

## BIOSYSTEMATIC STUDIES OF THE RUMEX ACETOSELLACOMPLEX. I. ANGIOCARPY AND CHROMOSOME NUMBERS IN FRANCE

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### SUMMARY

As a sequel to biotaxonomic studies in Belgium, about 110 random population samples of *Rumex acetosella* L. s.l. from a large part of France were studied. Representatives of this polyploid complex were of common occurrence everywhere except in areas with a subsoil rich in lime. Angiocarpy is wide-spread, but gymnocarpy was only recorded from the French Alps. In contrast to the situation in Belgium, no correlation between the incidence of angiocarpy and a more fertile kind of soil could be established.

Diploids ( $2n = 14$ ) were found in the SE: Massif Central, Montagne Noire, Massif du Maure, and Massif du Mercantour in the Alpes Maritimes (altogether 36 populations); tetraploids ( $2n = 28$ , 23 populations recorded) are almost exclusively encountered in the Pyrenees and in the NE part of the Massif Central; and hexaploids ( $2n = 42$ , in 32 populations) appeared to be scattered over the remainder of the area studied, with a certain amount of sympatric overlap with the areas of the diploid and of the tetraploid chromosomal races in the Massif Central.

In the zones of overlap an appreciable number of hybrids between  $2n$  and  $4n$ , and between  $4n$  and  $6n$  plants were encountered (in 11 populations).

By far the large majority of the plants bear angiocarpous fruits irrespective of the level of ploidy, so that the alleged coupling between angiocarpy and diploidy (in the pertaining literature regarded as "*R. angiocarpus* Murb.", with  $2n = 14$ ) must be rejected. In the Alpes Maritimes gymnocarpous diploids were found, which may be considered to represent a more primitive taxon among the aggregate.

As far as can be ascertained, the distribution pattern of populations of the *R. acetosella* aggregate is, generally speaking, characteristic of a complex species differentiated during and after the last Ice Ages. In the discussion attention is paid to the possible causes underlying the differences in the distributional patterns (such as vegetative reproduction at higher ploidy levels). In order to obtain a more complete picture of the complex the investigations are being pursued.

### RÉSUMÉ

Comme suite aux recherches biotaxinomiques faites en Belgique, approximativement 110 échantillons des populations du *Rumex acetosella* L. s.l., provenant d'une grande partie de la France, ont été étudiés.

Représentants de cet agglomérat polyploïde étaient partout d'une présence fréquente, à l'exception de régions avec un sous-sol calcifère. La forme angiocarpe se présente très fréquemment, tandis que la forme gymnocarpe ne se trouve que dans les Alpes Maritimes.

Contraire à la situation en Belgique, la corrélation entre l'incidence d'angiocarpie et un sol plus fertile n'a pas été démontrée.

Des plantes diploïdes ( $2n = 14$ ) ont été trouvées dans le Sud-Est: le Massif Central, la Montagne Noire, le Massif du Maure et le Massif du Mercantour dans les Alpes Maritimes (36 populations au total). Des tétraploïdes ( $2n = 28$ , 23 populations) se trouvent presque

exclusivement dans les Pyrénées et dans le Nord-Est du Massif Central.

Des hexaploïdes ( $2n = 42$ , 32 populations) étaient répandues dans le reste de la région étudiée, avec des présences sympatriques dans le Massif Central où les aires de la cytotype diploïde, tétraploïde et hexaploïde se rencontrent.

Dans cette région un grand nombre d'hybrides a été trouvé entre des plantes diploïdes et tétraploïdes ainsi qu'entre des plantes tétraploïdes et hexaploïdes (dans 11 populations au total). L'immense majorité des plantes a des fruits angiocarpes, indépendamment du niveau de ploïdie, de sorte que la corrélation du caractère angiocarpe avec le taxon diploïde (considéré dans la littérature concernante comme *Rumex angiocarpus* Murbeck,  $2n = 14$ ) n'existe pas. Dans les Alpes Maritimes des diploïdes gymnocarpes ont été trouvés qui peuvent être considérés comme un taxon primitif dans l'agglomérat en question.

