 population ♀ 46 Puławy × × ♂ 3 Choroszcz (index 2.60).

In the F_1 populations of the crosses between *R. acetosa* and *R. arifolius* the average value of the leaf shape index ranged from 1.56 (♀ Hala Kopienica × ♂ Choroszcz) to 2.94 (♀ Niedzica × ♂ Jaktorów). This was undoubtedly the result of the considerable variability between the *R. arifolius* parents from the various stands. The differences in the values of the leaf shape index of the F_1 hybrids between *R. acetosa* and *R. arifolius* from the Tatra Mts. were much smaller.

In the case of reciprocal crosses between *R. thyrsiflorus* and *R. acetosa* or *R. arifolius* the leaf shape index value in F_1 hybrids was shifted towards the values of maternal population. The same was observed in F_2 populations of corresponding crosses. The shift of the index value in F_1 and F_2 hybrids of the four reciprocal crosses is illustrated on the graphs (Figs. 31, 32) and in Figs. 33, 34.

F_2 Hybrids and backcrosses

Table 5 lists the crosses for which the analyses covered the F_1 and F_2 generations and in some cases the backcrosses. Contrary to the F_1 hybrids, which were all characterized by normal, undisturbed growth, some of the F_2 populations comprised segregants with malformed leaves and (or) inflorescences; in Table 5 these populations are marked disturbed. Malformation occurred among the hybrids *R. acetosa* × *R. thyrsiflorus* and *R. thyrsiflorus* × *R. arifolius*.

The F_2 generation of the cross *R. acetosa* Choroszcz × *R. thyrsiflorus* Jaktorów included, besides the normal segregants, also aberrant plants with an entirely changed growth habit. The aberrant plants had very wide, almost round leaves growing on very reduced petioles. The aberrant types amounted to about 15 per cent of the F_2 segregants. The normal segregants in F_2 and some of the aberrant types are illustrated in Fig. 35. The same aberrant types appeared also in the backcross F_1 × × *R. thyrsiflorus*. In the backcross F_1 × *R. acetosa* all the individuals had the normal growth habit and morphologically resembled *R. acetosa*. This seems to indicate that the factors causing the abnormal shape of leaves were carried by *R. thyrsiflorus* from Jaktorów. In the reciprocal cross *R. thyrsiflorus* Jaktorów × *R. acetosa* Choroszcz there were no aberrant plants, but some of the segregants had very little vigour: the sublethal types amounted to about 13 per cent of the F_2 progeny of this cross.

In the cross *R. thyrsiflorus* Puławy × *R. acetosa* Choroszcz two F_2 lines were obtained: one diploid, the other polyploid (12×16) with the

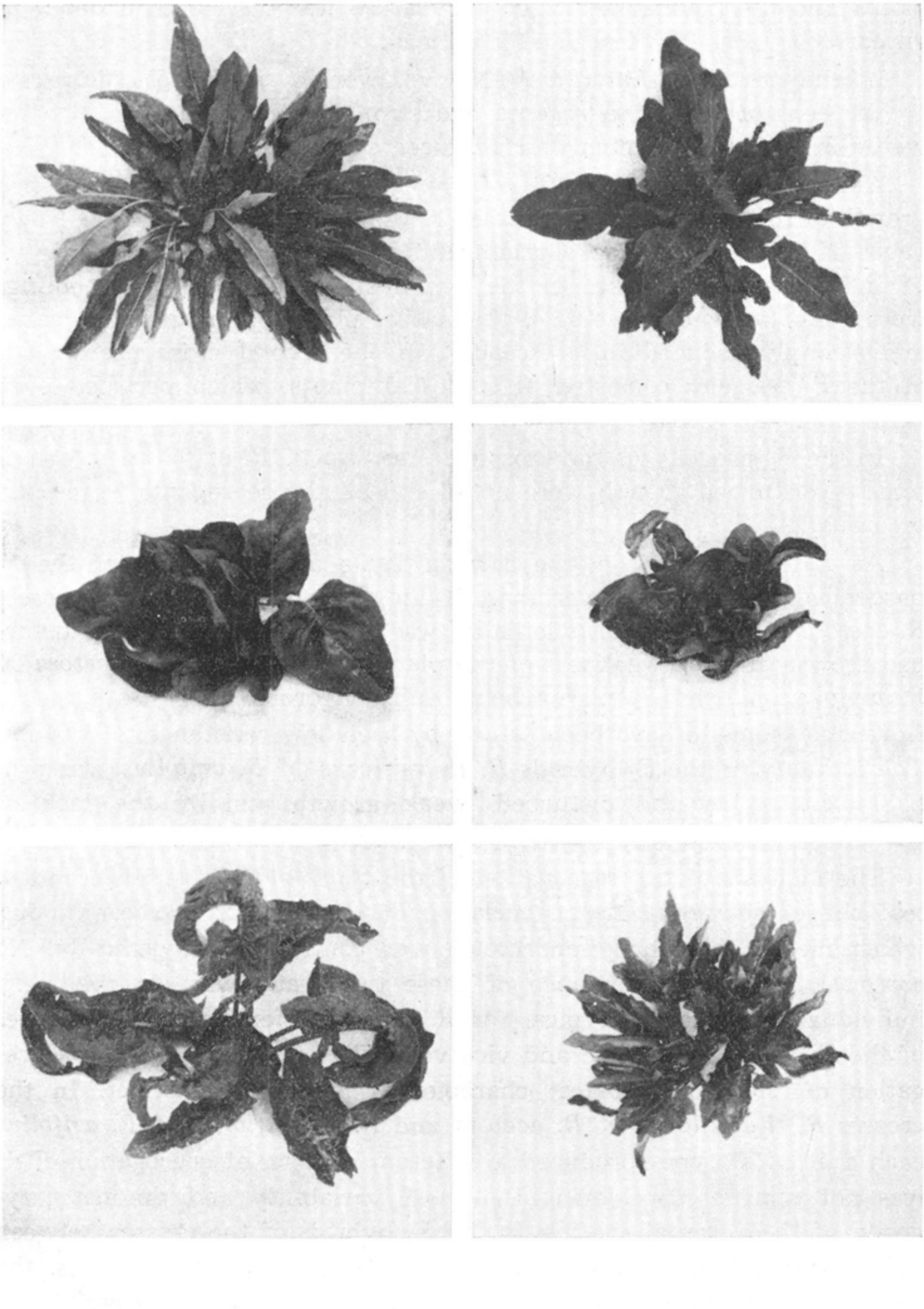


Fig 35. Some normal and aberrant segregants in F_2 *R. acetosa* Choroszcz. × *R. thyrsiflorus* Jaktorów (explanation in text).

chromosome numbers approaching tetraploids. The morphology of these plants and the manner in which they arose was discussed in detail in an earlier report (Świetlińska 1960).

In the cross *R. thyrsiflorus* Nowy Dwór × *R. acetosa* Jaktorów 15 per cent of the F_2 segregants had strongly reduced leaves but flowered in the usual manner and produced seeds.

Among the hybrids *R. thyrsiflorus* × *R. arifolius* the disturbed growth of the F_2 segregants accurred in the crosses *R. thyrsiflorus* Nowy Dwór × *R. arifolius* Kozi Grzbiet and *R. tyhrsiflorus* Nowy Dwór × × *R. arifolius* Szałasiska. In the first instance some of the seedlings were albinotic, whereas some of the mature plants had malformed leaves and strongly reduced inflorescences. In the second cross nearly half of the F_2 progeny consisted of sublethal plants, which perished even before they flowered.

In the F_2 progeny of the crosses *R. acetosa* × *R. arifolius* no symptoms of disturbed growth were noted and all the segregants were fully vigorous.

As is to be seen from the data in Table 5 the viability of the F_2 progenies was usually lower than of the F_1 generation. In the crosses *R. acetosa* × *R. thyrsiflorus* lethality was mainly associated with disturbed growth and the weakness of the plants. In the crosses *R. acetosa* × *R. arifolius* all the F_2 plants being fully vigorous their death before flowering seems to have been caused by their low resistance to drought. The lethality of the F_2 hybrids *R. thyrsiflorus* × *R. arifolius* was probably caused by the disturbed, weak growth and by the lack of resistance to drought.

The analysis of the segregation of the types of inflorescence and of leaf shapes showed that the variation of these traits was continuous, which means that their inheritance was controlled polygenically. No correlation in the inheritance of these two traits was observed, e.g. individuals with leaves typical for *R. acetosa* often had inflorescences of the *R. thyrsiflorus* type and vice versa. Not in all crosses the segregation of the morphological characters was equally distinct. In the crosses *R. thyrsiflorus* × *R. acetosa* and *R. thyrsiflorus* × *R. arifolius* each pair of biotypes produced a different pattern of segregation. This was not unusual considering the great variability and the heterozygosity of the parental species. In the F_2 hybrids of the crosses between *R. acetosa* and *R. arifolius* from the Gorce and the Pieniny Mts. the segregation of the morphological traits was virtually impossible to define: the range of variation of the leaf shape index in the F_2 populations was practically speaking the same as in F_1 and the parental populations.

4. Sex ratio in hybrid generations

The percentages of the male individuals in the F_1 and F_2 populations from the various crosses are listed in Table 5. As is to be seen the differences in the proportion of the male individuals are considerable: the male individuals were the most numerous in F_1 of the cross *R. thyrsiflorus* Nowy Dwór × *R. arifolius* Szałasiska, where they amounted to 61.0 per cent; the opposite extreme was the F_2 generation (24×62) *R. arifolius* Niedzica × *R. thyrsiflorus* Nowy Dwór where among 193 plants there was not one male individual. This F_2 generation was also remarkable for its great uniformity of growth habit and seed colour, a behaviour difficult to explain, since another F_2 generation of the same cross manifested the usual segregation of morphological characters and a rather high proportion of the male individuals. The data in Table 5 indicate that in some hybrid populations the low proportion of the male plants was associated with some definite paternal parent. E.g. in the cross *R. thyrsiflorus* Puławy × *R. acetosa* Choroszcz the backcross *R. thyrsiflorus* ♀ 46 × F_1 ♂ 15 and F_2 generation (12 × 15) were both obtained by pollinating the female individuals with the pollen of the same male individual $F_1/15$ and in both progenies there was a similarly low proportion of male plants (5.1 and 5.7 per cent). In the cross ♀ 210 Kozi Grzbiet × ♂ 162 Nowy Dwór and in the cross ♀ 129 Niedzica × ♂ 162 Nowy Dwór (the same male parent) in both F_1 progenies the male plants were few amounting to 6 and 5.8 per cent respectively. These two examples seem to indicate that the low proportion of the male individuals is determined by the genotype of the male parent, but more detailed investigations into this problem are necessary.

