BIOSYSTEMATIC STUDIES OF THE RUMEX ACETOSELLA-COMPLEX II. THE ALPINE REGION

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SUMMARY

The present paper is a sequal to similar ones dealing with populations in Belgium and France. About 80 population samples were gathered in the following areas: the southern part of the German Federal Republic, the Swiss, Austrian and (partly) Italian Alps, and northern Austria. Of these samples the occurrence of angiocarpy vs. gymnocarpy and the chromosome numbers were determined, special attention being paid to the incidence of foliar multifidy. In the Alpine region proper the large majority of the individuals is gymnocarpic. In southern Germany and Lower Austria the plants are nearly always angiocarpic, however. The distribution of the levels of ploidy is rather intricate and roughly as follows: gymnocarpic diploids occur in the southernmost French Alps, in the southern and western Swiss Alps, and in a single population in the Austrian Wachau on the NE escarpment of the Alps; gymnocarpic tetraploids in the Austrian Alps, and rather numerous hexaploids, with some angiocarpy, in the intervening border area of the central Alps. In southern Germany and Lower Austria mostly angiocarpic hexaploids were encountered, with predominantly gymnocarpic tetraploids especially in the border area between Austria and Czechoslovakia (the Bohemian Forest). In the latter region hybridisation between tetra- and hexaploids frequently takes place.

There are correlations between this chorological pattern and certain consistent phytogeographical phenomena in the Alpine region associated with its Pleistocene geological history, such as the presence of several refugia and the so-called Rein-Traun gap in the central Alps. In addition it is suspected that antropogenous influences have disturbed the original situation to an appreciable extent.

The degree of dissection of the leaves, as a character included in the population analyses for the first time, is present to the same extent in alpine di- and tetraploids (in which the leaves are more or less multifid), but in the Alpine and the German and Lower Austrian hexaploids, foliar multifidy is hardly developed. Some possible causes and plausible conclusions are discussed. The single population in the Wachau refugium contains a singularly high percentage of plants with multifid foliage and this is, among other things, the reason why this population is considered to belong to a different population complex than do the Alpine ones. In the discussion some space is devoted to difficulties that may be expected if a future, novel taxonomic classification of the complex is attempted.

1. INTRODUCTION

The studies reported in the present paper form a continuation and extension of the biosystematic investigations of the *Rumex acetosella* aggregate in W-Europe. After the Netherlands (STERK et al. 1969), Belgium (STERK & DEN NIJS 1971), France (DEN NIJS 1974) and NW Germany (DEN NIJS et al., in prep.),

the Alps and some adjoining areas have been explored. A rather fine-meshed distributional pattern of the areas of the di-, tetra- and hexaploids is manifest in France, but it is clear that a better insight into the distributional intricacies could only be obtained after a survey of a much larger region. It has been shown in the last few decades that the centres of origin of a large number of European polyploid species complexes lie in the Alps. Roughly speaking, this can be explained by the fact that unglaciated areas may have served as refugia where certain taxa could survive even during the periods of maximum glaciation (see, e.g., FAVARGER 1969). Such taxa, thus having become relicts, or new ones deriv-ed from them, subsequently colonised the land that became inhabitable during the milder interglacials (and the postglacial).

One of the interesting aspects emanated from the studies in France is the presence in the Alpes Maritimes of a diploid gymnocarpic race which may be regarded as a relatively primitive taxon (DEN NIJS 1974). This provided one of the discrete starting points for the detailed survey of the Alpine region which forms the subject of the present paper. Another problem studied by the present author is the incidence of divided basal lobes of the leaves (multifidness). In the above-mentioned, previous publications this character has not been included in the investigation because it occurred only sporadically or not at all.

The normal type of leaf blade in *R. acetosella* s.l. is provided with a single basal pair of patent lobes, but there are forms in which these lobes are bisected to multifid so that the lamina bears 2, 3, or more pairs of lobes at its base. This character is mentioned in the relevant taxonomic literature as "multifidus". Linnaeus assigned to plants with this character the status of a species (*Rumex multifidus*), but since De Candolle made it a variety there has been considerable disagreement concerning the status of plants with this leaf character and such specimens are treated as varieties or formae.

The character in question is emphasised in local floras of the countries explored, as will be pointed out presently. HARRIS (1968) studied the character of dissected leaves in herbarium material and drew the preliminary conclusion that multifidy of the leaves is of a clinal nature, i.e., changes gradually in Europe from populations with almost entire basal lobes in the NW to popula-tions in the SE with a high proportion of individuals with very much dissected lobes. He assumed that the highest frequency of occurrence of multifidy occurs in the E Balkans and Asia Minor, and based on this idea, to an appreciable extent, his hypothesis of the possible location of the centre of origin of the *R. acetosella* complex in this region. The present study partly deals with the incidence and relative frequency of occurrence of multifidy in most of the population samples collected in the explored areas.

Material was obtained from the following regions: the northwestern Italian, the Swiss, and the Austrian Alps, the Black Forest, the SE part of the G.F.R. and northern Austria. Hitherto only very little detailed information concerning the *R. acetosella* aggregate was available. Chromosome counts had hardly been made, and fine-meshed analyses of the distribution of angio- and gymno-

carpy, and of the degree of dissection of the leaves (= lobing ratio) were alto-
gether non-existent.

According to distribution maps published by Löve (1944), the occurrence
in the area studied of R. angiocarpus Murb. (2n = 14), R. tenuifolius (Wallr.)
Löve (2n = 28), and of R. acetosella L.s.s. (2n = 42) may be expected, the
Alps forming the farthest southwestern extension of the range of R. tenuifolius
and R. acetosella s.s. The following concise survey is a summary of the most
important information gleaned from local floral works and other floristic
literature covering S-central Europe:

RECHINGER in HEGI (1957) retained the classification as three species, follow-
ing Löve (1941a, 1941b), and distinguished in R. acetosella s.s. two formae,
viz., f. multifidus (the more common form) and f. integrifolius (less common in
the area covered); otherwise this taxon is said to be wide-spread. As habitats
are mentioned: poor, acid, sandy to loamy, dry to moderately moist soil types
(the two formae behave similarly in this respect); these habitats are very often
anthropogenously disturbed. R. tenuifolius is said to have a most incompletely
known distribution, which is largely attributable to the inconsistent evalua-
tion of the various microspecies by different phanerogamists. It is said to occur
fairly wide-spread in warm sites particularly on sandy soils poor in lime, and
supposed to be a characteristic species of the order Festuco-Sedetalia (the so-
called "Silbergrasfluren" and Sedum acre communities). Localities are given
from Lower and Upper Austria, Graubünden, and the Simplon region. R.
angiocarpus is reported as being of only sporadic occurrence in the area cover-
ed by the flora; the NE borderzone of its area runs through it. The ecology is
insufficiently known. RECHINGER (1964) maintains the same subdivision into
three species, but he mentions the occurrence of the dissected leaf character
in both R. angiocarpus and R. acetosella s.s. (not in R. tenuifolius) and does not
give specimens with this character any taxonomic status any longer.

HESS et al. (1972), dealing with the Swiss flora, follow RECHINGER (1957) more
or less closely, but do not give special information about R. angiocarpus;
R. tenuifolius is reported as occurring in the foothills and lower montane zone
up to about 1700 m. alt., whereas R. acetosella extends into the subalpine belt
up to about 2400 m alt.

HÖFLER & KNOLL (1956–1960) distinguish, following Löve 1944, the "var.
multifidus" (L.) DC. in the common R. acetosella s.s. and state that it is oc-
casionally found together with the typical form. R. tenuifolius is only recorded
from Lower and Upper Austria. R. angiocarpus is said to occur here and there
in most of the Bundesländer.

ROTHMAHLER (1963) also follows the subdivision into three species and
recognises three formae in R. acetosella viz., f. acetosella, f. integrifolius, and
f. multifidus, which are all reported to be found on neutral to calcareous soils.
R. angiocarpus is said to be rare and recorded from Thuringia, Anhalt, the
Black Forest, and Bavaria, and R. tenuifolius is considered to be calcifugous
and recorded as occurring on dry sandy soils and on land lying fallow, but its
distribution is said to be insufficiently known.

GARCKE (1972) distinguishes *R. acetosella* s.s. with a forma *multifidus* (L.) Murb. which is given as "occasional". The ecological data are practically the same as those of RECHINGER 1957, but also with the restriction that the ranges of distribution and the ecology of the other species have inadequately been studied.

OLTMANS (1922) and GRADMAN (1936) recorded for, respectively, the Black Forest and the Swabian Alb a number of localities of *R. acetosella* s.l. Especially in the latter region its occurrence is restricted by the predominantly basic nature of the soil. Summarising the literature on the subject, one can draw the conclusion that in the local floras three species are generally accepted, but the distribution and ecology of these is apparently very incompletely known. The present author expects that his own contribution will also throw some light on these questions.

2. METHODS

The field studies were carried out during the summers of 1973 and 1974 and yielded material from about 85 localities. Of these population samples about 45 contained 30–100 individuals, the remainder contained fewer plants (usually 10–15). It was the purpose of the sampling to obtain a finer meshwork of records of principally the cytological races, the smaller samples gathered "in between" providing material for a cytological, but not for a statistically reliable, morphological analysis. Moreover, the population size often appeared to be so small in the area studied that it was impossible or unwarranted to collect a large enough population sample. Also in this case quantities of seeds were received from fellow-botanists (see *table 1*); as a rule not accompanied by reference (herbarium) specimens.