Selon la connaissance actuelle, la distribution de l'agglomérat polyploïde du *Rumex acetosella* peut être indiquée comme caractéristique de celle d'un complexe qui s'est développé pendant et après les dernières périodes glaciaires.

Dans les discussions attention a été prêtée aux causes éventuelles de ces différences de distribution (p.e. l'augmentation végétative aux niveaux de ploïdie plus élevés).

Afin d'obtenir une opinion plus complète sur ce complexe les recherches seront continuées.

## 1. INTRODUCTION

The present report is a continuation of the biotaxonomic studies of the *Rumex acetosella* complex in the Low Countries and Belgium (STERK et al. 1969; STERK & DEN NIJS 1971), and constitutes a part of an extensive biosystematic analysis of the aggregate in the whole of W. Europe.

LÖVE (1941a, 1941b, 1944) has distinguished four species in this polyploid complex with basic chromosome number ( $x$ ) = 7, viz., *R. angiocarpus* Murb. (supposed to be  $2n = 14$  and angiocarpous, as against gymnocarpy in the other three), *R. tenuifolius* (Wallr.) Löve ( $2n = 28$ ), *R. acetosella* L. s.s. ( $2n = 42$ ), and *R. graminifolius* Lamb. ( $2n = 56$ ), which have, according to distribution maps in LÖVE (1944), largely separate ranges in Eurasia. Angiocarpy, supposed to be a characteristic diagnostic feature of the diploid taxon by LÖVE (1941b), is the coalescence of the inner three perigone lobes with the exocarp at seed maturity.

Previous studies (STERK et al. 1969, STERK & DEN NIJS 1971) have shown that the combination of diploidy and angiocarpy does not hold for angiocarpous populations of the Low Countries, where the populations sampled appeared to be predominantly hexaploid, and sometimes tetraploid, and nearly all angiocarpous particularly in the southern regions of Belgium. Several workers, after having studied material from other parts of the world, e.g., from Canada (MULLIGAN 1959), Australia (JOHNSON & BRIGGS 1962), N. Zealand (MOORE 1954, HARRIS 1969), Central and S. Europe (e.g., HARRIS 1969), and S. Africa (STERK 1970), also mention angiocarpy in tetraploids and hexaploids. Up to now only two localities of angiocarpous diploids had been recorded viz., one near Lisbon (LÖVE 1944) and one on Mont Lozère, Dépt. Lozère, S. France (HARRIS 1969). The data reported in the relevant literature indicate a much smaller area of distribution of the diploid form than suggested in Löve's map of 1944.

The record of diploids from Mt. Lozère was one of the principal reasons to extend our investigations into the distribution and the ecology of the complex to populations in France. A second important fact is the relative scarcity of

tetraploids in the regions previously studied. STERK & DEN NIJS (1971) suggested that a narrower ecological amplitude is associated with a more restricted range of distribution. The question arises whether the tetraploid chromosomal race is also of restricted occurrence elsewhere in the range of the aggregate taxon.

A third reason for an extension of our studies is the correlation observed in central and S. Belgium between loamy soils and the occurrence of angiocarpy. Some previously obtained data from Les Landes, S.W. France and central Europe (HARRIS 1969), where angiocarpous populations were recorded from very different soil types, might be taken as pointed to the marginal distribution of the angiocarpous populations in Belgium where, conceivably, replacement of ecological factors by other ones resulted in a correlation typical of the border area.

In brief, the exact distribution and genecology of the levels of ploidy in W. Europe is inadequately known, so that the present classification is insufficiently based on biotaxonomic data.

The present study deals with the distribution of angiocarpy and of the different ploidy levels in France. Similar investigations covering Germany and the Alpine area are in progress and in addition ecological and genetical research. For the present investigation population samples were collected in a large part of France including the French Alps, the Pyrenees and the adjacent Spanish territory. According to LÖVE (1944) nearly exclusively *R. angiocarpus* Murb. (with  $2n = 14$ ) occurs in this region, with an admixture of both *R. tenuifolius* (Wallr.) Löve (with  $2n = 28$ ) and *R. acetosella* L. s.s. (with  $2n = 42$ ) in Alsace, the extreme NE of France, and the French Alps.