Among the hybrids from some crosses *R. thyrsiflorus* × *R. acetosa* and *R. thyrsiflorus* × *R. arifolius* bisexual individuals occurred sporadically, but no bisexual individuals were found among the progeny of the crosses *R. acetosa* × *R. arifolius*.

5. Inheritance of the seed colour

Mention has already been made that the seeds of *R. acetosa* and *R. thyrsiflorus* are dark brown. In the populations of *R. arifolius* there are some plants with dark brown seeds and others with light coloured seeds of different shades. It seems, therefore, that *R. arifolius* must manifest a high degree of heterozygosity with regard to the factors determining the colour of seeds.

As we see (Table 7) it is difficult to establish the genetic basis of seed colour inheritance. In some crosses between *R. arifolius* and *R. thyrsiflorus* the light colour is dominant (♀ 183 × ♂ 211) whereas in

Table 7

Seed color in F_1 and F_2 hybrids R. thyrsiflorus × arifolius and R. acetosa × arifolius

Cross		No. of plants with seeds			
		F_1		F_2	
♀	♂	light	brown	light	brown
R. thyrsiflorus × arifolius					
183 /brown seeds/	× 211	60	-	77	81
176	× 86	-	11	-	102
R. arifolius × thyrsiflorus					
210 /light seeds/	× 162	-	90	115	82
129	× 162	28	63	108^{*}	-
				10^{**}	12
R. acetosa × arifolius					
12 /brown seeds/	× 149	90	-	40	-
R. arifolius × acetosa					
97 /light seeds/	× 19	59	4	11	33
127	× 63	11	14	2	75
104 /brown seeds/	× 20	7	-	30	3

$^{*}F_1$ - light seeds.

$^{**}F_1$ - brown seeds.

other (♀ 210 × ♂ 162) the reverse situation was found. The same situation was stated in hybrids between *R. arifolius* and *R. acetosa*. Also the segregations in F_2 were irregular and difficult to explain. It seems that the genetic basis of seed colour is not monogenic.

6. Time of flowering

R. thyrsiflorus begins to flower much later than *R. acetosa* or *R. arifolius*. Moreover, unlike the two other species, *R. thyrsiflorus* when sown out in the spring flowers and produces well developed seeds already in the first year of growth. In view of these differences it was to be expected that the hybrids *R. acetosa* × *R. thyrsiflorus* and *R. arifolius* × *R. thyrsiflorus* would differ from the parental plants in both the flowering date and the ability to flower in their first year.

The behaviour of the hybrids *R. acetosa* × *R. thyrsiflorus* in what concerns their flowering dates is here illustrated by the behaviour of two reciprocal crosses between *R. acetosa* from Choroszcz and *R. thyrsiflorus* from Jaktorów. The flowering of the F_1 and F_2 crosses and of two backcrosses is illustrated by Fig. 36. For comparison this graph also shows the flowering of the corresponding parental populations. As is to be seen the behaviour of the F_1 hybrids in the first year was the same as the behaviour of *R. thyrsiflorus*. In both F_1 hybrid populations all the plants flowered but the dates of flowering differed depending on the direction of the cross. In F_1 of the cross *R. acetosa* × × *R. thyrsiflorus* flowering was simultaneous with the parental *R. thyrsiflorus* population. The flowering of the F_1 progeny of the reciprocal cross with *R. thyrsiflorus* as the maternal parent was somewhat earlier and appreciably shorter.

In the F_2 populations the segregation with regard to the data of flowering was very distinct already in the first year of vegetation. The nature of this segregation differed, however, according to the direction of the cross. In the F_2 generation of the cross *R. acetosa* × *R. thyrsiflorus* only 12 per cent of the plants flowered in the first year and the date of flowering was distinctly later than in F_1. The behaviour of the majority of the plants was thus similar to the behaviour of typical *R. acetosa*. In F_2 of the reciprocal cross 89 per cent of the plants flowered in the

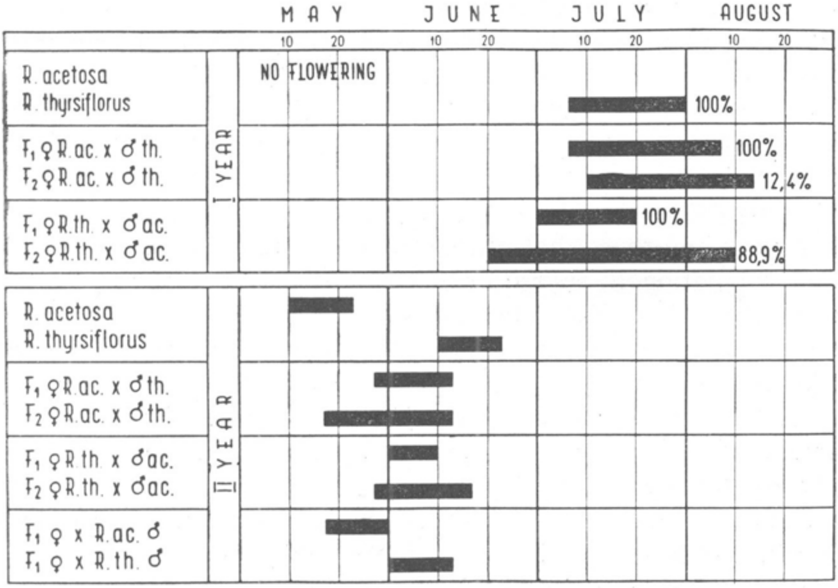


Fig. 36. Flowering time of *R. acetosa* from Choroszcz, *R. thyrsiflorus* from Jaktorów, F_1 and F_2 of their reciprocal hybrids and two backcrosses (explanation in text.)

first year and they began to flower much earlier. This means that in both cases the influence of the maternal plant was strong. In both reciprocal crosses among the plants that did not flower in the first year there were some individuals, which developed flower shoots, but did not develop flowers.

In the second year the date when the F_1 plants began to flower was intermediate between the flowering of the parental populations, with a well marked shift towards the date of flowering of the maternal parent. The F_2 plants in their second year manifested well marked differences in their flowering dates. In F_2 of the cross *R. acetosa* × *R. thyrsiflorus* about 27 per cent of the plants flowered simultaneously with the *R. acetosa* population, 48 per cent simultaneously with the F_1 progeny, and about 25 per cent simultaneously with the *R. thyrsiflorus* population. In F_2 of the reciprocal cross there was a higher proportion of plants flowering simultaneously with the *R. thyrsiflorus* population, and this behaviour again confirmed the influence of the maternal plant.

So far as the flowering date was concerned the behaviour of the backcrosses was the same as of the F_2 progeny. Thus, the backcross F_1 × *R. acetosa* flowered in its second year much earlier than the backcross F_1 × *R. thyrsiflorus*.

The behaviour of the hybrids *R. thyrsiflorus* Puławy × *R. acetosa* Choroszcz was the same as the behaviour of the hybrids *R. thyrsiflorus* Jaktorów × *R. acetosa* Choroszcz. In the F_2 generation the polyploid line flowered much later than the diploid lines: this was clearly apparent in both the first and the second year of growth.

The cross *R. thyrsiflorus* Nowy Dwór × *R. acetosa* Jaktorów merits special attention. As has been said before, *R. thyrsiflorus* from Nowy Dwór flowered much earlier than the populations of this species from Puławy and Jaktorów. Not all the F_1 plants of this cross flowered in the first year and those that did began flowering much earlier than the parental population *R. thyrsiflorus*. Only 34 per cent of the F_2 hybrids flowered in the first year and nearly 2/3 of the F_2 plants behaved like *R. acetosa*, which in this cross was the paternal species. In the second year the flowering time of the F_1 plants was on the whole intermediate with regard to the parental species, whereas the flowering of the F_2 population was exceptionally early, since the plants began to flower even before *R. acetosa*.

Contrary to what was the case in the other crosses, in the hybrids *R. tyhrsiflorus* Nowy Dwór × *R. acetosa* Jaktorów the traits of the paternal parent were distinctly dominant. The domination of the paternal traits in this cross was also confirmed by the morphological analysis. The different behaviour of these hybrids must have been caused by the special properties of the paternal population. Observations revealed that the particular populations of *R. acetosa* did not differ in their flowering dates, whereas *R. thyrsiflorus* from Nowy Dwór flowered much earlier than *R. thyrsiflorus* from other stands. The genotype of *R. thyrsiflorus* from Nowy Dwór seems to have been enriched by introgression with genes carrying some characters of *R. acetosa*. The crossing of this population of *R. thyrsiflorus* with *R. acetosa* could have resulted in the domination of the accumulated characters of *R. acetosa* in the hybrids.

Fig. 37 illustrates the flowering dates of the hybrids *R. thyrsiflorus* Nowy Dwór × *R. arifolius* Kozi Grzbiet and of the reciprocal cross. As is to be seen on this graph almost all the plants of both F_1 populations flowered in their first year. When *R. arifolius* was the maternal parent the F_1 progeny flowered nearly a month later than the progeny of the reciprocal cross, though both F_1 populations were sown out and planted out at the same time.