During the field studies the same ecological data were recorded as those assembled in France (see DEN NIJS 1974). For the estimation of the sampling density differences in altitude were much more important than in France. On the other hand, the low accessibility of large stretches was often a limiting factor during sampling excursions owing to the time allotted for the field trips. The assessment of the degree of angiocarpy was carried out as explained in STERK et al. 1969. Chromosome counts were always made in seedling root tips, so that the mother plants could be preserved as vouchers in the Hugo de Vries-Laboratory (AMD). Only of population 418 counts were obtained from plants sampled in situ owing to the lack of mature seed. The method of counting is described in DEN NIJS 1974. For the sake of clearness the pretreatment of the seeds is reported here: stratification for some time in a refrigerator, after which germination follows after a sojourn for 2 or 3 days at 25°C.

The presence of dissected basal lobes on the leaf blade (lobing ratio) was assessed by studying herbarium material consisting of the dried population samples. Not all individuals of a population are suited for such an analysis owing to the advanced growing season, sampling being done when ripe seeds are likely to be present. In such cases the leaves are mostly wilted or even shed,

and sometimes eaten away. The character is not pronounced to the same extent in all leaves of the same individual. The registration of the character was made irrespective of the total number of leaves of a specimen with multifid leaves. A lobing ratio was, accordingly, not determined *per plant*, but only the incidence of multifidy was recorded (even if occurring in only a single leaf) and also the expression of the character in the number of lobes.

3. RESULTS

3.1 Local distribution of R. acetosella in the area explored

More or less extensively the following areas were visited: the Swiss and Austrian Alps, and the Italian Alps from the Aosta region to the Lago Maggiore and the southern Tyrol; in addition the Alp escarpment in Switzerland ("Mittelland"), Austria, and, somewhat less intensively, the Federal German Republic. Of the more northernly situated areas the Black Forest and the border areas between Germany and Austria and Czechoslovakia were explored, from Bayreuth (Bavaria) through the Regensburg area along the Danube to Vienna. As might be expected, after the experience obtained in France, populations of representatives of the complex are almost or completely lacking in parts of the regions studied. It could be confirmed once more that *R. acetosella* s.l. is practically absent on limestone and other very basic formations with the possible exception of some incidental, anthropogenically determined cases. This conclusion agrees with the calcifugy of the complex reported in the above cited floral works.

In GRADMAN's (1936) localities in the Swabian Alb, as far as they could be located, no populations of *R. acetosella* s.l. could be found. These localities are situated on a limestone formation where locally the soils are leached out to an appreciable extent, but such sites may be too rare and too far apart to be easily detected. Elsewhere in southern Germany with its predominantly basic soils few populations were encountered, with the exceptions of the zone between Passau and Bayreuth (the Bavarian Forest, etc.) where the subsoil consists of outcrops of acid rocks such as granites and metamorphic rock formations.

In the Alps proper *R. acetosella* s.l. is fairly common in the areas poor in lime and frequently occurs in large populations. In the more basic areas hardly any specimens are encountered which means that in a broad belt ranging from the southernmost point of Lac Leman via Chur and Salzburg to Vienna no sampling was possible. This belt is formed by the basic outer Alp chains consisting of limestone, dolomite, and basic shales and *Flyschen*. The same holds for similar situations, such as found in NW Switzerland and the southern Tyrol. Although certainly not all the alpine escarpments of Switzerland consist of basic subsoils, and the occurrence of *R. acetosella* s.l. has been reported (RECHINGER 1957, Favarger, priv. comm.), hardly any specimens were encountered. The complex must be rare in that area and presumably only occurs in small populations.

The area covered by the present study is so large, and the locating and samp-

Table 1. Population and seed samples: origin, percentage of angiocarpy, chromosome numbers and leaf-lobing percentages (Including a Section 'Mixed and Hybrid populations').

				Angiocarpy/ Gymnocarpy		Chromosome counts				leave lobing rates (in percentages) "Multifidus"		
Population number	Locality	Height in metres	Country, magisterial department	Sample size ♀ plants	Percentage angiocarpic plants	Number of seedlings counted	Number of parent plants	2n Number of chromosomes	Ang. + gymn.- plant	Sample size	Percentage* 2 pairs	Percentage* ≥ 3 pairs
(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)
408	Cogne, Val d'Aosta	1380	Aosta, It.	63	0	30	6	14 (21)	–	68	10	0
409	Villair, Val d'Aosta	650	Aosta, It.	26	0	10	3	14	–	28	20	0
410	Cuzzago	220	Novara, It.	13	0	26	7	14 (15, 21)	–	17	35	0
411	Macugnaga	1220	Novara, It.	48	0	11	3	14	–	50	10	0
412	Domodossola	280	Novara, It.	38	0	10	3	14	–	42	25	15
413	Simplon-Dorf	1280	Wallis, Sw.	17	0	7	3	14	–	18	0	0
414	Simplon-Pass	2000	Wallis, Sw.	17	0	6	2	14	–	50	0	0
415	Fiesch	1020	Wallis, Sw.	53	0	8	3	14 (15)	–	67	10	0
083	Grächen	1600	Wallis, Sw.	–		5	?	14	–	–		
049	Saas-Fee	1800	Wallis, Sw.	–		3	?	14	–	–		
419	Faido	800	Ticino, Sw.	30	0	11	3	14 (15)	–	62	10	0
421	Soazza	500	Graubün-den, Sw.	17	0	13	3	14	–	18	0	0
450	Dürnstein	250	Nieder-Oesterreich	22	0	11	4	14	–	30	20	65
424	Kappl	1170	Tirol, Oesterreich	39	0	13	3	28	–	55	40	10
428	Umhausen,	900	Tirol, Oesterreich	47	0	7	2	28 (29)	–	47	0	2
430	Moos in Passeier	1500	S.-Tirol It.	1	0	2	1	28	–	–		
523	Maria Alm	950	Salzburg, Oesterreich	1	0	3	1	28 (29)	–	–		

439	Goldegg i. Pg.	850	Salzburg, Oesterreich	18	0	8	3	28	–	20	25	5
442	Sauerfeld	1240	Salzburg, Oesterreich	44	0	17	3	28	–	45	2	0
434	Mittewald a.d. Drau	1250	O.-Tirol, Oesterreich	17	0	6	2	28	–	22	25	0
435	Greifenburg	750	Kärnten, Oesterreich	19	0	5	2	28	–	25	10	0
436	Kolbnitz	650	Kärnten, Oesterreich	44	0	12	3	28 (27, 29)	–	38	0	0
437	Stall	800	Kärnten, Oesterreich	32	0	11	3	28	–	41	5	0
443	Kremsbrücke	1080	Kärnten, Oesterreich	6	0	6	2	28	–	9	0	0
444	Afritz	840	Kärnten, Oesterreich	33	0	11	3	28 (29)	–	42	10	0
445	Klippitztörl	1080	Kärnten, Oesterreich	5	0	5	2	28	–	3	0	0
440	Groszsölk	920	Steiermark, Oesterreich	47	0	7	3	28	–	46	10	5
447	Gaberl-Haus, Plan Kogel	1330	Steiermark, Oesterreich	7	0	7	2	28 (35)	–	6	0	0
448	St. Johann a. Tauern	1000	Steiermark, Oesterreich	35	0	11	3	28	–	43	10	5
449	Kraubath	650	Steiermark, Oesterreich	7	0	3	1	28	–	8	10	0
508	Neumarkt i.d. Oberpflaz	400	Bayern, BRD	25	0	8	2	28	–	37	15	0
522	Waldkraiburg	400	Bayern, BRD	29	100	1	1	28	+	26	0	0
461	Ried	450	Ober-österreich	51	0	5	2	28	–	47	20	10
459	Klaffer	640	Ober-österreich	15	0	5	2	28	–	16	20	5
458	Hinter-weissenbach	700	Ober-österreich	31	60	11	3	28 (c. 29)	–	45	5	0
457	Wullowitz	600	Ober-österreich	13	25	10	3	28 (35)	–	17	30	5

				Angiocarpy/ Gymnocarpy		Chromosome counts					leave lobing rates (in percentage) "Multifidus"		
Popu- lation number	Locality	Height in metres	Country, magisterial department	Sample size ♀ plants	Percentage angiocarpic plants	Number of seedlings counted	Number of parent plants	2n Number of chromo- somes	Ang. + gymn.- plant	Sample size	Percent- age* 2 pairs	Percent- age* ≥ 3 pairs
(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)
403	Haslach, Black Forest	230	Baden-Wür- temberg, BRD	11	100	3	2	42	+	13	0	0
404	St. Peter, Black Forest	625	Baden-Wür- temberg, BRD	3	100	5	2	42	+	-		
405	Schluchsee, Black Forest	900	Baden-Wür- temberg, BRD	66	83	5	2	42	-	69	0	0
407	Liddes	1300	Valais, Sw.	53	75	4	2	42	-	56	0	0
417	Gadmen	1250	Bern, Sw.	10	100	8	2	42 (34, 41)	+	16	0	0
418	St. Gotthard- Pass	1950	Ticino- Sw.	-	-	4	4	42	?	20	0	0
422	San Bernardino	1630	Graubünden, Sw.	38	0	20	5	42 (40)	-	49	0	0
423	Fluëlapass	1900	Graubünden, Sw.	9	0	5	2	42	-	16	0	0
425	Galtür	1600	Tirol, Oesterreich	28	100	12	3	42	+	28	0	0
426	St. Leonhard im Pitztal	1270	Tirol, Oesterreich	31	0	4	2	42	-	45	2	0
427	Mittelberg im Pitztal	1680	Tirol, Oesterreich	8	86	8	2	42 (39)	+	14	0	0
429	Obergurgl	1950	Tirol, Oesterreich	8	0	2	1	42 (40)	-	30	0	0
429b	Hochgurgl	2050	Tirol, Oesterreich	11	0	8	3	42 (c. 37)	-	10	0	0
432	Gerlos-Platte	1500	Salzburg, Oesterreich	25	80	8	3	42 (38)	+	22	0	0