FOURNIER (1961) only mentions *R. acetosella* L. without subdivision. The same holds for COSTE (1937). BONNIER (1934) gives *R. acetosella* L. with the varieties *integrifolius* (Wallr.), *multifidus*. DC., and *repens* DC. which are said to occur only scatteringly. In addition, *R. angiocarpus* is recorded as rare (one must bear in mind that at that time the chromosome number [ $2n = 14$ ] was not coupled with that name). TUTIN et al. (1964) maintain Löve's classification but remark that the distribution is insufficiently known. DE LANGHE et al. (1973) also retain Löve's classification of 1944, though not as species but at the subspecies level, and state that large-scale studies are necessary to establish the occurrence of these elements of the complex in the area covered by their flora.

## 2. MATERIAL AND METHODS

The present author collected material from about 115 sites in 1971 and 1972. The collections consisted mainly of random samples of natural populations, usually with a sample size of 50 to 75 individuals, but for various reasons a small number of samples contained only a few plants. In each locality a soil sample was taken and a record of the stand of vegetation was made. A more detailed evaluation of these data will be presented in a forthcoming publication.

As a rule the distance between the sampling sites was at least 30 to 50 km, but

in a number of cases, namely in mountainous areas, this principle was disregarded when differences in elevation were thought to be of greater importance than mere distances measured along the ground.

The density of sampling was appreciably lower in the W. and in the N., because these regions were not so intensively explored for various reasons to be explained later.

Apart from these population samples an additional 30 samples collected by other workers became available, e.g., material gathered in Brittany and Les Landes by Dr. A. A. Sterk, samples from scattered localities in W. and N. France supplied by Dr. M. Kergu len of the Station Nationale d'Essais de Semences (Versailles), and some from the Swiss canton of Valais obtained through the Botanical Garden, Geneva. The samples in question consisted of seed collected from an unknown number of plants, so that no voucher specimens were retained unless mature plants had been raised from such a sample.

The incidence of angiocarpy was assessed as previously indicated (compare STERK et al. 1969). Individual plants producing both angiocarpous and gymnocarpous fruits were, as before, recorded as "angiocarpous". The present author found some indications of a certain amount of suppression of a genotypically determined angiocarpy in the phenotype in special circumstances (DEN NIJS, 1970).

Chromosome counts were usually performed on root tip material of young seedlings which after a cold treatment for 3 – 5 days followed by a sojourn at 25°C for 2 – 3 days and subjection to a light regime of 12 hrs per day, had produced rootlets with a usable length of 5 – 10 mm.

The voucher specimens preserved in the Hugo de Vries-laboratorium (AMD) are nearly always the mother plants from which seed for chromosome counts was taken.

For the counting of the chromosomes the following technique was employed: a pretreatment of the harvested root tips with 1-bromonaphthalene for 2 – 3 hrs. followed by fixation in acetic acid/absolute alcohol 1:3 for 30 – 50 min. (if unavoidable, storage in the fixative at –20°C until the sample could be worked up), maceration in N HCl at 60°C for 9 min., staining in basic fuchsin according to Feulgen, squashing in 45% acetic acid, and microscopic observation (with phase contrast) under a Zeiss RA research microscope. Some of the better slides were made permanent by freeze-drying with CO<sub>2</sub> snow followed by mounting in Euparal.

### 3. RESULTS

#### 3.1. The distribution of the angiocarpous and the gymnocarpous forms in France

The localities of the population samples and the lots of seeds and the corresponding occurrence of angiocarpy or gymnocarpy arranged according to the magisterial departments, are shown in *tables 1* and *2*, respectively. *Map no. 1* shows the localities in question. It is evident that in certain regions there are

Table 1. Population samples: Origin, Percentage of angiocarp and Chromosome numbers.