The F_2 populations segregated distincly into plants that flowered and into those that did not flower in their first year. In F_2 of the cross *R. thyrsiflorus* × *R. arifolius* the proportion of plants that flowered in their first year was 56.9 per cent and in F_2 of the reciprocal cross this proportion was much lower, i.e. only 37 per cent, and the plants flowered at a much later date. These results showed that the F_1 generation behaved like *R. thyrsiflorus*, since all the plants flowered in their first year, but the time of flowering depended on the direction of the cross. When the maternal parent was *R. arifolius* the F_1 progeny flowered

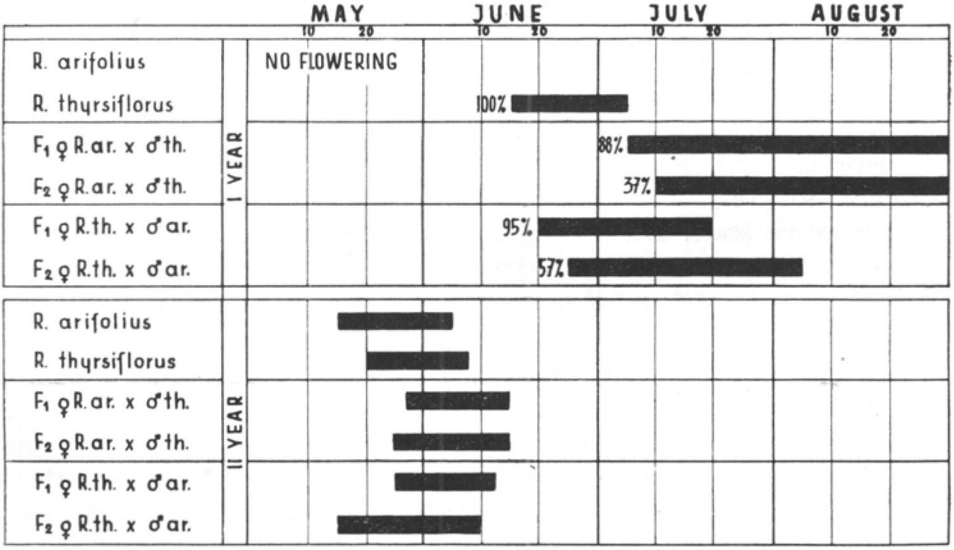


Fig. 37. Flowering time of *R. arifolius* from Kozi Grzbiet, *R. thyrsiflorus* from Jaktorów, F_1 and F_2 of their reciprocal hybrids (explanation in text).

much later than in the case of the reciprocal cross. A similar regularity was observed in the behaviour of the F_2 generation: when *R. arifolius* was the maternal parent the flowering of the F_2 progeny was much later and fewer plants flowered than in F_2 of the reciprocal cross. The conclusion to be drawn from these results is, therefore, that the hybrids *R. thyrsiflorus* × *R. arifolius*, like the hybrids of *R. thyrsiflorus* and *R. acetosa*, manifest in reciprocal crosses a strong domination of the influence of the maternal plant.

In the second year the time of flowering of the F_1 and F_2 generations did not differ significantly from the time of flowering of the parental populations. The only exception was the F_2 progeny of the cross *R. thyrsiflorus* × *R. arifolius*, which flowered very early, though the earlier flowering of the F_2 progeny from the reciprocal cross was to be expected. The behaviour of this population was, thus, similar to the behaviour of the F_2 generation of the cross *R. thyrsiflorus* Nowy Dwór × *R. acetosa* Jaktorów, which contrary to expectation flowered earlier than either parental population.

The F_1 and F_2 hybrids of *R. acetosa* × *R. arifolius* flowered, when sown out in the spring, in their second year. These hybrids flowered at the same time as *R. acetosa* or somewhat earlier. No significant differences in the time of flowering of the particular F_1 populations were observed.

7. Hybrid fertility

Female plants

Mention has been made earlier in this report of the difficulties in determining the fertility of the female plants. The differences of fertility between the F_1 and F_2 generations from the particular crosses were, however, so great that they could be estimated and represented on a comparative scale. The setting of seeds in the hybrids was estimated by reference to the parental species. On this basis the plants were discriminated into four classes: fertile, semifertile, semisterile and sterile.

It was found that in the hybrids *R. acetosa* × *R. thyrsiflorus* and *R. arifolius* × *R. thyrsiflorus* the ability to set seeds was much higher in the second than in the first year. This was specially true in the case of the F_2 generation, in which not all the plants flowered in their first year. Many of the plants, which flowered in their first year, had strongly reduced inflorescences with few flowers and produced few seeds. The fertility of the female plants was, therefore, estimated in the second year of their growth. The data illustrating the setting of seeds by the different hybrids are assembled in Table 8. This Table lists only the data for the crosses *R. thyrsiflorus* × *R. acetosa* and *R. thyrsiflorus* × *R. arifolius*, since a certain degree of sterility was manifested by almost all these hybrids. On the other hand none of the hybrids from the crosses *R. arifolius* × *R. acetosa* manifested a significant drop in their ability to set seeds either in F_1 or F_2. As is to be seen in Table 8 the degree of sterility in the hybrids was closely associated with the biotypes used for the crosses.

Among the hybrids *R. acetosa* × *R. thyrsiflorus* the setting of seeds was at the lowest level in the cross *R. acetosa* Choroszcz × *R. thyrsiflorus* Jaktorów, specially in the F_2 generation: more than a half of these

Table 8

Fertility of female plants in F_1 and F_2 hybrids R. thyrsiflorus × R. acetosa and R. thyrsiflorus × R. arifolius.

Cross		Hybrid generation	No. of plants	No. of plants			
♀	♂			fertile	semi-fertile	semi-sterile	sterile
R. acetosa × R. thyrsiflorus							
22 Choroszcz	× 61 Jaktorów	F_1	22	1	1	18	2
		F_2	176	-	12	57	107
R. thyrsiflorus × R. acetosa							
59 Jaktorów	× 3 Choroszcz	F_1	21	10	8	3	-
		F_2	200	40	85	58	17
163 Nowy Dwór	× 63 Jaktorów	F_1	78	3	27	48	-
		F_2	194	77	60	57	11
R. thyrsiflorus × R. arifolius							
183 Nowy Dwór	× 211 Kozi Grzbiet	F_1	56	2	10	43	1
		F_2	162	5	35	121	1
176 Nowy Dwór	× 86 Szałasiska	F_1	14	5	5	4	-
		F_2	104	8	18	71	7
R. arifolius × R. thyrsiflorus							
210 Kozi Grzbiet	× 162 Nowy Dwór	F_1	62	23	27	12	-
		F_2	205	87	102	16	-
129 Niedzica	× 162 Nówy Dwór	F_1	72	4	29	39	-
		F_2	130	76	51	3	-

F_2 plants did not set seeds at all, though they flowered quite regularly, whereas the other plants of both the F_1 and F_2 generations either manifested a reduced ability to set seeds or were semisterile. Controlled pollination carried out to obtain the F_3 generation produced not more than twenty or even fewer seeds per plant, whereas the number of seeds from controlled pollination of F_1 plants could even be a few hundred. In the backcross F_1 × *R. thyrsiflorus* the setting of seeds was at an equally low level as in F_2: most of these plants produced no seeds at all and the others were semisterile. In the backcross F_1 × *R. acetosa* the setting of seeds of most plants was at the normal level and there were no sterile plants.

Among the hybrids *R. thyrsiflorus* × *R. arifolius* the setting of seeds was at the lowest level in the cross *R. thyrsiflorus* Nowy Dwór × × *R. arifolius* Kozi Grzbiet: about 2/3 of the F_1 as well as of the F_2 plants had to be classified as semisterile. The setting of seeds by the semisterile plants of the F_2 generation was much lower than of the F_1 generation. Under conditions of controlled pollination the F_1 plants produced a few hundred seeds each, whereas the F_2 plants usually produced less than a score and very seldom more than 200 seeds.

A high level of sterility was also manifested by the cross *R. thyrsiflorus* Nowy Dwór × *R. arifolius* Szałasiska: in F_2 nearly 2/3 of the plants were semisterile and there were also some sterile individuals, which did not even produce floral shoots. The fertility of the F_1 plants was also reduced.

Generally speaking, ability to produce seeds was the most reduced in the crosses which included segregants with malformed leaves and inflorescences. This correlation seems to indicate that there was a certain degree of linkage between the factors causing sterility and the factors causing the malformation of the plants. In the F_2 generation the setting of seeds was always weaker than in F_1. Observations showed that in the F_3 generation the fertility of the female plants improved and could be even higher than of the F_1 generation.

Not all the seeds produced by the hybrids were well developed and in all the crosses the female plants produced a certain amount of empty seeds. The malformed seeds consisted only of the seed coat without the embryo or endosperm. The empty seeds were developed from both controlled and free pollination. The various plants of the same F_1 or F_2 population produced empty seeds in different proportions. No determinations were made of the amount of empty seeds, but rough estimates showed that the hybrids, in which the setting of seeds was at the lowest level, had the highest proportion of empty seeds. In the F_3 progenies, parallelly to the general improvement of fertility, the amount of empty seeds decreased. Empty seeds were also produced by some of the hybrids *R. acetosa* × *R. arifolius,* but here the number of plants producing empty seeds as well as the amount of empty seeds was very much lower than in the crosses with *R. thyrsiflorus.*

To obtain more information about the fertility of the female plants the germination rates of seeds obtained from controlled pollination were also determined (Table 9). The differences in the germination rates of the different crosses were on the whole small. Similarly, there were no significant differences of the germination rate between the seeds collected from hybrids and the seeds collected from intraspecific crosses. In the case of the hybrids *R. acetosa* × *R. thyrsiflorus* the germination rate of the seeds of the F_2 progeny was lower than of the F_1 progeny, but this effect was not observed in the case of the cross *R. thyrsiflorus* × *R. arifolius*: the seeds of two F_2 populations of the latter cross germinated even better than the seeds of the F_1 generation. In the case of the hybrids *R. acetosa* × *R. arifolius* the seeds from F_2 plants had a lower germination rate than in F_1, similarly to what was the case with the hybrids *R. acetosa* × *R. thyrsiflorus.*

Table 9

Seed germination in F_1 and F_2 hybrids among R. thyrsiflorus, R. acetosa and R. arifolius.

Cross		% germination	
♀	♂	F_1	F_2
R. acetosa × thyrsiflorus			
22 Choroszcze ×	61 Jaktorów	51,0	38,0
R. thyrsiflorus × acetosa			
59 Jaktorów ×	3 Choroszcz	50,0	-
163 Nowy Dwór ×	63 Jaktorów	44,2	28,8
R. thyrsiflorus × arifolius			
183 Nowy Dwór ×	211 Kozi Grzbiet	33,5	29,0
176 Nowy Dwór ×	86 Szałasiska	26,3	37,3
R. arifolius × thyrsiflorus			
210 Kozi Grzbiet ×	162 Nowy Dwór	32,7	57,0
129 Niedzica ×	162 Nowy Dwór	33,4	40,7
R. arifolius × acetosa /9 crosses/		46,3	30,0
R. acetosa × arifolius /4 crosses/			

Male plants

The fertility of the male plants, like of the female ones, differed greatly in the various crosses. There even were considerable differences of pollen fertility between the various flowers of the same plant. Plants were found with as much as 90 per cent of fertile pollen in some buds, whereas in the other buds nearly all the pollen was degenerated and only a few grains looked as if they were fertile. Sometimes the microspores degenerated already at the stage of tetrads. These extreme differences made the correct determination of the actual fertility of the particular plants very difficult, specially since only two buds from every plant were examined. E.g. in some crosses a certain amount of seeds was produced from controlled pollination under an isolator, though on acetocarmine smears all the pollen of the male plant used in this cross had been found to be completely degenerated. Moreover, the fertility of the male plants, like the fertility of the female plants, proved to be higher in the second than in the first year of growth. To obtain reliable comparative data on pollen fertility in the particular crosses the male individuals were divided in to three classes of fertility (Table 10):

1) plants with normal or little reduced pollen fertility,
2) plants producing semifertile pollen in some buds and completely degenerated pollen in other buds,
3) plants producing almost completely degenerated pollen.