No.	Locality	Region						2n				
078	Lauscha, Thüringerwald	Suhl, DDR	·	—	—		?	42 (43)	—	—		0
524	Dinkelsbühl	Bayern, BRD	450	5	80	2	1	42	+	5	0	0
501	Bayreuth	Bayern, BRD	350	10	10	1	1	42	—	7	0	0
502	Zinst, Ober Franken	Bayern, BRD	500	10	70	4	1	42 (41, 43)	+	11	0	0
503	Waldershof, Ober Franken	Bayern, BRD	500	1	100	7	1	42 (41)	+	—		
504	Tirschenreuth	Bayern, BRD	530	25	100	13	3	42 (38–41)	+	38	0	0
505	Floss	Bayern, BRD	550	36	100	9	3	42 (35, 40, 43)	+	39	3	0
506	Winklarn	Bayern, BRD	500	22	90	3	3	42	+	24	0	0
507	Ensdorf	Bayern, BRD	420	23	100	3	2	42 (41)	+	26	0	0
509	Beilngries	Bayern, BRD	480	26	96	11	3	42	+	32	0	0
512	Michelsneukirchen	Bayern, BRD	600	44	100	7	2	42 (43)	+	41	2	0
514	Scheibensattel	Bayern, BRD	1050	1	100	3	1	42 (41)	+	—	0	0
515	Schwarzach	Bayern, BRD	480	36	92	4	2	42	‡	41	0	0
516	Lalling	Bayern, BRD	600	26	27	1	1	42	?	24	0	0
517	Hohenau	Bayern, BRD	800	47	95	4	2	41 (42)	‡	60	0	0
518	Hauzenberg	Bayern, BRD	500	54	90	6	2	42 (41)	+	60	0	0
519	Vilshofen	Bayern, BRD	320	12	100	3	2	42 (41)	+	12	0	0
455	Pabneukirchen	Ober-österreich	620	34	100	7	3	42	+	42	0	0
456	Gallneukirchen	Ober-österreich	400	5	100	1	1	42	+	4	0	0
460	St. Gotthard i. Mühlkreis	Ober-österreich	470	59	100	8	2	42 (41)	+	58	2	0

Section mixed and hybrid populations

No.	Locality	Region						2n				
406	Les Valettes	Valais, Sw.	570	80	14	7, 3, 6	2, 1, 2	14, 42, 14	—, +, —	86	15	1
420	Biasca	Ticino, Sw.	350	62	30	1, 1	1, 1	c. 37, 42	—, +	G: 54, A: 19	15, 0	0, 0
431	St. Leonhard i. Passeier	Südtirol, It.	1750	57	0	2, 3, 1	1, 1, 1	28 (35), 30–33, 35	—, —, —	59	5	0

Popul-ation number	Locality	Height in metres	Country magisterial department	Angiocarpy/Gymnocarpy		Chromosome counts				leave lobing rates (in percentage) "Multifidus"		
				Sample size ♀ plants	Percentage angiocarpic plants	Number of seedlings counted	Number of parent plants	2n Number of chromosomes	Ang. + gymn.- plant	Sample size	Percent-age* 2 pairs	Percent-age* ≥ 3 pairs
(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)
438	Bad Gastein	1020	Salzburg, Oesterreich	7	0	5	1	28	−	3	65	0
						2	1	28 (36)	−			
441	Schröder	1200	Steiermark, Oesterreich	7	0	1	1	28	−	7	0	0
						3	1	37	−			
446	Preitenegg	1080	Kärnten, Oesterreich	56	91	3	1	42 (35)	+	63	0	0
						4	1	34	+			
510	Münchmünster	360	Bayern, BRD	16	100	3	1	42	+	16	20	5
						9	2	42 (c. 35)	+			
520	Frontenhausen	500	Bayern, BRD	10	100	2	1	28	+	18	0	0
451	Grafenschlag	780	Niederösterreich	67	90	3	1	30–32	−	74	1	0
						2	1	32 (c. 35)	−			
						1	1	35	+			
						3	1	37 (32)	+			
						4	1	36 (42)	+			
						4	1	42 (41, 35)	+			
						4	1	42	∓			
452	Schrems	550	Niederösterreich	16	80	1	1	35	+	15	0	0
						3	1	c. 36 (40)	−			
						8	2	42	−			
453	Grossgerungs	680	Niederösterreich	41	15	4	1	28	−	63	15	5
						10	2	28 (30, c. 35)	∓			
454	Arbesbach	350	Niederösterreich	12	75	5	1	30 (28, 34)	−	5	0	0
						6	1	30–33 (38)	−			
						4	1	35 (28)	−			
						4	1	35 (31–34)	−			
						4	1	35 (39)	+			

* The remainder is l-paired or completely entire.

ling of the populations so time-consuming, that the present author cannot possibly claim that his results are sufficiently complete. Some areas have not been adequately explored, among other things, but nevertheless it is felt that enough data have been compiled for future, promising inquiries.

3.2. The incidence of angiocarpy and gymnocarpy

In *table 1* the localities of all populations studied are shown and the percentages of angiocarpic and gymnocarpic individuals are indicated. The sequence in the table is from W. to E. and according to the country districts in the Swiss cantons and the federal districts of Germany and Austria. On map 1 the sites are shown with the corresponding population sample number. The relative incidence of the angio- and the gymnocarpic forms is indicated by symbols representing five classes of percentages of angiocarpic individuals in the populations (see the legend of the map). These classes were chosen for their suitability for visual representation, not because of theoretical considerations.

As regards the distribution and ratio of angiocarpy and gymnocarpy, a general pattern emerges. Nearly all populations in the Alps proper exclusively contain gymnocarpic individuals, whereas in S Germany angiocarpy prevails. The zone lying just to the N of the central Alp chains which is nearly or completely void of *R. acetosella* s.l. forms a clear-cut boundary between the two population groups. In Lower and Upper Austria there is no such a manifest line of separation. In connection with the importance of cytological data associated with these alternative characteristics of the fruit, this point will be discussed in greater detail on p. 434.

Other areas which are singular owing to the common incidence of angiocarpy, viz., the Vallée d'Entremont (Valais), the area around the Gotthard massive (Ticino, Uri), and the SW. Tyrol, will also be treated in conjunction with cytological data on the pages 431 and 433, respectively.

3.3 Chromosome numbers
3.3.1 General data

The chromosome numbers of 81 population samples were determined by counting, when possible, 3–5 seedlings each of 1 to 4 progenies.

The distribution of the ploidy levels is as follows:
diploid ($2n = 14$) were 13 samples, tetraploid ($2n = 28$) 23 samples, and hexaploid ($2n = 42$) 33 samples. In 12 samples either more than one ploidy level was present in a high frequency, or hybrids occurred. These aberrant samples are separately treated on p. 434.

Table 2 is a survey of the numbers of individuals counted and also shows the degree of variation of the somatic numbers at each ploidy level. Interindividual variation has been determined separately.