Locality	Magisterial department	Population number	Population samples		Individual plants				
			Number of ♀ plants	% Angioc. plants	Number of seedlings counted	Number of parent plants	2n number of chromosomes	Plant: ang. + gym.-	
1	2	3	4	5	6	7	8	9	
Avallon	260 m	Yonne	363	10	100	11	3	14	+
Bort-les-Orgues	550 m	Cantal	348	36	100	10	3	14	+
Allanche	1020 m	Cantal	347	59	100	8	3	14	+
Mons	930 m	Cantal	344	4	100	9	3	14	+
Montsalvy	800 m	Cantal	335	47	100	9	3	14 (15, 16)	+
Chanaleilles	1150 m	Lozère	126	62	100	6	3	14	+
Gandrieu	1150 m	Lozère	127	68	100	6	3	14	+
St.-Chely-d'Apcher	1030 m	Lozère	125	73	100	6	3	14	+
Combrettes	1110 m	Lozère	124	42	100	6	3	14	+
Gourgons	1200 m	Lozère	128	75	100	6	3	14	+
Finiels-Mont Lozère	1250 m	Lozère	123	75	100	8	3	14	+
Pont-de-Montver	750 m	Lozère	122	44	100	4	3	14	+
Mont Aigoual (Cabrillac)	1220 m	Lozère	121	76	100	8	3	14	+
Mont Aigoual (Observatoire)	1570 m	Gard	120	64	100	6	3	14	+
Mont Aigoual (L'Esperou)	1190 m	Gard	119	53	100	6	3	14	+
Mont Aigoual (Mas Mejean)	470 m	Gard	118	57	100	5	3	14	+
Mont Aigoual (Valléraugue)	250 m	Gard	117	27	100	5	3	14	+
Mont Aigoual (Le Vigan)	250 m	Gard	116	64	100	5	3	14	+
Astet	1050 m	Ardèche	130	58	100	6	3	14	+
Laval-Roquecèzière	770 m	Aveyron	324	38	100	7	3	14	+
Faveyrolles	280 m	Aveyron	329	25	100	9	3	14 (15-17)	+
Bois du Four	870 m	Aveyron	330	36	100	8	3	14	+
Le Cayrol	820 m	Aveyron	336	15	100	13	4	14	+
Mirepoix-s.-Tarn	110 m	Hte-Garonne	327	32	100	13	4	14	+
Moulin-Mage	820 m	Tarn	323	50	100	9	3	14	+
Lavaur	150 m	Tarn	326	19	100	7	3	14	+
Mazamet	400 m	Tarn	114	49	100	7	3	14	+
St.-Gervais	530 m	Hérault	322	24	100	9	4	14	+
St.-Pons	600 m	Hérault	115	46	100	6	3	14	+
Cuxac	530 m	Aude	113	46	100	9	3	14	+
Col de Babaou	400 m	Var	112	34	100	2	1	14	+
						3	1	14(15)	+
						3	1	15	+
Le Pra (Val de Tinée)	1600 m	Alpes-Mar.	107	18	0	3	2	14	-
St. Etienne de Tinée	1100 m	Alpes-Mar.	106	47	0	6	4	14	-
Isola (Val de Tinée)	830 m	Alpes-Mar.	105	1	0	1	1	14	-
Le Boréon	1400 m	Alpes-Mar.	109	56	0	4	3	14	-
Le Boréon	1550 m	Alpes-Mar.	108	43	0	5	4	14	-
Les Voisins	250 m	Allier	146	54	100	10	3	28	+
Planfait	430 m	Allier	144	50	100	6	3	28 (30)	+
Digoin	240 m	Saône-et-Loire	145	52	100	8	3	28 (29)	+