In the cross *R. acetosa* × *R. thyrsiflorus* the greatest difference in male fertility was manifested by the F_1 progeny *R. acetosa* Choroszcz × *R. thyrsiflorus* Jaktorów, where pollen fertility ranged from almost normal (92.6 per cent) to almost completely sterile. Similar differences of pollen fertility were also observed in the F_2 generation the average pollen fertility of this generation being distinctly lower than the fertility in F_1. In the sterile buds the microspores usually degenerated already at the stage of tetrads. The degenerating tetrads often were malformed and consisted of different numbers of microspores, which were of different sizes. In the backcross F_1 × *R. thyrsiflorus* the degeneration of the microspores followed a similar pattern to that in F_2. On the other hand, in the backcross with *R. acetosa* the pollen degenerated at a later stage, when the tetrads had already separated, and the pollen grains always were well developed; the only exception here were two plants producing well developed and well staining pollen, which consisted of unseparated tetrads.

Among the hybrids *R. thyrsiflorus* × *R. arifolius* the lowest male fertility was manifested by the plants of the cross *R. thyrsiflorus* Nowy Dwór × *R. arifolius* Kozi Grzbiet: plants producing no fertile pollen occurred in the F_1, F_2 and F_3 generations. The sterility of these plants

T a b l e 10

Pollen fertility in F_1 and F_2 hybrids R. thyrsiflorus × acetosa and R. thyrsiflorus × arifolius.

Cross			Year of wege-tation	No. of male plants	Plants with normal buds		Plants with normal and degenerated buds		No. of sterile plants
♀	♂				No. of plants	% of good pollen	No. of plants	% of good pollen	
R. acetosa × R. thyrsiflorus									
		F_1	II	7	1	92.6	4	71.0	2
22 Choroszcz	× 61 Jaktorów	F_2	II	13	4	63.8	2	54.8	5
		F_3	II	0	-	-	-	-	-
18 F_1	× 61 Jaktorów	B	II	18	7	65.8	2	55.0	9
21 F_1	× 31 Choroszcz	B	II	5	2	80.0	-	-	3
R. thyrsiflorus × R. acetosa									
59 Jaktorów	× 3 Choroszcz	F_1	I	6	-	-	3	78.6	3
		F_2	I	8	1	79.8	3	57.1	4
		F_1	I	3	-	-	-	-	3
		F_1	II	3	3	73.3	-	-	-
163 Nowy Dwór	× 63 Jaktorów	F_2	I	9	4	71.3	-	-	5
		F_2	II	29	29	68.3	-	-	-
		F_3	II	5	5	84.2	-	-	-

cont. T a b l e 10

Cross			Year of wege-tation	No. of male plants	Plants with normal buds		Plants with normal and degenerated buds		No. of sterile plants
♀	♂				No. of plants	% of good pollen	No. of plants	% of good pollen	
R. thyrsiflorus × R. arifolius									
183 Nowy Dwór	× 211 Kozi Grzbiet	F_1	I	4	-	-	-	-	4
		F_1	II	2	1	71.6	-	-	1
		F_2	I	8	-	-	2	58.4	6
		F_2	II	14	8	50.3	5	51.6	1
		F_3	II	9	8	73.4	-	-	1
176 Nowy Dwór	× 86 Szałasiska	F_1	I	3	-	-	-	-	3
		F_1	II	7	3	69.8	2	62.5	2
		F_2	II	10	9	72.2	-	-	-
R. arifolius × R. thyrsiflorus									
210 Kozi Grzbiet	× 162 Nowy Dwór	F_1	I	2	1	85.6	1	82.1	-
		F_1	II	5	5	78.6	-	-	-
		F_2	II	12	12	78.2	-	-	-
		F_3	I	2	2	92.2	-	-	-
129 Niedzica	× 162 Nowy Dwór	F_1	I	2	-	-	-	-	2
		F_1	II	5	5	82.6	-	-	-
		F_2	II	2	2	82.1	-	-	-
		F_3	I	2	2	89.0	-	-	-
R. acetosa × R. arifolius		F_1	II	47	26	93.5	9	88.1	12
R. arifolius × R. acetosa		F_2	II	36	35	84.8	1	72.5	-

sometimes consisted in the drying off of the anthers before the pollen had time to develop. The fertility was specially low in the F_2 generation. In the F_3 generation pollen fertility distinctly improved.

The results indicate that in all the F_1 populations pollen fertility was lower than in the parental populations. In the F_2 generation male fertility was further reduced, but in the F_3 generation pollen fertility again appreciably improved. Thus, male fertility manifested the same regularity that was observed for female plants.

When comparing the male and female fertility of the plants from the particular crosses it is seen that on the whole it was at the same level. The reduced fertility of the female plants was usually associated with the semisterility of pollen. The great differences in the fertility of the hybrids from the particular crosses reflected the genetic differentiation of the parental taxa.

In the case of the hybrids *R. acetosa* × *R. arifolius* the fertility of the male plants from the particular crosses did not differ significantly. In F_1 populations more than a half of male plants had the normal pollen fertility (Table 10). In the remaining plants the pollen grains were always well developed, but in some buds they did not stain well making difficult the distinction of the sterile grains from the seemingly fertile ones. Such plants were classed as semisterile or sterile. Pollen fertility of the F_2 male plants was somewhat lower than in F_1. In two out of the thirteen examined F_2 plants of the cross *R. arifolius* Długa Hala × *R. acetosa* Jaktorów large pollen grains and pollen grains consisting of unseparated, often irregular dyads and tetrads were found. Large pollen grains were also found in a few F_1 and F_2 plants of the cross *R. acetosa* Choroszcz × *R. arifolius* Krościenko.

In general, the pollen fertility of the progenies of the crosses between *R. acetosa* and *R. arifolius* was not much lower than the fertility of the parental plants and this also applies to the fertility of seeds.

8. Cytology

Mitosis

The somatic chromosome number was established for 96 plants of 18 F_1 populations and in 59 plants of eight F_2 populations. Nearly all of the examined hybrids were diploids (Table 11). Of the F_1 hybrids only one plant from the cross *R. arifolius* Hala Długa × *R. acetosa* Jaktorów was a tetraploid ($2n = 28$). It was a female plant and its phenotype did not differ from the diploid individuals. It probably arose from the union of unreduced gametes produced by both the parental plants. In the F_1 hybrids *R. arifolius* Szałasiska × *R. acetosa* Choroszcz many T chromosomes and additional fragments were found (Fig. 38).

Table 11

Karyotypes of F_1 and F_2 hybrids among R. thyrsiflorus, R. acetosa and R. arifolius.

Cross		Generation	No. of plants examined	2n	Karyotypes established
♀	♂				
R. acetosa × R. thyrsiflorus					
22 Choroszcz	× 61 Jaktorów	F_1	8	14-15	2X+10i+j+v/3/*; 2X+9i+j+v+T/2/
		F_2	12		2X+11i+v/1/
R. thyrsiflorus × R. acetosa					
59 Jaktorów	× 3 Choroszcz	F_1	5		2X+10i+j+v/1/
		F_2	5		2X+12i/1/; 2X+10i+j+T/1/; 2X+10i+v+T/1/; 2X+9i+j+v+T/2/;
163 Nowy Dwór	× 63 Jaktorów	F_1	8		
		F_2	6		
R. thyrsiflorus × R. arifolius					
183 Nowy Dwór	× 211 Kozi Grzbiet	F_1	4		2X+8i+3j+v/1/
		F_2	12		X+2Y+11i+v/1/; X+2Y+11i+j/1/; 2X+10i+2v/1/
176 Nowy Dwór	× 86 Szałasiska	F_1	not examined		
		F_2	5	14-15	2X+12i/1/; 2X+8i+2v+j+T/2/; 2X+9i+j+v+T/1/
R. arifolius × R. thyrsiflorus					
210 Kozi Grzbiet	× 162 Nowy Dwór	F_1	7		2X+10i+j+T/1/; 2X+9i+j+2T/1/
		F_2	5		2X+11i+j/2/; 2X+12i/1/
129 Niedzica	× 162 Nowy Dwór	F_1	8		2X+11i+v/1/
		F_2	3		2X+11i+v/1/; 2X+10i+v+T/1/; 2X+9i+v+2T/1/
			1	22	2X+2Y+2v+16i/1/

cont. Table 11

Cross ♀	Cross ♂	Generation	No. of plants examined	2n	Karyotypes established
R. acetosa × R. arifolius					
12 Choroszcz	× 149 Krościenko	F_1	3	14-15	2X+11i+j/1/
8 Choroszcz	× 86 Szałasiska	F_1	4		2X+9i+j+2T/1/; 2X+11i+j/1/
R. arifolius × R. acetosa					
91 Szałasiska	× 3 Choroszcz	F_1	3	14-15	2X+8i+4T/1/; 2X+9i+j+2T/1/; 2X+8i+4T+3 fragments /1/
104 Niedzica	× 20 Choroszcz	F_1	4		2X+11i+j/1/
91 Szałasiska	× 19 Choroszcz	F_1	4		2X+10i+j+T/1/
135 Niedzica	× 63 Jaktorów	F_1	7		2X+10i+v+j/1/; 2X+11i+v/3/; 2X+10i+v+T/1/
154 Pustelnia	× 63 Jaktorów	F_1	6		2X+10i+j+v/2/
99 Rezerwat Orkana	× 24 Choroszcz	F_1	6		2X+9i+2j+T/1/; 2X+11i+j/1/; 2X+11i+v/1/
97 Rezerwat Orkana	× 19 Choroszcz	F_1	5		2X+10i+j+T/1/; 2X+9i+j+v+T/1/
		F_2	3		2X+10i+j+T/1/
123 Hala Długa	× 20 Choroszcz	F_1	5		2X+11i+T/1/; X+2Y+9i+j+2T
127 Hala Długa	× 63 Jaktorów	F_1	5		
127 Hala Długa	× 63 Jaktorów	F_1	1	28	

[*] No. of plants with the same karyotype.