Since the purpose of the table is to show only the variation of the somatic chromosome numbers, undisturbed by hybridisation, care has been taken to include only samples with a homogeneous (subconstant) ploidy level. The pre-
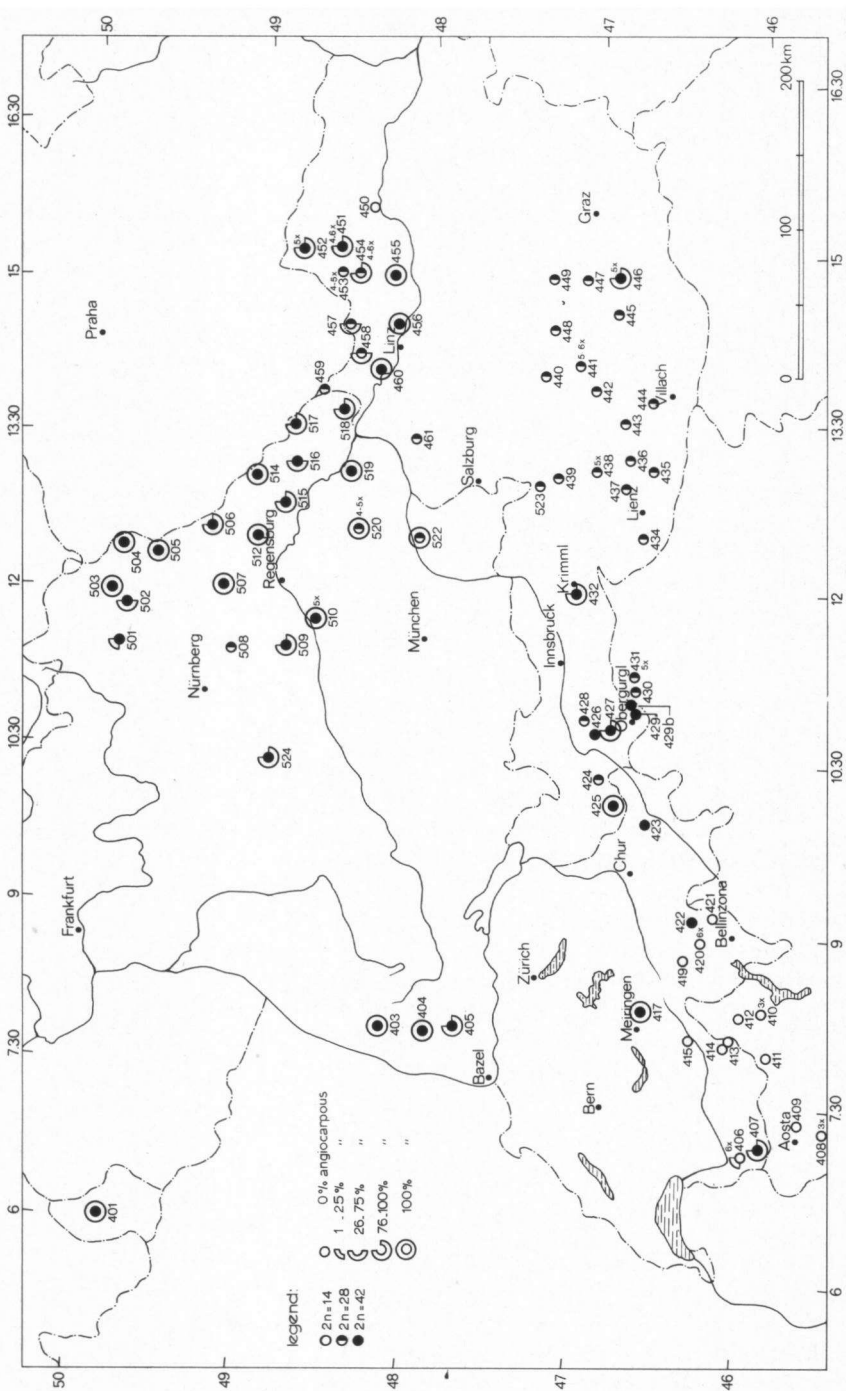
Map 1. The population samples: distribution of angiocarpy and gymnocarpy and of the ploidy levels.

Table 2. Inter-individual and intra-individual variation of the somatic chromosome numbers at the various ploidy levels (in per cents).

Ploidy level	inter- or intra-individual	Number of chromosomes (in per cents)									Percentage total	Total numbers
		2n−4	2n−3	2n−2	2n−1	2n	2n+1	2n+2	2n+3	2n+ ≧4		
Diploids 2n = 14	inter					98	2				100	152 ind.
	intra				<1	94	5	<1			c. 100	462 cells
Tetraploids 2n = 28	inter				<1	97	2	<1			c. 100	135 ind.
	intra			1	5	89	5	<1			c. 100	351 cells
Hexaploids 2n = 42	inter		<1	3	9	82	3	<1	<1	<1	c. 100	173 ind.
	intra	<1	<1	5	15	68	6	2	1	1	c. 100	401 cells
Diploids DEN NIJS 1974	inter					96	3	1			100	254 ind.
	intra					94	4	1.5	<1	<<1	c. 100	c. 700 cells
Hexaploids SINGH 1964		<<1	2.5		13	64	19	1			c. 100	204 ind.

sent author (DEN NIJS, 1974) found in hybridogenous populations in France, apart from, say, pentaploids, also individuals with a few more chromosomes than 28 or a few less than 42, for which phenomena back-crossing was suggested as the responsible cause. It is by no means unlikely that the hitherto recorded data include cases of aberration in chromosome number caused by back-crossing that took place perhaps several generations ago. The data relating to tetra- and hexaploid populations are, therefore, presented with some reserve. For this reason the tetraploids of pops. 447, 457, and 458, and the hexaploids of pop. 417 have already been omitted. The practical problems associated with the counting of hexaploids, such as a poor segregation and clustering of the chromosomes, which rendered the mentioning of figures for French populations unreliable (DEN NIJS 1974), do not play a part here, because exclusively numbers obtained from accurate counts are included in the calculations.

The higher the ploidy level, the greater the variation in the chromosome numbers recorded. The distribution of variance of the diploids agrees satisfactorily with the data from France. Observations of the diploid metaphase plates indicate that there are two probable causes of a higher count, viz. (a) fragmentation of a chromosome (in a number of cases such a fragment was present as a relatively small fifteenth chromosome); and (b) irregularities during mitosis, sometimes a fifteenth chromosome not being distinguishable from the other 14. In tetraploids and hexaploids fragmentation has not been established with certainty; the somatic chromosomes are mostly smaller than in the diploids, which renders the recognition of (smaller) fragments much more difficult.

It is striking that SINGH (1964) found a greater percentage of deviations than the present author did, which may be explained by the relatively much smaller number of samples with an incidental greater inhomogeneity Singh had at his disposal. The well-known fact that seedlings, in particular their rootlets, exhibit relatively many deviations from the euploid somatic number of chromosomes (NICHOLS 1941, SWANSON 1957), must be taken into account in all chromosome numbers reported here. EHRENDORFER (1959) reported, for instance, that in the *Achillea millefolium* complex the seedlings (especially their radicles) show variations in chromosome number which become more frequent as the storage time of the seed increases. Deviations in chromosome numbers, therefore, do not necessarily imply that irregular numbers are present in the generative cycle during meiosis, since much of the variation is apparently regulated back to the normal diploid number in the course of development of the the plant.

The counts recorded are tabulated in *table 1*. For the understanding of this table the following items are important:
(a) if within a single population progenies with different chromosome numbers were present, these progenies are noted down in separate lines (compare, e.g., pop. 406 Les Valettes);
(b) if variation within a single progeny was found, the deviating number is given between brackets; as a rule such an abnormal number occurred in a

minority of the individuals studied; and

(c) intra-individual aneuploidy has not been included into the table.

Also in this region studied there is no positive correlation between the various ploidy levels and the incidence of angio- or gymnocarpy. However, several population complexes are either completely angiocarpic or exclusively gymnocarpic as we shall see.

Map I shows the distribution pattern of the three ploidy levels, combined with the percentages of angiocarpic individuals. Diploids are, with one exception, restricted to the SW Alps in the area under discussion (Valais, Ticino, Aosta, Novara) and appear to be common there. All populations are gymnocarpic. It is highly probable that they form a part of a population complex which also includes the diploid gymnocarpic forms of the French Alpes Maritimes (see DEN NIJS 1974). The locally occurring angiocarpic hexaploids do not fit into this pattern and will be discussed on p. 432. Apart from this large gymnocarpic population complex a single gymnocarpic, diploid population (no 450) was encountered near Dürnstein on the Danube, which on account of the large distance from the above-mentioned complex must be supposed to belong to a different population group of which it happens to be the only representative in the area explored. Two populations (nos. 408, and 410) yielded seedlings with $2n = 21$ (triploid) chromosomes. Since tetraploids were not present in a wide surrounding area (see *map 1*) it is more plausible that in these populations individuals occur which occasionally produce viable 'unreduced' (diploid), functional gametes than that the triploids are of hybrid origin.

Tetraploids are of common occurrence in the Austrian Alps and more occasionally in northern Austria and SE Bavaria. In the Austrian Alps the tetraploids are all gymnocarpic; other ploidy levels are almost completely absent. The more dispersed tetraploid populations (mostly gymnocarpic) in N Austria are probably extensions of the alpine population complex. The angiocarpic tetraploid populations 520 and 522 of SE Bavaria link up with similar ones in central Germany (unpublished) and central France.

Hexaploids are quite common in SE Germany and N Austria provided the soil conditions are favourable. They are predominantly angiocarpic and clearly represent an extension of the hexaploid angiocarpic populations in France which form a broad barrier belt between the gymnocarpic populations in NW Europe and those in the Alpine region.

In the Alps only sporadically hexaploids are encountered, mostly in the SW Tyrol and the adjoining part of Switserland (see p. 433) and less frequently in southern Switserland (see the following paragraph).

3.3.2 Mixed populations in southern Switserland

A number of populations in southern Switserland, where otherwise only diploid gymnocarpic populations are found, are completely or partly hexaploid and/or angiocarpic.

Pop. 420 (Biasca) is heterogeneous. It was collected at a relatively undisturbed site covered with dry grassland vegetation. At the edge of the stand of vege-

tation, alongside a road, gravel dumped in heaps for road mending was sparsely overgrown. In both sites *R. acetosella* was present: in the presumably natural grass vegetation as rather small plants which were invariably gymnocarpic, and in the disturbed gravelly roadside as larger angiocarpic ones. Chromosome counts revealed that the smaller gymnocarpic plants were diploids, and the larger (ruderal) angiocarpic individuals hexaploids.

Population 406 from Les Valettes, collected on a slope which had been partly worked over, showed the same phenomenon: the sample contained 69 gymnocarpic and 11 angiocarpic plants, and the cytological analysis yielded 23 cases of diploidy combined with gymnocarpy against 4 cases of hexaploidy combined with angiocarpy.

Pop. 407 (Liddes), from a similar habitat, also contained angio- and gymnocarpic individuals. A sample analysis indicated that there both phenotypes were hexaploid, however.