	1	2	3	4	5	6	7	8	9
Vendranges	450 m	Loire	142	32	100	8	3	28	+
Noirétable	730 m	Loire	140	53	100	10	3	28	+
Les Halles	600 m	Rhône	141	58	100	9	3	28	+
St.-Beauzire	580 m	Hte-Loire	346	76	100	10	3	28	+
Pinols	970 m	Hte-Loire	345	68	100	10	4	28	+
Lavillatte	1300 m	Ardèche	129	53	94	5	3	28	+
Bourg-St.-Maurice	1700 m	Savoie	102	76	100	6	3	28	+
Les Auberts	1380 m	Htes-Alpes	103	76	95	8	3	28	+
						2	1	28	-
St.-Chaillol	1290 m	Htes-Alpes	104	51	100	2	1	28	+
La Séoube	1020 m	Htes- Pyrénées	310	67	100	6	3	28	+
Fabian	1150 m	Htes- Pyrénées	308	15	100	1	1	28	+
Arreau (Col d'Aspin)	850 m	Htes- Pyrénées	309	21	100	7	3	28	+
Laspaüles	1400 m	Huesca (Spain)	304	42	100	4	2	28	+
Viella	1280 m	Lérida (Spain)	305	38	100	2	1	28	+
Mournicou	1050 m	Ariège	313	87	100	2	2	28	+
Ax-les-Thermes	720 m	Ariège	314	6	100	14	4	28 (35)	+
Puyvalador	1420 m	Pyrénées-Or.	318	13	100	8	4	28	+
Col de la Quillance	1700 m	Pyrénées-Or.	319	83	100	9	3	28	+
Prats-de-mollo-la-Preste	700 m	Pyrénées-Or.	320	43	100	7	3	28	+
Escoulobre	1000 m	Aude	317	22	100	8	3	28	+
Le Bonhomme	970 m	Haut-Rhin	364	26	100	8	3	42 (43)	+
Lac Blanc	1100 m	Haut-Rhin	365	51	100	9	3	42	+
Le Valtin	800 m	Vosges	366	59	100	11	4	42 (41)	+
Pouilly-en-Auxois	430 m	Côte-d'Or	100	76	100	6	3	42	+
Moulon-s.-Yonne	240 m	Nièvre	362	70	100	10	3	42	+
Mesires	300 m	Saône-et- Loire	147	68	100	10	4	42	+
Le Châtelet	200 m	Cher	359	8	88	1	1	42	+
Vallon-en-Sully	250 m	Allier	360	69	100	8	3	42	+
Le Theil	400 m	Allier	354	72	100	7	3	42 (43)	+
Viersat	430 m	Creuse	355	32	100	5	3	42 (43)	+
St.-Vaurey	470 m	Creuse	356	67	100	7	3	42	+
Croix-de-la-Gétte	280 m	Hte-Vienne	358	14	100	8	3	42	+
St.-Junien	275 m	Hte-Vienne	357	49	90	9	3	42	+
Cours	560 m	Rhône	143	57	100	8	3	42	+
Chaponnay	340 m	Rhône	101	37	100	6	4	42	+
St.-Avit	720 m	Puy-de-Dôme	352	76	100	8	3	42 (40)	+
Pérols-sur-Vézeur	850 m	Corrèze	349	84	100	9	3	42	+
Laval	400 m	Corrèze	342	33	100	6	2	42	+
Le Teulet	640 m	Corrèze	340	96	100	10	3	42	+
Vézac	750 m	Cantal	339	59	100	10	3	42	+
St.-Martin-s.-Vigourou	950 m	Cantal	338	62	100	7	3	42 (41)	+
Valette	900 m	Cantal	343	73	100	8	3	42 (41)	+
Maurs	450 m	Cantal	334	60	100	10	3	42	+
Allègre	800 m	Hte-Loire	134	71	100	2	1	42	+
Villefranche-de-Rouergue	590 m	Aveyron	332	79	100	10	3	42 (44)	+
Baraqueville	680 m	Aveyron	331	63	98	8	3	42 (41)	+
Gaulène	410 m	Tarn	328	74	100	8	4	42	+

	1	2	3	4	5	6	7	8	9
Lomers	250 m	Tarn	325	30	100	8	3	42	+
Lannemezan	540 m	Htes-Pyrénées	311	30	100	4	2	42	+
Canet-plage	0 m	Pyrénées-Or.	321	23	100	8	3	42	+
S. Celoni	165 m	Barcelona (Spain)	302	6	100	8	4	42 (44)	+
Montseny	700 m	Barcelona (Spain)	303	56	100	9	4	42 (43)	+

Table 2. Seed-samples origin, angiocarpy or gymnocarpy, ploidy level.