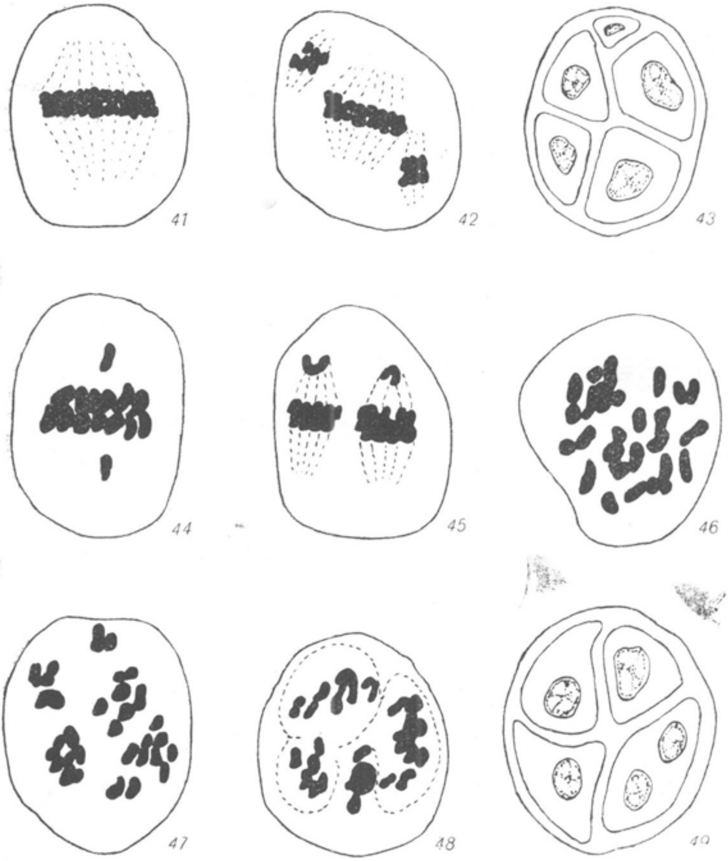


Fig. 38-40. Root tips metaphases. 38 — F_1 *R. arifolius* Szałasiska × *R. acetosa* Choroszcz ♀ 2n = 14 ($2X + 8i + 4T$ + 3 fragments); 39-40 — *R. arifolius* Niedzica × *R. thyrsiflorus* Nowy Dwór: 39 — F_1 2n = 22 ($2X + 2Y + 2v + 16i$), 40 — F_2 - 2n = 16 ($X + 2Y + 9i + 2j + v + T$). × 1870

Fig. 41-49. Meiotic disturbances in PMCs of F_1 and F_2 hybrids *R. acetosa* Choroszcz × *R. thyrsiflorus* Jaktorów. 41 — F_1 — MII with chromosomes in one plate; 42 — F_1 — MII with three plates; 43 — F_1 — abnormal tetrad; 44 — F_2 — univalentes in MI; 45 — F_2 — MII with chromosomes outside the plates; 46 — F_2 — PMC with double somatic chromosome number; 47 — F_2 — PMC with spindle disturbances and abnormal chromosome separation; 48 — F_2 — abnormal tetrad formation in PMCs with disturbed chromosome separation; 49 — F_2 abnormal tetrad. × 1870

The T chromosomes and the additional fragments were probably introduced by *R. arifolius*, since the male parent of *R. acetosa* had the simple karyotype $X + 2Y + 12i$. The presence of the additional fragments had no influence on the morphology of the plants and their fertility.

In the F_2 generation there was one plant with the polyploid chromosome number: it was a bisexual plant found in the F_2 progeny of the cross *R. arifolius* Niedzica × *R. thyrsiflorus* Nowy Dwór and was a semifertile triploid with $2n = 22(2X + 2Y + 2v + 16i)$ (Fig. 39). The progeny of the triploid consisted of four plants obtained from free pollination; in two plants the karyotypes were found to be $2n = 16(X + 2Y + 9i + 2j + v + T)$ (Fig. 40) and $2n = 18(X + 2Y + 14i + v)$, i.e. they were aneuploids. The bisexual plants in the F_2 progenies of the crosses *R. thyrsiflorus* Nowy Dwór × *R. acetosa* Jaktorów and *R. thyrsiflorus* Nowy Dwór × *R. arifolius* Szałasiska probably also were polyploids, but their chromosome number was not established. The special type of polyploidy found among the F_2 hybrids *R. thyrsiflorus* Puławy × *R. acetosa* Choroszcz was described in an earlier report (Świetlińska 1960), but the problem is still being investigated.

The counts of the chromosome numbers in the hybrids and in the parental plants indicate that polyploidy occurs more frequently in hybrids (in particular in the crosses *R. acetosa* × *R. thyrsiflorus* and *R. arifolius* × *R. thyrsiflorus*) than in the natural populations of the parental species.

Table 11 lists the karyotypes that were found in the hybrids. The various F_1 and F_2 plants of the same cross often had different karyotypes. This is comprehensible in view of the asymmetrical karyotypes found in the parental populations (Table 3). Fig. 24 shows metaphasal plate of F_2 hybrid *R. arifolius* Szałasiska × *R. acetosa* Choroszcz with karyotype $2X + 10i + j + T$

Microsporogenesis

The results of the investigations on microsporogenesis in the hybrids are listed in Table 12. These data indicate that in the hybrids *R. acetosa* × *R. thyrsiflorus* and *R. arifolius* × *R. thyrsiflorus* meiotic irregularities in PMCs were of frequent occurrence. The greatest meiotic irregularities occurred on the whole in the crosses with a high degree of malformation of the F_2 segregants and a high sterility.

In hybrid populations not all the F_1 and F_2 plants manifested meiotic irregularities. It was found, moreover, that in most plants microsporogenesis could have a different course in the various buds of the same plant and even in the various anthers of the same flower. The mass degeneration of pollen and of the whole anthers in plants with a regular meiosis was also of frequent occurrence.

In the hybrids the conjugation of chromosomes was usually regular. At diakinesis one trivalent *Y—X—Y* and six bivalents were formed. Single univalents at metaphase I were found only in a few PMCs of the hybrids *R. acetosa* Choroszcz × *R. thyrsiflorus* Jaktorów. The disturbance of microsporogenesis observed in the hybrids consisted mainly in the irregular parting of the chromosomes after the first and the second meiotic divisions.

In two F_1 hybrids *R. acetosa* Choroszcz × *R. thyrsiflorus* Jaktorów complete degeneration of the tetrads occurred in many buds, though no meiotic irregularities were observed. In a third plant in most of the buds the meiotic divisions were regular, but in some buds irregularities of the second division were observed: at metaphase II the chromosomes sometimes formed one common plate resembling the metaphase plate of a restitution nucleus (Fig. 41) or besides the large common plate also a few smaller ones were formed (Fig. 42) indicating that the parting of chromosomes at anaphase I had been disturbed. The irregular tetrads that were often formed contained additional nuclei (Fig. 43). The irregular tetrads degenerated without separating into individual microspores. In many buds regularly developed tetrads also degenerated.

In two F_2 hybrids about six per cent of the PMCs had single univalents at metaphase I (Fig. 25, 44). In some PMCs parting of chromosomes at anaphase I was regular and lagging bivalents and chromatin bridges were not observed more often than in the parental taxa. At metaphase II chromosomes laying outside the plate were sometimes found (Fig. 45). In some buds there were PMCs in which instead of regular stages of the second divisions all the chromosomes scattered about in disorder (Fig. 46): sometimes in such cells the number of chromosomes was double their normal, diploid number. In these PMCs the division of the chromosomes occurred probably without the division of the nuclei. Such irregularities were probably associated with the misfunction of the spindle in the first and the second divisions. In the PMCs of some buds the chromosomes assembled in chance groups (Fig. 26, 27, 47) and after some time cell walls began to form inbetween them (Fig. 48); the final effect of this behaviour was the formation of irregular "tetrads" composed of different numbers of microspores (Fig. 49). Tetrads of this kind usually degenerated before they separated into the individual microspores.

In the backcross F_1 × *R. thyrsiflorus* the meiotic irregularities were similar to what was found in F_2 and consisted in the complete break-down of the functions of the spindle. The normal formation of the tetrads was observed only in very few buds. On the other hand, in the backcross F_1 × *R. acetosa* no characteristic irregularities of meiosis were found, but even so the pollen produced by these plants was partly

T a b l e 12

Meiosis in PMCs of F_1 and F_2 hybrids among R. thyrsiflorus, R. acetosa and R. arifolius.

Cross		Hybrid generation	No. of plants		Meiotic disturbances
♀	♂		examined	with meiotic disturbances	
R. acetosa × R. thyrsiflorus					
22 Choroszcz	× 61 Jaktorów	F_1	3	1	spindle disturbances abnormal tetrads
		F_2	4	2	univalents in MI, spindle disturbances in AI and II, abnormal tetrads
18 F_1	× 61 Jaktorów	B	3	2	
21 F_1	× 31 Choroszcz	B	2	-	
R. thyrsiflorus × R. acetosa					
57 Jaktorów	× 3 Choroszcz	F_1	2	2	univalents in MI, lagging bivalents and inversion bridges in AI, bridges in TI
		F_2	1	-	
163 Nowy Dwór	× 63 Jaktorów	F_1	1	-	
		F_2	4	-	

cont. T a b l e 12

Cross		Hybrid generation	No. of plants		Meiotic disturbances
♀	♂		examined	with meiotic disturbances	
R. thyrsiflorus × R. arifolius					
183 Nowy Dwór	× 211 Kozi Grzbiet	F_1	1	1	lagging bivalents and inversion bridges in AI, bridges in TII
		F_2	7	5	inversion bridges AI, bridges in AII, restitution nuclei, diads
176 Nowy Dwór	× 86 Szałasiska	F_1	4	-	
		F_2	3	1	inversion bridges in AI, bridges in interkinesis and TII
R. arifolius × R. thyrsiflorus					
210 Kozi Grzbiet	× 162 Nowy Dwór	F_1	3	3	lagging bivalents and inversion bridges in AI
		F_2	3	1	abnormal tetrads
129 Niedzica	× 162 Nowy Dwór	F_1	3	3	lagging bivalents and inversion bridges in AI, bridges in interkinesis, MII, AII, restitution nuclei, diads
		F_2	3	-	
R. arifolius × R. acetosa		F_1	9	-	
R. acetosa × R. arifolius		F_2	10	2	abnormal tetrads

sterile or the seemingly normal pollen grains consisted of unseparated tetrads.