In the author's opinion such "mixed" populations are manifest examples of the autonomous or anthropogenic importation of (in the cases mentioned mostly angiocarpic) hexaploids in sites disturbed by human interference, because in all other population samples collected in mostly less disturbed or undisturbed localities, neither hexaploidy nor angiocarpy occurred. *Map 1* clearly shows that generally speaking in the whole Alpine region only gymnocarpic populations are present. In this connection another three populations may be mentioned: 417 (Gadman, from much-trodden meadow edges), 418 (from the road sides along the St. Gotthard Pass), and 422 (sides of newly constructed parking areas near the entrance of the tunnel underneath the San Bernardino Pass). In these, still strongly anthropogenic, habitats the local populations contain only hexaploids. Such populations, in conjunction with the above-mentioned "mixed" ones, point to a development still progressively proceeding under the disturbing influence of human activities, which may ultimately lead to a reduction of the area of the diploid gymnocarpic taxon if not to its total disappearance, at least in all more or less strongly disturbed habitats. On the one hand, the diploid populations cannot cope with anthropogenically influenced situations as far as can be ascertained and deteriorate, and on the other especially the hexaploids have an enormous capacity of vegetative propagation by producing underground runners (DEN NIJS, unpublished). After having penetrated into a site inhabited by diploids (for instance, by anthropochory), the hexaploids may conceivable oust out the diploids by competition. It seems recommendable to follow such a development by repeated sampling in the same localities and also by means of competition experiments.

3.3.3 Some speculations concerning the distribution of the ploidy levels

The established chorology of the three ploidy levels appears to be rather closely correlated with the history of the Alpine region during the pleistocene periods of glaciation. The phytogeographical analysis of the alp flora has revealed a number of species-groups whose more primitive elements are found

to this day in, or in close proximity of, glacial refugia and did not manage to extend their range to any appreciable extent, whereas younger (newly originated) taxa did increase their distributional area considerably (compare, e.g., MERXMUELLER 1952; EHRENDORFER 1949, 1958, 1964; FAVARGER 1964, 1967).

Several valleys and mountain massives in the area of the large diploid, gymnocarpic population complex of *R. acetosella* s.l. (the southwestern Alps) apparently were never covered by the Alpine ice-cap and may have served as refugia for the gymnocarpic 2n = 14 populations. The refugia include in this case valleys of the Cogne and Visp and several massives in the Alpes Maritimes (HESS et al. 1972). Apart from several other ones, there must also have been a refugium in the northeastern Alps, e.g., the Wiener Schneeberg and the area towards Krems (Wachau) were ice-free (GAMS 1936, MERXMUELLER 1952, FAVARGER 1969, NIKLFELD 1972). In this region lies the only find of a second diploid gymnocarpic population complex that is presumably much larger than was hitherto established, since the present author also found gymnocarpic 2n = 14 specimens from the Bohemian Forest (Czechoslovakia) in a sample received without a more precise indication of the locality.

During one of the Pleistocene interglacials a tetraploid taxon must have settled and subsequently maintained itself in the Austrian Alps. Conceivably its area of distribution later became restricted to a few ice-free valleys or nunataks in the southern Alps during a following period of glaciation, as EHRENDORFER (1958) has shown in the case of the *Galium anisophyllum* aggregate in the Brenner Pass region. A similar hypothesis may be proposed for the tetraploid angiocarpic population complex in the Pyrenees (DEN NIJS 1974).

The Alpine distributional area of the tetraploids is separated from the western diploid populations by a zone in E. Switzerland and W. Austria. In this zone 10 populations were recorded of which 6 contain only hexaploids, 4 of which are gymnocarpic (423, 426, 429, 429b) and two angiocarpic (425 and 427).

It is noteworthy that in the Pitz valley one population is gymnocarpic (no. 426), and the other (no. 427) angiocarpic: see *map 1*. This inhomogeneity, in conjunction with the observation that elsewhere in the Alps hexaploidy or angiocarpy are hardly ever encountered, suggests that this area is exceptional. It seems as if between the ranges of Alpine diploids and tetraploids there is a gap in this central part of the Alps. MERXMUELLER (1952) pointed out similar distributional patterns in numerous other species. The area in question, roughly comprising the upper regions of the rivers Rhine, Enn, Traun and Salzach, conceivably only became accessible to plant life a fairly long time after the termination of the last glacial period, when this centrally situated area was heavily glaciated. It would also have acted as a geographical barrier till some time after the glacial phase, because it is precisely along this area that western and north-eastern taxa are separated by a phytogeographical discontinuity, the so-called "Rhine-Traun gap" (MERXMUELLER 1952). Some demonstrative examples of cytological differences on either side of the gap are *Chrysanthemum alpinum* (diploid in the W, tetraploid in the E, see CONTANDRIOPOULOS

& FAVARGER 1959; FAVARGER 1964) and *Trisetum distichophyllum* with tetra-
ploids in the W. and octoploids in the E. (BEURET 1974). This situation would
in the case of *Rumex acetosella* s.l. not only have resulted in a spatial separation
of di- and tetraploid populations, but also have permitted, in a later phase, the
invasion of the intervening area by the hexaploid of more recent origin and
with a greater penetrating power.

Some samples were available from populations outside of the area studied in
detail. Cytological analysis of these samples yielded the following data: in
Portugal diploids and hexaploids occur, in Bulgaria di- and tetraploids, and in
two Aegaean islands (Mykonos and Delos) hexaploids. This evidence strongly
suggests that there are still many voids in our knowledge of the distribution
of the various ploidy levels and of the morphological variation in and between
populations as will become clear later. Further studies in the Iberian Peninsula
and in S-E Europe are required before a better insight into the micro-evolution
of the *R. acetosella* aggregate can be obtained.

3.4 Hybrid populations
In two regions hybrid populations were encountered, viz., in the eastern Alps
and in the border areas between the German Federal Republic, Czechoslova-
kia, and Austria. These two groups of populations will be discussed separately.

3.4.1 Eastern Alpine region
In only 4 localities within the area of the tetraploids hybrids between different
ploidy levels were found, namely in pops. 431, 438, 441, and 446 (see *table 1*,
section "Mixed and hybrid populations"). In all these cases crosses between
tetra- and hexaploids occurred, resulting in pentaploids in the offspring. In
one sample (no. 431) descendants of back-crosses were noted (as previously
recorded in France); in the case under discussion apparently only with a tetra-
ploid parent judging by the somatic chromosome numbers 2n = 30, 32, 33.
In one locality, viz., the one near Preitenegg (no. 446), the character of angio-
carpy is introduced into the population by these crosses.

3.4.2 Border areas of Czechoslovakia
The great diversity of aneuploid numbers combined with the absence of eu-
ploid ones in a number of progenies (e.g., of pop. no. 454, Arbesbach) suggests
that in such cases the mother plant was already a pentaploid (at least an F1
plant), and the progeny, accordingly, consisted of F2- and BC-plants. Hybrid
pollen grains will only be able to fertilise a part of the ovules of a euploid mother
plant already on account of the relatively much lower quantities available, not
to mention possible fertility problems, so that of such a euploid mother only a
portion of the plants will be hybridogenous. That this situation is actually
present is evident from pops. 451 (Grafenschlag) and 453 (Großgerungs) in
which the same progeny contains, apart from hybrids, also hexaploids or
tetraploids, respectively.

After the populations 510 (Münchmünster) and 520 (Frontenhausen) with,

respectively, pentaploids and decendants of backcrosses towards the tetra-
ploid level (which fits into the frequently recorded pattern), the situation in
Lower Austria strongly draws the attention owing to the large number of hy-
brids present (see *map 1*), not only in respect of the Alps but also in respect
of the corresponding area in the German Federal Republic, the Bavarian
Forest in a wider sence. Not counting the diploid (relict?) population 450 from
Dürnstein, of the 10 samples within the Austrian territory four (451, 452, 453,
and 454) are to an appreciable extent, and two (459, 458) to a lesser extent,
hybridogenic. One of these 10 samples is purely tetraploid (no. 459) and the
remainder, like all samples in the adjoining Germain area, hexaploid (see also
table 1, section "mixed and hybrid populations"). In the samples 451, 452 and
454 the hybridogenous element consists mainly of pentaploids with some back-
crosses towards the levels of both parent types. Only few tetraploids were
found in these samples. In pop. no. 453 (Großgerungs) it are the hexaploids
that are conspicuous by their absence, and many descendants of back-crosses
were found.

Taking the general pattern of distribution of the ploidy levels into account,
it is striking that the purely hexaploid populations, generally speaking, are
situated along the Danube, whereas the single purely tetraploid one was found
in the densely afforested border area against the Czech border, as well as the
two almost pure tetraploid populations nos. 457 and 458. It is fairly obvious
to assume that in the lower Bohemian Mountains of old a tetraploid popula-
tion complex is present, and that from the Danube valley hexaploids have
penetrated into that region, partly also aided by an increasing anthropogenic
disturbance. Also in this connection a study of the situation inside Czechoslo-
vakia is clearly indicated.

A consideration of the characters of angiocarpy *versus* gymnocarpy yields
a rather similar situation: the hexaploids appear to be angiocarpic, and the
tetraploids gymnocarpic. According as a hybrid population contains more
pentaploids, the percentage of angiocarpic individuals rises: in pops. 453, 454,
452, and 451, 15%, 75%, 80% and 90% of angiocarpic plants were found,
respectively.