Origin		Magisterial Department	sample number	seeds ang. + gym.-	ploidy level
Val d'Entremont	1730 m	Valais (Suisse)	031	—	2×
Val d'Entremont	1300 m	Valais (Suisse)	032	—	2×
Mont Aigoual	1500 m	Gard	07	+	2×
Mont Aigoual (Mandagout)	600 m	Gard	09	+	2×
Le Môle	30 m	Var	111a	+	2×
Les (Val d'Aran)	650 m	Huesca (Spain)	046	+	4×
Bouafles	—	Eure	01	+	6×
Plougrescant	—	Côtes-du-Nord	02	+	6×
Suscinió	—	Morbihan	027	+	6×
Pointe-St.-Jacques	—	Morbihan	026	+	6×
Ploërmel	—	Morbihan	047	+	6×
La Grée	—	Morbihan	021	+	6×
La Chapelle-Blanche	—	Indre-et-Loire	014	+	6×
Bélin	—	Gironde	024	+	6×
Sables-d'Olonne	—	Vendée	028	+	6×
Petit-Auverné	—	Loire-Atl.	011	+	6×
Vieux-Boucau	—	Landes	022	+	6×
Léon	—	Landes	025	+	6×
Soustons	—	Landes	030	+	6×
Villargoix	—	Côte-d'Or	150	+	6×
Molinot	—	Côte-d'Or	04	+	6×
Mhère	—	Nièvre	05	+	6×
Chatellux	—	Yonne	06	+	6×
Campnac	—	Aveyron	010	+	6×
Viazac-gare	230 m	Lot	333	+	6×
Vizzavona	850 m	Corsica	057	+	6×
Vizzavona	1050 m	Corsica	058	+	6×
Tossa de Mar	—	Barcelona (Spain)	056	+	6×

none, or hardly any, sampling sites. For the W. and N.W. this is simply a matter of insufficient sampling. It is, for instance, known that in some areas of these parts of France, e.g., in Brittany, *R. acetosella* L. s.l. does occur frequently

(Dr. Sterk, pers. comm.). In other parts of the country which were explored more thoroughly, elements of this taxon are much less common or distinctly rare owing to unsuitable soil conditions, however, particularly on limestone or other very basic formations representatives of the complex under discussion are only found in exceptional cases and, if so, certainly not in large populations. In areas where substrates poor in lime (such as granites, sandstones, and sandy soils) occur, on the other hand, *R. acetosella* L. s.l. is wide-spread and often forms populations of an appreciable size. Some illustrative examples are the following: elements of the aggregate were encountered in the whole of the Massif Central (which consists largely of granitic rocks, acid sands, and eruptive sediments), but they appear to be conspicuous by their absence in the area of the so-called "Causses", limestone plateaus situated in the southern part of the Massif Central. Also in the foreland of the Pyrenees, towards Pau and Tarbes, where a large number of rivers streaming to the north deposited thick packets of Tertiary and Quaternary deposits of material eroded off the limestone-rich first chain of mountains lying to the S., *R. acetosella* L. s.l. is poorly represented.

Rich populations of the *R. acetosella* aggregate occur in the eastern Pyrenees, but only a few in the western part which consists chiefly of limestone rocks. In the French Alps many populations were encountered in a few granite massifs, namely the Massif du Mercantour and the Massif du Champsaur.