In the F_1 hybrids *R. thyrsiflorus* Jaktorów × *R. acetosa* Choroszcz some few PMCs had single univalents at metaphase I. At anaphase I of some PMCs bridges and acentric fragments were found (Fig. 50). At anaphase I lagging bivalents and chromatin bridges persisting to the late telophase (Fig. 51) were of frequent occurence. The course of the second meiotic division was regular. Normal tetrads were produced in all the buds. Microsporogenesis was examined in only one F_2 plant and no irregularities were found.

In F_1 hybrids *R. thyrsiflorus* Nowy Dwór × *R. arifolius* Kozi Grzbiet at anaphase I there were lagging bivalents and in many PMCs bridges with acentric fragments indicating that inversion had taken place. Chromatin bridges without fragments often persisted into the interphase stage. The second meiotic division proceeded without disturbance and regular tetrads were formed. In many buds the wholesale degeneration of tetrads however occurred. In some PMCs of F_2 hybrids there were chromatin bridges, lagging bivalents, and bridges with acentric fragments. Chromatin bridges were often found also in the second meiotic division (Fig. 52). The parting of chromosomes at anaphase II was in some cases so irregular that triads instead of tetrads were formed (Fig. 53). In some PMCs owing to the irregular separation of chromosomes at anaphase I restitution nuclei were formed. The division of the restitution nuclei was usually greatly retarded as compared to the cells with regular meiosis. In the anthers there were among the developing tetrads some single PMCs at the stages of metaphase or anaphase of the restitution nucleus. At metaphase of the restitution nuclei chromosomes lying outside the plate were frequent (Fig. 54) and at anaphase there were chromatin bridges and single fragments or whole chromosomes remaining on the spindle (Fig. 55). After the division of the restitution nuclei diads were formed (Fig. 56).

In some hybrids of the cross *R. thyrsiflorus* Puławy × *R. acetosa* Choroszcz after the first meiotic division diads were formed and the second division was completely omitted. By such plants unreduced gametes were produced and in the next hybrid generation polyploids occurred (Świetlińska 1960).

In the cross *R. arifolius* Kozi Grzbiet × *R. thyrsiflorus* Nowy Dwór at anaphase I there were lagging bivalents and frequent bridges with acentric fragments, but these were the only irregularities of meiosis that were observed. The analysis of the metaphase plates of the mitotic divisions in pollen showed, however, that in not all the PMCs the chromosomes were regularly segregated during microsporogenesis. Usually there were eight or seven chromosomes (Figs 60, 61), but there were grains with nine (Fig. 62), ten (Fig. 63) or more chromosomes.

Fig. 50-59. Meiotic disturbances in **P**MCs of F_1 and F_2 hybrids among *R. acetosa*, *R. arifolius* and *R. thyrsiflorus*. 50-51. F_1 *R. thyrsiflorus* Jaktorów × *R. acetosa* Choroszcz: 50 — inversion bridge with acentric fragment in AI, 51 — chromatin bridge in TI; 52-56 — F_2 *R. thyrsiflorus* Nowy Dwór × *R. arifolius* Kozi Grzbiet: 52 — chromatin bridge in TII, 53 — abnormal tetrad, 54 — restitution nucleus metaphase with few chromosomes outside the plate, 55 — restitution nucleus with lagging chromosome, 56 — diad resulting from restitution nucleus division; 57-58 — F_2 *R. thyrsiflorus* Nowy Dwór × *R. arifolius* Szałasiska: 57 — chromatin bridge in AII, 58 — chromatin bridge in MII; 59 — F_1 *R. arifolius* Niedzica × *R. thyrsiflorus* Nowy Dwór — chromatin bridges in TII. × 1870

Fig. 60-63. Pollen grains metaphases in F_1 *R. arifolius* Kozi Grzbiet × *R. thyrsiflorus* Nowy Dwór. 60 — $n = 8(2Y + j + 5i)$; 61 — $n = 7(X + 5i + j)$; 62 — $n = 9(2Y + 7i)$; 63 — $n = 10(2Y + 2j + 6i)$. × 1000

In one plant of the F_2 generation irregular microspores were found: among the normally developed pollen grains there were also some enormous microspores of irregular shapes containing several nuclei. These usually degenerated, but in a few the mitotic division of some nuclei was observed.

In the F_1 hybrids *R. thyrsiflorus* Nowy Dwór × *R. arifolius* Szałasiska all the pollen in some buds was completely degenerated, though no irregularities of meiosis were observed. In the F_2 plants bridges with acentric fragments and chromatin bridges without fragments were of frequent occurrence at anaphase I. The bridges often persisted into the interphase and are visible in metaphase II (Fig. 58). Chromatin bridges were also observed at anaphase II (Fig. 57). In some buds all the pollen degenerated as in the F_1 plants. Fig. 29 shows an anther in which the pollen was developing regularly; the nuclei of these pollen grains are at the prophase stage of the mitotic division. Fig. 30 shows another anther with completely degenerated pollen the degeneration of the anther tissue being also visible.

In the F_1 hybrids *R. arifolius* Niedzica × *R. thyrsiflorus* Nowy Dwór the parting of the bivalents at anaphase I was obstructed. Chromatin bridges (Fig. 28), lagging chromosomes, and bridges with acentric fragments were of frequent occurrence. The bridges from anaphase I persisted into the interphase and were still visible at metaphase II. In many PMCs chromatin bridges were visible at telophase II (Fig. 59). In some anthers there were rare PMCs in which, owing to the failure of the chromosomes to part at anaphase I, restitution nuclei were formed. The division of the restitution nuclei was usually simultaneous with the telophase of the second division in the other PMCs. After the division of restitution nuclei diads were formed. Such F_1 plants probably produced sometimes unreduced gametes with 15 chromosomes ($X + 2Y + 12a$). It seems, therefore that the bisexual plant with 22 chromosomes ($2X + 2Y + 18a$) found among F_2 hybrids developed by the union of a normal female gamete $X + 6a$ with the unreduced male gamete $X + 2Y + 12a$. In the F_2 generation no irregularities of microsporogenesis were observed, but similarly as in the F_1 generation the pollen of some buds was completely degenerated.

In the case of the crosses between *R. acetosa* and *R. arifolius* the microsporogenesis of the F_1 plants was as regular as in the parental plants. In one of the F_1 plants of the cross *R. acetosa* Choroszcz × *R. arifolius* Krościenko some large pollen grains were found; it seems that in this individudal unreduced gametes must have developed as the result of the infrequent irregularities of microsporogenesis; however, the microsporogenesis of this plant was not investigated. In the F_2 generation the microsporogenesis was wholly regular similarly as in the F_1 hybrids. The only exceptions were two F_2 plants of the cross *R. arifolius* Długa

Hala × *R. acetosa* Jaktorów, which in pollen examinations were found to produce irregular tetrads; this seems to indicate that in this cross disturbances of microsporogenesis may have occurred in some plants, but that their incidence was low.

The general conclusion to be drawn from the cytological investigations is that in the F_1 and F_2 progenies *R. acetosa* × *R. arifolius* the disturbances of microsporogenesis were much less frequent than in the hybrids *R. acetosa* × *R. thyrsiflorus* and *R. arifolius* × *R. thyrsiflorus*. The incidence of these irregularities was so low that they were revealed only by the large scale examinations of pollen fertility.

DISCUSSION

1. The crossability of the parental species

The crosses carried out between *R. arifolius*, *R. thyrsiflorus*, and *R. acetosa* show that these taxa are not separated by barriers making impossible the obtaining of hybrids. The crossability is not, however, the same for all the various populations of the parental species. E.g. *R. acetosa* is the easiest to cross with *R. thyrsiflorus* from Nowy Dwór: the high crossability in this case is obviously caused by that the exceptionally early flowering of the Nowy Dwór population eliminates the seasonal isolation, which under natural conditions makes the crosses difficult.

The seeds obtained from the interspecific crosses are always well developed and their germination rate varies over the same range as in the case of the intraspecific crosses. The differences in the germination rates of seeds manifested by the intraspecific as well as by the interspecific crosses and the different behaviours of the hybrids obtained from the various crosses evidence that the genetic variability of the investigated group of plants is high.

This kind of differentiation is common to dioecious species and often causes different results in intra- and interspecific crosses. E.g. V. Grant and A. Grant (1960) have found complete isolation barriers between some geographic races of *Gilia exilis*, whereas other races of this species crossed without any difficulty.

2. The vigour and the viability of the hybrids

In all the combinations of the studied taxa the F_1 hybrids manifest a normal viability. The vigour of the hybrids is not lower than of the parents and in some of the crosses hybrids even manifest distinct heterosis. The F_1 hybrids *R. arifolius* × *R. acetosa* have different environmental requirements: the progenies of some combinations when planted on too dry a soil prospered in the summer but perished in the winter, whereas when planted on a more suitable soil they vegetated normally through two full seasons. This means that some combinations of the hybrids of the mountain *R. arifolius* and the lowland *R. acetosa* have a reduced toleration range to environmental conditions.

A similar example of the different behaviour of hybrids in different environments is provided by the crosses between the lowland and mountain races of *Potentilla glaudulosa* (Clausen 1949, Clausen & Hiesey 1958): the clones of the same F_1 individuals grew either very vigourously or very weakly depending on the altitude above sea level.

The F_2 hybrids of the crosses *R. acetosa* × *R. arifolius* are as vigourous and as viable as the F_1 progenies, but in some crosses *R. thyrsiflorus* × *R. acetosa* and *R. thyrsiflorus* × *R. arifolius* the F_2 generation has, as compared to F_1, a much reduced vigour and viability manifested by small, dwarf, or malformed plants or death of seedlings in the first weeks after germination. In one cross *R. acetosa* × *R. thyrsiflorus* the malformations affect a large proportion of plants and in some cases change the morphology of the aberrant plants so much that they in no way resemble the parental species. The aberrant types usually arise as the result of the recombination of the genetic factors and have been reported in many interspecific crosses. Clausen (1926) describes aberrant types of the hybrids *Viola arvensis* × *Viola tricolor* and Stebbins (1958a) quotes several other examples.