In pop. 457 (Wullowitz) and 458 (Hinterweissenbach) the angiocarpy per-
centages were 25% and 60%, respectively, with only few demonstrably hybri-
dogenous individuals, which condition may be taken as an indication of the
genetic dominance of the character of angiocarpy over gymnocarpy. All these
data notwithstanding, it cannot be deduced with certainty if (and if so, what
form of) introgression has taken place when angiocarpy or gymnocarpy pre-
vails: has, with the penetration of hexaploids, angiocarpy become introduced
in (gymnocarpic) tetraploid populations, or did the invading hexaploids beco-
me gymnocarpic? Back-crosses from the pentaploid F1 plants to both parental
ploidy levels can take place (see in *table 1*, e.g., the pops. nos. 451, 453, and
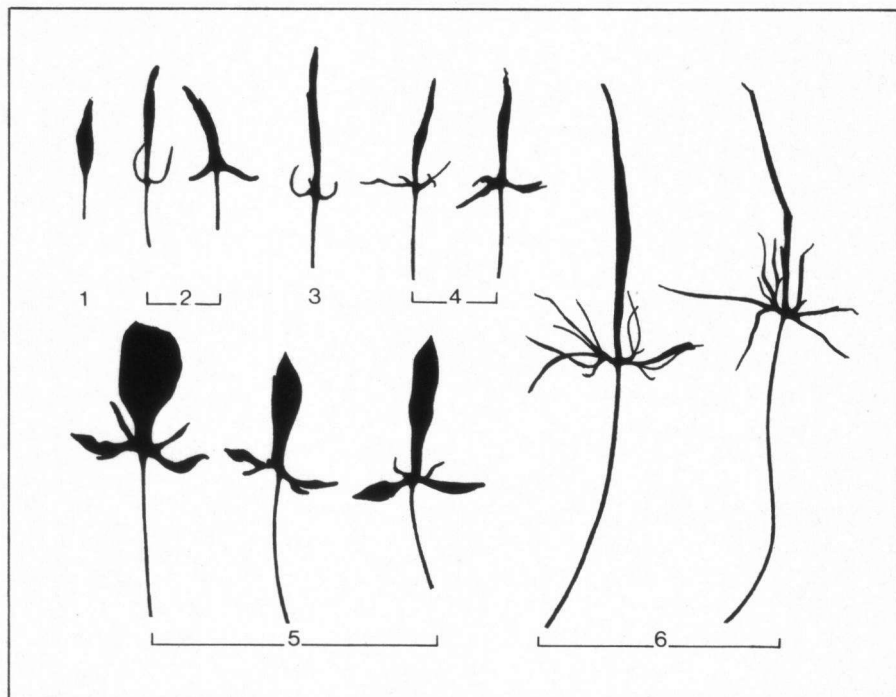454), so that both forms of gene-flow are possible.

Fig. 1. Leaf types from some population samples.
1. entire lamina ("integrifolius"), pop. 408;
2. one pair of leaf lobes, pop. 408;
3. one pair of lobes with a little secondary lobe, pop. 409;
4. multifid leaves ("multifidus") i.e. 2 or partly 3 pairs of lobes, pop. 412;
5. multified, – mostly 2 pairs –, pop. 424;
6. multifid leaves with 6 pairs of lobes, pop. 450 (Dürnstein).

3.5 The dissected leaf lobes character (multifidness)

3.5.1 Introduction and generalities

As already stated on p. 419, several local floral works mention that apart from specimens of *R. acetosella s.l.* with the "normal" type of leaf-lobing occasionally individuals with dissected leaf-lobes are encountered. Relevant data concerning the relative frequency and distribution of this form are scarce, and information about the genetical and ecological background was almost completely lacking. HARRIS (1968, 1973) deduced from a study of herbarium material that the character has a clinal distribution, and increases in Europe in frequency from NW to SE. He figured multifid leaf types of tetraploid populations from Hungary and Yugoslavia, and posed that the focal centre of the leaf variability lies somewhere in the Balkans or in Asia Minor.

In the Netherlands, Belgium and France individuals with dissected lobes are of extremely rare occurrence, but in the Alpine areas the frequency of incidence

may be strikingly high locally. Of the samples from the Alps the degree of dissection of the basal lobes has been assessed as described on p. 420, and expressed as a lobing ratio in percentages in which 1, 2, 3 or more basal lobe pairs were present.

Before presenting the results, the author seems it worthwhile to consider the nature of the character of dissected leaf lobes in some detail. In *fig. 1* a number of leaf-types are shown which were found in the population samples. It is clear that transitions occur between the nominal leaf shape with only a single pair of basal lobes and a form with bifid lobes through leaves with only a small additional (second) lobe-pair or through a form in which only one lobe is bifid and the other one entire. It is also obvious that the number of lobes can attain a rather high value by a repeated dissection of the secondary and tertiary lobes.

The problems associated with the multiple lobing are largely caused by the phenotypic inconstancy of expression of the character. Not even all leaves of the same individual with dissected leaves are divided to the same extent. In many cases only a few leaves of a plant bear multifid lobes whereas all other leaves have entire basal lobes. This is not unexpected as far as the bracteoid phyllomes of the flowering stalks are concerned because they become increasingly smaller and less developed higher up. As a rule, multifidy is expressed most strongly in the third, fourth, or fifth stem leaf of the flowering stalks dependent on the density of the foliage. A similar phenomenon is exhibited by the rosette leaves: the outer, oldest ones are usually hardly dissected if at all, whereas the younger leaves may show various degrees of multifidy. This infra-individual variability, in combination with the somewhat inappropriate time of collecting of the population samples (for the sake of obtaining mature seeds in the late summer when most of the leaves are already withered or damaged), renders an assessment of the degree of leaf variability in the population samples rather unreliable.

Conceivably, genetically "multifid" specimens may produce fewer leaves when growing under unfavourable circumstances and not or hardly exhibit the characteristic of dissected leaf-lobes. These objections apply to all population samples from the Alps but not to a large extent to pop. no. 450 (Dürnstein) in which practically all leaves present are manifestly multisect. In the latter case the variation expresses itself in the degree of lobing of the leaves, the number of lobes varying from 3 to 8 pairs per leaf. In a few plants hailing from Mykonos (Greece) the variation even extends to 12 or 13 pairs of lobes per leaf.

A series of cultivation experiments has been started in which plants are being cultivated under uniform conditions in order to gain some insight into the genetic variation and phenotypic expression of the character.

In *table 1*, columns 11, 12 and 13 show the observations of the character of leaf dissection (viz., the percentage of dissected leaf-lobes expressed as pairs, the so-called lobing ratio) of all populations that provided several individuals for the assessment. To make the data better surveyable the results are somewhat simplified in the table in that only two categories are distinguished, viz., a group with bifid basal lobes (2 pairs) and a group with tri- to plurisect lobes; moreover, the category of nominal leaf shapes (constituting the balance of the

100 percent) has been omitted (this last category also includes the usually small number of plants without any basal leaf lobes, "f. *integrifolius*").

3.5.2 Multifidy and ploidy level

From the data compiled in *table 1* a remarkable fact emerges, *viz.*, that the lobing ratio differs appreciably from population to population. In both the diploid and the tetraploid ones the percentage of plants with bifid leaf lobes varies from 0 to 40, with, in addition, sometimes a small percentage of plants with a higher degree of lobing.

In diploid populations the highest percentages of multifid forms were recorded on the southern slopes of the Alps in northern Italy in relatively low-lying sites: Val d'Aosta, and the region to the NW of Lago Maggiore. This agrees with a report by LANDOLT (1967) concerning a number of montane taxa: populations from more elevated habitats show a tendency towards less dissected leaves as compared to populations from lower elevations. It is possible that smaller amounts of annual precipitation and relatively high temperatures favour the formation of leaves with a smaller surface area, but the small number of samples does not permit a more definite conclusion.

Pop. no. 450 (Dürnstein) contains a conspicuously high number of plants with much-dissected leaves, which emphasises the isolated position of this locality once more (see p. 431 and p. 433).

The variation in the records pertaining to tetraploid populations does not permit any conclusion as regards any ecological relation. The incidence of multifid leaves in tetraploids (as also found by HARRIS 1973) is, incidentally, quite at variance with what has been stated in, e.g., Flora Europaea (RECHINGER 1964).

In the hexaploid populations so far studied hardly any specimens with multifid leaf lobes have been encountered.

Map 2 shows of those populations which (a) contained at least 20 plants suitable for an assessment of the lobing ratio and (b) were cytologically homogeneous the overall percentages of multifidy. The peculiarities mentioned above are manifestly illustrated by this map.