After the poor representation of the *R. acetosella* aggr. in regions rich in limestone rocks and basic deposits had been established, large parts of France where such formations are wide-spread were not explored any more. This is the case in the Paris Basin and the adjoining territory to the W. and N.W. of the Massif Central. For this reason these (and similar) areas are almost devoid of sample sites on *map no. 1*. The percentage of angiocarpous individuals was determined in altogether 112 population samples. Of these 112, 102 contained exclusively angiocarpous plants (= 100% angiocarpy), and 5 none at all (= 0% angiocarpy, i.e., consistent gymnocarpy); the remaining 5 populations upon the whole exhibited only a small rate of gymnocarpy, varying from 2% to 12%.

Twenty-eight seed samples were studied, but owing to the fact that the seeds were gathered from an unknown number of individual plants the angiocarpy of the individual plants of the population could not be assessed. Of the 28 lots, 26 were exclusively angiocarpous and two completely gymnocarpous. On *map 1* (see pag. 664) the areas where gymnocarpy was recorded are hatched. The absence of gymnocarpy in most of the French territory and the adjoining Spanish Pyrenees is striking. Only five gymnocarpous populations have been found in a restricted area in the Alpes Maritimes: Massif du Champsaur, Val de Tinée, and Val de Vésubie. In this area not a single angiocarpous plant was encountered. The two lots of gymnocarpous seed are from Val d'Entremont (Valais) in Switzerland. Elsewhere in the French Alps the situation is not different from that in the rest of France, albeit that the populations are of less common occurrence in these mountains.

No correlation between the incidence of angiocarpy or gymnocarpy and a more fine-grained (or coarse-grained) soil (as is apparent in Belgium), and neither



a correlation between the occurrence of angiocarpous populations and soil fertility could be established. Complete angiocarpy was found in populations growing on soils ranging from very rich to very poor. Possible consequences of these results will be mentioned in the discussion.

### 3.2. Chromosome numbers

In all 105 population samples and 28 seed samples were studied. Whenever possible, seedlings from the progeny of 3 to 4 plants of each population sample were examined; by doing so counts were made of the progenies of a total of 313 plants. Two to six seedlings of each mother plant were used, so that per population the chromosomes were counted of 5 to 15 seedlings representing 3 to 4 separate progenies. In all about 785 seedlings were studied.

Of each seed sample the chromosome number was determined in 3–10 individual seedlings.

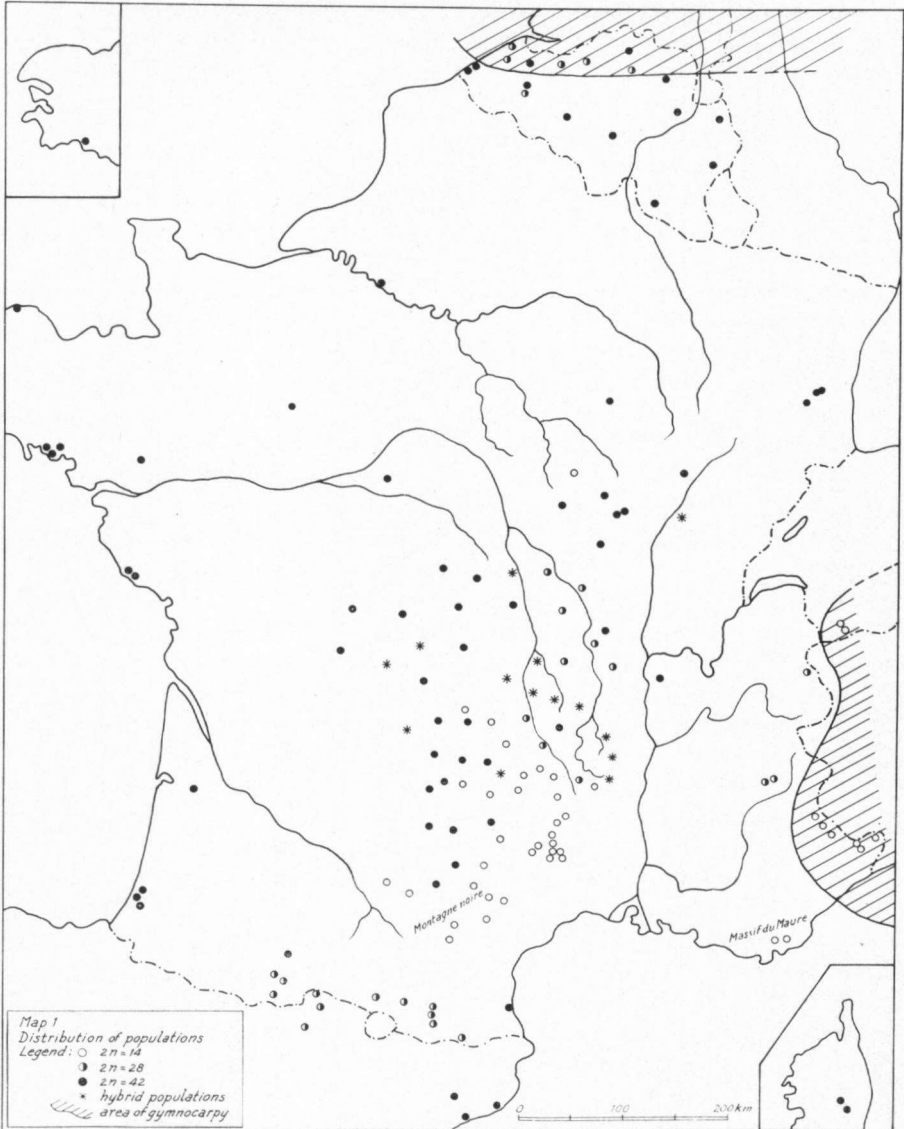
The results of the counts of the population samples and the seed samples are shown in *tables 1* and *2*, respectively, with the exception of 14 “mixed” populations separately tabulated in *table 3* (see pag. 667).