The drop of the viability and vigour of the F_2 hybrids has been observed in many plant groups. Stebbins (1958b) defines this phenomenon as hybrid breakdown including under this term the degeneration and the sterility of the F_2 and further hybrid generations.

The lethality and the weakness of the hybrids is generally attributed to gene incompatibility of the parental species or in less frequent instances to the specific influence of genes. In the case of *Rumex* it seems that some populations or even the particular biotypes carry genes or sets of genes which in combination with the genome of the representatives of another species cause the reduced viability or the malformation of the hybrids. In the F_1 generation these factors occur in the heterozygous state and do not manifest themselves phenotypically, whereas in the F_2 generation homozygous combinations are segregated and if they are not eliminated at the germination stage they cause the lethality or the weakness of the plants. The low germination of the seeds of the F_2 generation points to the even stronger elimination of the zygotes: in F_3 this leads to the less frequent occurrence of individuals with disharmonious combinations of genes. The normal level of viability in the F_2 generation of the crosses between *R. acetosa* and *R. arifolius* indicates that the genes of these two taxa do form harmonious combinations in the hybrids.

3. The inheritance of morphological and physiological characters

Morphological characters

The shape of leaves and the inflorescence type in the F_1 hybrids are developed intermediately between the parents. In the F_2 generation these traits manifested a continuous variation, which means that they are inherited polygenically.

The shape of leaves of F_1 plants from almost all the crosses tends to resemble the maternal rather than the paternal parent. Similarly, in F_2 the segregants with leaves shaped as in the maternal parent usually predominate. These differences are most strongly manifested in the backcrosses.

The seeds colour analysis indicate that in *Rumex* the seed colour is not inherited polygenically, but is seems to depend on a few determining factors. However, on the ground of the experiments reported here no more precise conclusion can be drawn about the nature of these factors and the way their influence is exerted, the parental species being highly heterozygous and the assembled data too fragmentary.

Flowering

R. acetosa and *R. arifolius* have different light and temperature requirements than *R. thyrsiflorus*, the former two species contrary to the latter flowering only after a period of low temperatures and short days.

The F_1 hybrids from almost all the various crosses *R. thyrsiflorus* × × *R. acetosa* and *R. thyrsiflorus* × *R. arifolius* flower in their first year similarly as *R. thyrsiflorus*. The date of flowering of the F_1 plants very distinctly depends on the direction of the cross. When *R. thyrsiflorus* is the female parent the F_1 progenies almost always flower earlier than in the reciprocal crosses.

In the first year of growth of the F_2 generation segregation occurs into plants that do not produce the flower shoots (like *R. acetosa* and *R. arifolius*), into those that produced the flower shoots but do not flower (intermediate), and into those that flower in the usual way (like *R. thyrsiflorus*). When reciprocal crosses are compared the proportion of plants flowering in their first year is appreciably higher when *R. thyrsiflorus* is the maternal parent.

In the second year of the F_1 generation the flowering time is intermediate between the parents with a slight shift towards the flowering time of the maternal parent. The F_2 progenies flower for a long time, some of the plants simultaneously with one or the other parent and the others intermediately between the parents.

In almost all the crosses the behaviour of the hybrids follows this typical pattern. The only exception worth mentioning is the cross *R. thyrsiflorus* Nowy Dwór × *R. acetosa* Choroszcz, which failed to manifest the influence of the maternal parent. This exception shows that among the parental species there are differences in physiological properties.

Under conditions of field experiments it is very difficult to establish the genetic basis of the processes that make the plants flower, since the time of flowering is highly variable and depends on seasonal conditions. The behaviour of the progenies of crosses between climatic and seasonal races has been fully investigated by Clausen and Hiesey (1958). The examples described by these workers indicate that the flowering of plants usually depends on numerous physiological stages each controlled by whole sets of genes and rarely by a few genes. A relatively simple instance is that of *Gilia capitata staminea* and *G. c. chamissonis* (Grant 1956), where the difference in the flowering time of these two varieties are determined by two genes only. The experience with the *Rumex* hybrids proves that they are a very convenient group of plants for this kind of investigations. It seems plausible to expect that a more detailed analysis of the hybrids would allow to establish, at least in the case of some ecotypes, the genetic basis of the physiological processes controlling the flowering of these plants.

The influence of the maternal parent

The strong influence of the maternal parent is clearly seen when the *Rumex* hybrids from reciprocal crosses are compared. The morphological traits and the physiological properties of the F_1 and F_2 generations resemble much more the population of the maternal parent. In the case of the *Rumex* hybrids the differences between the reciprocal crosses may be caused by cytoplasmic influences, but the possibility cannot be disregarded that they are merely the effect of the heterozygosis of the parental species. Since in all experiments various plants have been crossed, the results of reciprocal crosses refer in fact to whole populations and not actual genotypes. The well marked domination of the maternal characters in the shape of leaves and the flowering times recurring in almost all the crosses seems, however, to indicate that in these hybrids we have an instance of maternal influence or of cytoplasmic inheritance.

Polyploidy

Polyploid individuals have been found in two natural populations of *R. arifolius*, in the F_1 progeny of the cross *R. arifolius* × *R. acetosa*, in the F_2 and F_3 progenies of the cross *R. thyrsiflorus* × *R. acetosa*, and in the F_2 progeny of the cross *R. arifolius* × *R. thyrsiflorus*. With the exception of the cross *R. thyrsiflorus* Puławy × *R. acetosa* Choroszcz, where whole polyploid lines have been obtained in F_2 and F_3 (Świetlińska 1960), in all the other crosses the polyploid plants occur only sporadically.

Cytological investigations have shown that the polyploids arise from the union of unreduced gametes, which may develop either by the failure of the first division (restitution nuclei) or by the failure of the second division.

The process of the formation and the division of the restitution nuclei in *Rumex* has been investigated and described by Żuk (1963) who thinks that the formation of restitution nuclei is caused by the lack of synchronism between the conjugation of chromosomes and the formation of the spindle. In the cases observed by the author the cause of the formation of the restitution nuclei seems to be rather the presence of chromatic bridges; a similar interpretation was advanced by Andersson (1947) for *Picea* and by Darlington (1930) for *Prunus*.

The development of unreduced gametes owing to the failure of the second meiotic division in the hybrids *R. acetosa* × *R. thyrsiflorus* was described and interpreted in an earlier report (Świetlińska 1960); the same effect in the hybrids *R. arifolius* × *R. thyrsiflorus* was described by Żuk (1963).

Sterility of the hybrids and its causes

The fertility of the interspecific *Rumex* hybrids has been found to be strongly reduced. Many instances of seed and pollen sterility and of the degeneration of whole anthers soon after the end of meiosis have been described earlier in this report. A separate group of sterile plants consists of individuals, which fail to develop flower shoots and are thus unable to flower. The reduced fertility occurs mainly in the crosses *R. thyrsiflorus* × *R. acetosa* and *R. thyrsiflorus* × *R. arifolius*, but the degree of sterility is not everywhere the same and depends on the biotypes used for the crosses. In the particular F_1 and F_2 progenies there are differences of fertility among the male as well as the female plants. This behaviour pattern is attributed to the segregation of the genetic factors determining sterility. Similar differences in the fertility of hybrids have been found by Grant (1956) in the crosses *Gilia millefolia* × *G. achilleaefolia*: in this case the differentiation of fertility was caused by the segregation of independent genetic factors determining the sterility of pollen and seeds. In the hybrids *R. thyrsiflorus* × *R. acetosa* and *R. thyrsiflorus* × *R. arifolius*, which manifest a high degree of sterility in the F_1 and F_2 generations, a marked improvement of fertility occurs in the F_3 generation. The causes of the improving fertility in the further hybrid generations when the chromosome number is not doubled has been discussed by Stebbins (1958b) and by Grant (1958): these workers attribute the improved fertility to the supplementary factors of sterility, which can, when they segregate, give rise to wholly fertile lines in the progeny of semisterile F_1 and F_2 hybrids.

The causes of sterility in *Rumex* hybrids have not as yet been fully explained and what is known refers only to the male plants, whereas nothing is known about the causes of female sterility, since neither macrosporogenesis nor the development of seeds have been investigated.

The symptoms of the sterility of female plants are the malformation of the flowers, the low rate of seed setting, and the setting of malformed seeds. The completely sterile plants either do not set seeds at all, though their flowering is normal, or they set a small amount of seeds which do not germinate. Seed sterility may have different causes. Håkansson (1952) has found that in *Galeopsis pubescens* seed sterility is associated with the malformation of the embryo sac, the failures of fertilization, or the inhibited development of the endosperm or the embryo. The machanism of seed sterility in the *Rumex* hybrids may be similar but to confirm this supposition special embryological investigations would be necessary; nothing else is known at present than that the malformed seeds have only the fruit coat which contains neither endosperm nor embryo. It seems that in the *Rumex* hybrids the development of nothing but the fruit coat (the so-called parthenocarpy) may be stimulated by fertilization or by the initial stages of the development of the endosperm and the zygote. In plants, which set no seeds at all (not even parthenocarpic fruits), fertilization probably never takes place. Löve (1942, 1949) has found that in *Rumex* seeds can be set without pollination (agamospermy). The plants obtained from such seeds have the chromosome number 2n = 14 and their karyotype is identical with the karyotype of the maternal plant. In the plant material of this investigation no evidence pointing to the occurrence of agamospermy has been found.

Among the identified causes of male sterility there are instances of both genic and chromosome sterility. The occurrence of chromosome sterility has been deduced from the behaviour of the chromosomes in meiosis. Although, the conjugation of the chromosomes at diakinesis and metaphase I is usually regular, at anaphase I the structural differentiation of the chromosomes is evident: in many PMCs chromatin bridges with acentric fragments have been found. These irregularities indicate that the structural differentiation of chromosomes among other are inversions, which usually lead to the development of spores with duplications and deficiences. Inversions causing hybrid sterility occur in many plant groups: Clausen (1951) reported them in the crosses

Holocarpha virgata × *H. Heermanii*, Bernström (1952) in interspecific hybrids of *Lamium*, Brock (1954) in the *Lilium* hybrids, and Heiser (1949) in the crosses *Helianthus annus* × *H. Bolanderi*.

The variation in the autosome's morphology and the presence of bridges without acentric fragments at meiosis indicte the probable occurence of translocations which may also contribute to chromosomal sterility.