For comparisions on a larger scale of the character of multifidy between the various population complexes also three of such complexes from southern France have been included in the investigation. These include gymnocarpic diploids from the Alpes Maritimes, angiocarpic diploids from the Massif Central and Cévennes, and angiocarpic tetraploids from the Pyrenees. Together with the data from the Alpine region and S Germany, the recorded ratios, which were determined in population complexes defined by their ploidy level, by the predominance of angiocarpy and by their geographical distribution, are shown in *table 3*. The variation in the degree of dissection is shown by distinguishing several, differentiated categories. Only those populations are included which have a constant level of ploidy. The table permits the following deductions:

(a) The diploid population groups (from the Swiss-Italian Alps and from the
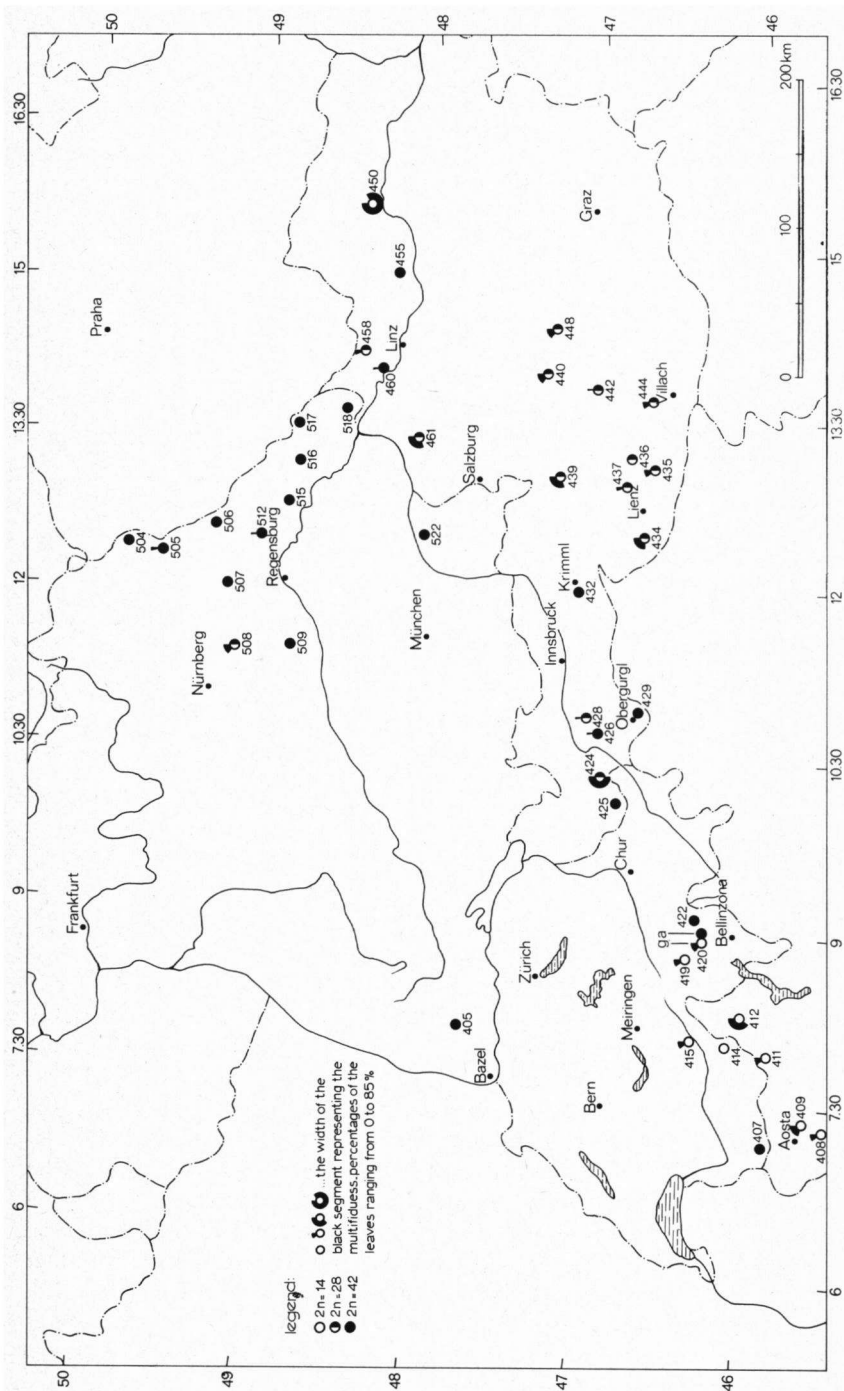
Map 2. Ploidy levels and the multifidus character in the bigger samples. The diverse multifidness grades compiled in one percentage multifidness as against entire leaf-lobes (one pair per leaf). The width of the circumposed segment correlates with the percentage multifidy, ranging from 0 up to 85% (see *table 1*).

Table 3. Lobing-percentages of a number of population complexes.

Ploidy level and fruit type	Population complex (geographical)	Number of lobe pairs per leave (in per cents)						Total percent-age	Total no. of plants examined
		0	1	2	3	4	≥5		
2n = 14, Gymnocarpic	Swiss and Italian Alps	2	85	11	2	–	–	100	413
	Alpes Maritimes (Fr.)*	1	83	15	1	–	–	100	207
	Dürnstein (A.), pop. no. 450	–	17	17	43	7	17	101	30
2n = 28, Gymnocarpic	Austrian Alps	1	84	12	3	–	–	100	454
	Upper Austria	–	78	17	5	–	–	100	125
2n = 42, Gymno- or Angiocarpic	Alpine Region (total)	9	91	<1	–	–	–	c. 100	316
2n = 42, Angiocarpic	Southern Germany and Upper Austria	7	93	<1	–	–	–	c. 100	614
2n = 14, Angiocarpic	Massif Central (Fr.)*	<1	97	2	–	–	–	c. 100	364
2n = 28, Angiocarpic	Pyrenees (Fr. + Sp.)*	4	95	<1	–	–	–	c. 100	426

* Material from DEN NIJS (1974)

Alpes Maritimes) exhibit a practically identical frequency distribution of the lobing percentages. It is not at all improbable that both groups belong to the same population complex, although the possibility of a convergent development of the character must also be reckoned with.

(b) The also gymnocarpic diploid pop. no. 450 Dürnstein differs so much in the variation of the character (43 per cent of the plants bore leaves with trifid lobes) that this strongly suggests that pop. no. 450 belongs to a different and geographically separated population complex.

(c) The variational distribution in the tetraploid populations from the Austrian Alps is identical with that of the first-mentioned diploid ones, so that – apart from the different ploidy levels – the Alps as a whole show a rather homogeneous picture. Once again one meets with the constancy of a certain characteristic within a certain geographical area irrespective of the level of ploidy (compare the distribution of angiocarpy and gymnocarpy on either side of a dividing line in the Belgian region: STERK & DEN NIJS 1971, DEN NIJS 1974). Although the number of tetraploid populations in Upper Austria is small, one may accept that they agree in their variation pattern with the Alpine tetraploids.

(d) The hexaploids from the Alpine zone show an altogether different pattern: the extremely low percentage of leaf multifidy (less than one per cent), and the corresponding low incidence of this feature in the population complex in S. Germany and Upper Austria (along the Danube) provide another argument pleading in favour of the assumption that the hexaploids in the Alps are independent of the di- and tetraploids found in that area, and perhaps invaded that region only recently, or, alternatively, are still penetrating into it (compare, e.g., the situation in pops. no. 407 Liddes, no. 418 St. Gotthard Pass, and no. 422 San Bernardino).

(e) As opposed to the continuity of incidence of the character in the Alpine di- and tetraploids we find a marked discontinuity in respect of the di- and tetraploid populations of the Pyrenees must be considered separately from the respectively. In these two areas the frequency of occurrence of plants with dissected leaf lobes is very low (2% and <1% respectively) and is about the same as that found in the hexaploids (<1%). The population complexes in question distinguish themselves from the di- and tetraploids of the Alps both in their angiocarpy and in the low incidence of dissected leaf lobes. In discussions regarding the micro-evolution of the *R. acetosella* aggregate these findings constitute important arguments in favour of the assumption that the tetraploid populations of the pyrenees must be considered separately from the tetraploids of the Alps; it is at any rate highly probable that these two groups and perhaps other ones not in discussion here originated independently by polytopy.

(f) It is noteworthy that the absence of leaf lobing ("f. *integrifolius*") in the material studied was almost exclusively recorded in hexaploid populations. In regional floras this form is mentioned for *R. acetosella* s.s. and said to occur only sporadically. Observations of plants growing wild (*e.g.* in the Netherlands) and in our experimental garden suggest to the present author that the plasticity of the phenotypic expression of the leaf shape is particularly high in hexaploids, so that extreme conditions (especially drought in combination with an open stand of vegetation) induce the plants to produce entire leaf-blades. In addition the incidental occurrence of West-European indivuals with genetical exclusively integrifoliate leaves must be noted. A much more important role is played by this character in the assumed integrifoliate group of *R. graminifolius* Lamb. s.l. found in the arctic regions of Asia and N America.

As an addition to the records in *table 3* it may be mentioned that 10 small samples (in all about 50 specimens), from the Greek islands of Mykonos (9 samples) and Delos (1 sample), of which in 6 and in one case, respectively, the chromosome number was determined (consistently = 42), consisted exclusively of individuals with multifid leaf lobes and with extremely numerous pairs of ultimate dissections (up to 12 or 13 per blade!). Such records seem to indicate that the prevailing ecological conditions play an important role in the phenotypic expression of the multifidy.

Surveying all accumulated data, HARRIS' (1968) notion of a clinal variation of the character (with a gradual increase towards the SE) seems to be correct.

For more cogent proof of this idea (and also to obtain arguments for pin-pointing the gene centre of the complex) a study of material from the Balkans and Asia Minor is undoubtedly required.