Genic sterility of the *Rumex* hybrids may be manifested in different ways. The degeneration of all the pollen in some anthers probably caused by the misfunctioning of the tapetum cells is certainly the result of genic sterility at the diplophase. Some irregularities in microsporogenesis also seem to be the manifestation of genic sterility at the diplophase: all the irregularities in the formation of the spindle are among the most important examples of the gene determined distrubances of meiosis.

The irregularities in the spindle function found in the cross *R. acetosa* Choroszcz × *R. thyrsiflorus* Jaktorów results in production of microspores with unbalanced chromosome numbers, absolutely incapable to perform their normal functions. Irregularities very much like the ones here described have been fully investigated by M. S. Walters (1958, 1960) in the intersectional crosses *Bromus trinii* × *B. carinatus*.

In the parental species *R. acetosa*, *R. arifolius* and *R. thyrsiflorus* and in the interspecific hybrids chromatin bridges without acentric fragments are of frequent occurence at anaphase I. In the parental taxa the chromatin bridges are usually associated with the retarded separation of some bivalents and they always break towards the end of anaphase I. In some instances bridges without fragments found in the interspecific hybrids are of different kind: they do not break at anaphase I, but persist into interkinesis and metaphase II and are still visible at anaphase of the second division. The chromatin bridges cause the irregular parting of the chromosomes and may be one of the reasons of the reduced viability of the gametes.

The chromatin bridges not associated with inversions have been often reported and are frequent in interspecific hybrids. Having observed bridges at anaphase I of the hybrids *G. millefolia* × *G. achilleaefolia* Grant (1952) atributes their formation to misfunctions in the mechanism of the chiasmata; the symptoms of these misfunctions are the difficulties in the formation of the chiasmata and the irregularities in their separation.

Another cause of the formation of the chromatin bridges may be the genetically controlled breaking of chromosomes at prophase of meiosis and the subsequent reunion of their ends: if in this process the ends of sister chromatids are united, then the bridges occur also at anaphase of the second division. This behaviour pattern has been observed by Brock (1954) in *Lillium*, by Lamm (1945) in *Solanum*, and by Rees (1955) in inbred rye. The breaking and the subsequent reunion of chromosomes is of a very frequent occurrence in the interspecific *Bromus* hybrids, where it has been studied in detail by M. S. Walters (1957), who thinks that this behaviour is determined by the collaboration of gene sets of the parental species combined in the hybrids. It is possible that the chromatin bridges observed in the *Rumex* hybrids are also associated with the breaking of chromosomes, but this is only a supposition requiring more detailed cytological investigations.

A high level of pollen sterility may occur in plants with no irregularities of meiosis. In these plants the sterility of the pollen must be attributed to the segregation to the gametes of the lethal combinations of genes, which means that this is a case of gene sterility at the haplophase, a source of sterility frequent in interspecific hybrids. In a comprehensive review of the sources of sterility in hybrids Stebbins (1958a) points out, however, that similar symptoms may be produced by small structural differences in chromosomes, since the segregation of these small differences is the same as of genes. In the case of the *Rumex* hybrids there are no data indicating whether the sterility of these plants is caused by genic factors of the haploid type or by chromosomal factors of the type defined by Stebbins as cryptic structural hybridity.

Taxonomic relationships

The experimental data indicate that there are no isolation barriers between *R. acetosa* and *R. arifolius*. Intercrossing between the two species is unobstructed, the viability of the hybrids is normal, and the hybrid fertility is not significantly reduced. In the F_1 and F_2 generations the course of meiosis is regular. The morphology of the pollen of the hybrids indicates that meiotic irregularities leading to the formation of unreduced gametes may occur sporadically similarly as is also the case in the parental species. The differences between *R. acetosa* and *R. arifolius* mainly consist in the shape of leaves, the colour of seeds, and the ecological requirements. The two species differ, moreover, by the incidence of the particular types of autosomes: the autosomes of types j and v are much more frequent in *R. arifolius* than in *R. acetosa*.

According to Pawłowski (1956) *R. acetosa* and *R. arifolius* have widely overlapping distributions in the Tatry Mts. The two species are very similar and difficult to distinguish in this area and Pawłowski thinks that they are connected by intermediate forms, which probably are hybrids. Kornaś (1957) found that in the Gorce Mts. *R. acetosa* is common in the foot-hills and in the lower part of the mountain-forest zone giving way to *R. arifolius* higher up in the lower mountain-forest zone. The highest altitudes at which stands of *R. acetosa* have been found are Mt. Wasielka (1010 meters above sea level) and the Hala Długa ridge (1200 meters above sea level). *R. arifolius* occurs in the lower and higher mountain-forest zones descending along streams to lawer altitudes. The highest stand of this species has been found on the Mt. Lubań (1220 meters above sea level). According to Kornaś opinion where the two taxa grow together their hybrids with intermediate traits may occur.

The present investigation fully confirms the suppositions made by Pawłowski and Kornaś about the crossability of *R. acetosa* and *R. arifolius*. The hybrids obtained experimentally very closely resemble in their external morphological traits and in their range of variation the natural *Rumex* populations from the lower altitutudes in the Gorce Mts. The experimental results and the field observations show that there is no strictly defined boundary separating *R. arifolius* and *R. acetosa*. Between the typical *R. acetosa* from the lowlands and the typical *R. arifolius* from higher altitudes there is a gradual series of intermediate forms. The assembled evidence justifies the conclusion that with increasing altitudes *R. acetosa* gradually passes into *R. arifolius*. The transition stands are occupied by forms intermediate in the external morphology. In the populations from the transition stands the range of variation is very wide. With the increasing altitude the environmental selection gradually limits the proportion in the populations of the individuals approaching *R. acetosa* favouring the individuals approaching *R. arifolius*, which is better adapted to the mountain conditions. The results of this investigation lead to the conclusion that *R. acetosa* and *R. arifolius* are not separate species and should be considered as being the lowland and the mountain subspecies of one species.

Rumex thyrsiflorus is a lowland species. On meadows it may occur together with *R. acetosa*, but the dry habitats with a sandy soil, such as field roads and railway embankments, are accessible only to *R. thyrsiflorus*. Under natural conditions the crosses between *R. thyrsiflorus* and *R. acetosa* are greatly restricted by their different times of flowering, but it has been found that this barrier does not affect all populations: e.g. there are no such limitations to crosses between *R. thyrsiflorus* from Nowy Dwór and *R. acetosa*. It seems possible that this population of *R. thyrsiflorus* is a fixed introgressive type, a supposition supported to some extent by the different behaviour of its hybrids with *R. acetosa*. As to morphology, *R. thyrsiflorus* differs in some of its traits from both *R. acetosa* and *R. arifolius*. Among the distinguishing traits of *R. thyrsiflorus* are the compound inflorescence, the tap root system, and the narrow leaves with sharply pointed tips. The differentiation of the karyotypes in *R. thyrsiflorus* is the same as in *R. arifolius*. The crosses of *R. thyrsiflorus* with each of the other species are obtained with equal ease, but the hybrids from some of the crosses have a reduced fertility, and a lower viability, or they are weak and malformed. Various irregularities may occur in the course of microsporogenesis.

The experimental results show that *R. thyrsiflorus* is isolated from *R. acetosa* and *R. arifolius* by ecological barriers and by the genetic barriers of semisterility and reduced viability of the hybrids. In view of the well marked diagnostic traits and of the partial isolating barriers *R. thyrsiflorus* should be treated as a separate species, but one closely related with *R. acetosa* and *R. arifolius*. So far as the two last mentioned species are concerned it seems correct to adopt the nomenclature suggested by Löve (1944), according to which *R. acetosa* L. is the name of the species and the names of the subspecies are subsp. *pratensis* and subsp. *arifolius*. The classification of the taxa covered by this investigation would then be

species: *Rumex acetosa* L.
subsp.: *pratensis*
subsp.: *arifolius*
species *R. thyrsiflorus* Fingerh.

SUMMARY

1. The plants for the experiments were collected from 22 natural stands of *R. acetosa, R. arifolius,* and *R. thyrsiflorus*. The investigated traits of the parental plants were the morphology, the karyotypes, the course of microsporogenesis, and the fertility of seeds and pollen.

2. Numerous interspecific crosses were made between the different ecotypes of the parental species. The crossability of the parental species was high; the only difficulty in crossing was the difference in the time of flowering between *R. thyrsiflorus* and the two other species.

3. The morphological analysis of 24 F_1, 12 F_2, and 9 F_3 populations showed that the shape of leaves and the type of the inflorescence were inherited polygenically. In reciprocal crosses the F_1 and F_2 progenies were more like the maternal parent; this reflected the strong maternal influence. In the F_2 generations of some of the crosses *R. acetosa* × *R. thyrsiflorus* and *R. arifolius* × *R. thyrsiflorus* the viability of the hybrids was reduced and malformed and aberrant plants appeared.

4. The behaviour of the hybrids of parents with different flowering times was investigated. In the crosses of *R. thyrsiflorus,* which flowers in its first year, with *R. acetosa* and *R. arifolius,* which flower in their second year, the F_1 hybrids flowered in the first year, similarly as *R. thyrsiflorus*. In reciprocal crosses the flowering times of the F_1 and F_2 generations in their first and second years were distinctly closer to the flowering time of the maternal parent.

5. In the crosses *R. thyrsiflorus* × *R. acetosa* and *R. thyrsiflorus* × *R. arifolius* the pollen and seed fertility of the F_1 and F_2 hybrids was strongly reduced. The degree of sterility differed in the crosses between the different biotypes. The fertility of the cross *R. acetosa* × *R. arifolius* was almost normal.

6. Various irregularities of microsporogenesis were observed in the hybrids *R. thyrsiflorus* × *R. acetosa* and *R. thyrsiflorus* × *R. arifolius*. At anaphase I chromatin bridges with acentric fragments were of frequent occurrence indicating

that inversion had taken place. Chromatin bridges of a different kind were also observed in the first and the second meiotic divisions; they were probably formed by the breaking and the subsequent reunion of the chromosomes. The disturbances in the parting of chromosomes sometimes led to the formation of restitution nuclei and subsequently of unreduced gametes. In some crosses the misfunctioning of the spindle resulting in the production of unviable spores was observed. In the crosses *R. acetosa* × *R. arifolius* the course of meiosis was regular.

7. The results of this investigation lead to the conclusion that *R. acetosa* and *R. arifolius* should be treated as two subspecies, subsp. *pratensis* and subsp. *arifolius,* of the species *R. acetosa* L. On the other hand *R. thyrsiflorus* is a distinctly separate but closely related species.

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