4. DISCUSSION

The geographical distribution of the characters of angio- and gymnocarpy in the area studied agrees fairly well the conclusions drawn by LÖVE (1944) on the basis of herbarium studies, with the restriction that angiocarpy is mentioned as being of wide-spread occurrence in the Alps although it is in fact rare and found only in adventitious populations. A linkage with certain chromosome numbers is altogether out of the question. The Alps can be regarded as an area in which initially only gymnocarpy occurred but became secondary invaded by angiocarpic forms, as witnessed by the situation in the central Alps and some "mixed" populations. Although this has not been examined in greater detail, it has become clear from information from the border areas and some published data that the situation in Czechoslovakia is most likely to be rather intricate, HADAČ & HAŠEK (1948) reported di-, tetra- and hexaploids from this country, and mention records of angio- and of gymnocarpic individuals. Their publication, incidentally, was the first to record gymnocarpic diploids. Later PAZUR-KOVA (1966) also reported their occurrence. Considering that in the adjoining parts of S Germany and the Austrian Danube valley the populations are pre-dominantly angiocarpic, one may expect to find the eastern limit of the area of angiocarpic forms somewhere in Czechoslovakia. As in France, the present area studied does not yield a correlation between the incidence of angiocarpy and a richer type of soil on the one hand, and the predominance of gymnocarpy on poorer soils, as found in Belgium on the other (STERK & DEN NIJS 1971). In the Alps a similar situation obtains as in France in that on a variety of soil types a single fruit type is found; in the former region nearly always gymnocarpy as against consistent angiocarpy in France. It seems as if the prevalence of angio-carpy (or gymnocarpy, respectively) in these regions is not so much decided by environmental conditions but rather by the Pleistocene glaciations which must have had a considerable influence on the distribution leading to relict areas and isolation of population complexes. Angiocarpic plants are certainly capa-ble of growing in the Alpine areas after their introduction (e.g., by human action). The possible ecological and perhaps adaptive significance of the character of angiocarpy thus remains an unresolved problem.

Also in the present study no positive correlation was found between the incidence of angiocarpy and the diploid chromosome number. Several regional floras follow LÖVE's (1944) classification, however, and consequently accept such a linkage (see, e.g. RECHINGER, 1957, 1964; ROTHMAHLER 1963; OBER-DORFER 1970; HESS et al. 1972). When chromosome numbers are at all given one must accept these with diffidence since at least a correlation with angio- or with gymnocarpy does not exist: in the area under discussion angiocarpy has been found in tetra- and hexaploids, and gymnocarpy at all three ploidy

levels. As regards the character of dissected leaf lobes the situation is rather similar: RECHINGER (1964) reports the presence of the "fa. *multifidus*" in only *R. angiocarpus* (2n = 14) and *R. acetosella* s.s. (2n = 42), i.e. not in *R. tenuifolius* (2n = 28), although in the numerous tetraploid populations of the eastern Alps a fairly high number of individuals with much dissected leaves was found (compare also HARRIS 1973). On the other hand in both the angiocarpic and the gymnocarpic hexaploids the dissected leaf type is decidedly scarce.

Another example of the problems arising from the most current classification of the complex is the occurrence of *R. tenuifolius* (Wallr.) Löve with 2n = 28. In Austria forms occur with very narrow leaf blades, high length to width ratios, which according to Löve's key would belong to *R. tenuifolius* (Gärtner, pers. comm.). The present author has checked such a situation near Dürnstein (pop. no. 450), and found that the plants keying out as such were diploid and had in addition very much dissected leaf blades (see *table 3*). HÖFLER & KNOLL (1956–1960) mention records of *R. tenuifolius* in Lower and Upper Austria, but in view of the above-mentioned experience one may expect that in this case they in fact also could refer to narrow-leaved diploid specimens, which is the more likely since one of the localities they mentioned (Welser Heide) lies in close proximity of Dürnstein. If one starts from the assumption that in NW Europe tetraploids are found which are conformable to the morphological description of *R. tenuifolius* (and such specimens do occur), it is not permissible to apply the same name to diploid plants *with multisect leaves*. It is quite clear that such diploids also morphologically belong to a different population complex which may even be rather far apart in a evolutionary sense if one takes the great rarity of the character of multisect leaves in north-west European tetraploid populations. Neither in the Netherlands (STERK et al. 1969) nor in Belgium (STERK & DEN NIJS 1971) has foliar multifidy been recorded in tetraploids.

In rough outlines the situation as regards the "accepted" classification of the *R. acetosella* complex in four species is thus as follows: the morphological variation exhibits a certain degree of discontinuity so that on the basis of this intranscendency a segregation into different taxa at the species level seems possible, but a number of conspicuous morphological features such as the leaf length-to-width ratio, angio- or gymnocarpy, and the number of basal leaf lobes varies right through the three ploidy levels. Some quantitative characters such as pollen size, length of the anthers, and fruit dimensions, on the other hand, vary in such a way that they agree much better with the ploidy levels (compare LÖVE 1941a, 1941b; HARRIS 1969; DEN NIJS, unpubl.), but they exhibit an appreciable overlap between the ploidy levels.

Taking these points into consideration in addition to the distribution of the various morphs and chromosomal races, the obvious corollary is that another classification of the complex must be considered. The cytological races are not distributed at random but in most cases in a certain area a single population complex with constant chromosome number is present, several of such population assemblies being geographically and often genetically isolated. Examples are provided by the gymnocarpic diploids in the W. Alps as against the angio-

carpic diploids in the French Massif Central and surrounding country, the gymnocarpic tetraploids in the eastern Alps as against the angiocarpic tetra-ploids in the Pyrenées, etc.

It is also to be expected that for a revised classification the differentiation into biospecies renders it difficult to arrange the forms into morphospecies. Nevertheless a new systematic arrangement must as closely as possible reflect the micro-evolutionary relationships of the taxa concerned (VALENTINE 1975), such as the probable polytopic origin of tetraploid population groups (and conceivably also of hexaploid complexes). It will be necessary to study more intensively the morphological characteristics and the ecological preferences of all taxonomic units to be recognised.

Attempts to arrive at a rational systematic classification will meet with appreciable difficulties owing to hybridisation of particularly tetra- and hexa-ploids. Although Löve (1944) only managed to produce very few pentaploids experimentally, which hybrids, moreover, appeared to be meiotically disturbed and already led to sterility in the F1 generation, the records of natural penta-ploids in France (DEN NIJS 1974) and now in the Czechoslovakian border area cannot be put aside as irrelevant. Artificial pentaploids, readily produced in the experimental garden, exhibited a fairly regular meiosis to the production of pollen grains with 16 to 19 chromosomes (DEN NIJS, unpubl.). The incidence of pentaploidy in some natural populations, and more particularly the obvious back-crosses of such F1-hybrids with the ploidy levels of the parent-individuals with about 30 ($= 16 + 14$) chromosomes and to a less extent specimens with about 38 ($= 16$ to $19 + 21$), render the conclusion obligatory that the popula-tion complexes involved are not altogether genetically separated. One must at least reckon with a possible hybridogenic introgression (see p. 435). It is inter-esting to note that in the polyploid complex of *Achillea collina* (4x) and *A. mille-folium* (6x) – even in the same area – similar hybridisation patterns have been found which must have resulted in gene flow and a weakening of the morpho-logical discontinuity between the tetra- and the hexaploid taxon (SCHNEIDER 1958). It is to be expected that also in the *R. acetosella* group such a diminish-ment of the differences has taken place in several parts of the overall range, especially because by a so-called "hybridisation of the habitat" the hexaploids will continuously increase their area of distribution at the cost of the di- and tetraploids. Examples of such a form of hybridisation sometimes succeeded by the disappearance of a less competitive species has been found in Canada: *Carduus acanthoides* versus *C. nutans* (see, e.g. MULLIGAN & MOORE 1961), and in Europe in the *Cardamine pratense* aggregate in which the incidence of neoge-nous contact zones between originally separated areas of occurrence has resulted in almost inextricable hybrid swarms (see LÖVQVIST 1956; LANDOLT & URBANSKA-WORYTKIEWICS 1971).

The historical phytogeography mentioned on p. 433 in connection with the so-called Rhine-Traun-Gap is substantiated by the data concerning foliar multifidy. The western diploids and the eastern tetraploids are, judging by their lobing ratios, apparently much more closely allied than each of them is to

the hexaploids found in the intervening country.

The situation regarding pop. no. 450 from Dürnstein, which is assumed to be a possible glacial relict, deserves some closer discussion. Not only does the presence of diploids in Czechoslovakia constitute an uncertain factor, but the locality lies in the Wachau which links up with the xerothermic Vienna Basin and the Czech Moravia. The latter areas contain an appreciable number of pannonic floral elements owing to the relatively favourable position on the SE flank of the Bohemian Massive. In this region there are numerous taxa of mediterranean or of steppe origin (which presumably invaded the area in post-glacial times) next to alpine elements which found refuge here during periods of maximum glaciation (POLATSCHEK 1966, NIKLFELD 1964, 1972, 1973). The area in question has, therefore, a fairly strong link with more easterly and southernly situated regions such as Hungary, Transsylvania, and the NE Balkans (KLIKA 1935). Considering that a few records from Bulgaria (from the Pirin Mts., among other localities) have already indicated the presence in that country of gymnocarpic, diploid, and 'multifid' plants (unpublished), one must also seriously consider the possibility that the Dürnstein population (and some neighbouring ones that may turn up) represent(s) a northwestern extension of a population complex with its principal range in the Balkans. It is, therefore, of the utmost importance to procure sufficient relevant data from the Balkan Peninsula, the more so since EHRENDORFER (1975) has summed up a series of arguments to emphasise the most interesting phytogeographical position of this region.

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