In each group with the same level of ploidy the samples are arranged in a sequence according to the magisterial districts, from N. to S.

- If all counts of a population sample yielded the same chromosome number, the number is given for all counted specimens together.
- If in the progeny of one, or of more, plant(s) of a sample a different number was found, this is indicated on a separate line (or on several lines).
- In a number of cases small deviations within the progeny of a single plant were recorded. If, for instance of 5 seeds examined one seedling had a chromosome number of  $2n = 15$  (instead of 14), or  $2n = 41$  (instead of 42), the deviating number is indicated between brackets behind the most frequent number counted and refers to only one or two of the seedlings counted.
- Variation of the number in one seedling (intra-individual or somatic aneuploidy) is not recorded in the table.

Within populations with only a single ploidy level a certain amount of variation was noted. In diploids ( $2n = 14$ ) 96% of the root tips had  $2n = 14$ , 3%  $2n = 15$ , and 1%  $2n = 16$ . Sometimes not all cells of the same root tip had the same number of chromosomes and the variation was even somewhat greater:  $2n = 14$  in 94%,  $2n = 15$  in 4%,  $2n = 16$  in 1.5%,  $2n = 17$  in 0.5%,  $2n = 18$  and  $2n = 19$  in 0.1% of the cases.

The total number of diploid seedlings recorded was 254, the number of individual cells counted amounted to about 700. Owing to the small number of chromosomes the counting is not difficult and deviations attributable to counting errors can be practically excluded. In tetraploid and hexaploid populations the variation seems to be greater. However, the polyploid nature of the sets of chromosomes often results in a poor separation of the chromosomes in the metaphase plates (by clustering), so that the exact number could not be estimated and such counts as “ $2n = 42 \pm 1$ ” were recorded. For this reason, more exact details concerning the range of aneuploid variation can as yet not be established.



Map 1: The population and seed samples: Distribution of gymnocarpy and angiocarpy and of the ploidy levels.

Of the population samples studied, 36 proved to be diploid ( $2n = 14$ ), 23 tetraploid ( $2n = 28$ ), and 32 hexaploid ( $2n = 42$ ). In the remaining 14 several ploidy levels were noted, while apparently in a number of these frequently hybridisations between individuals with different ploidy levels had taken place.

The seed samples yielded the following results: 5 of them were diploid, 1 was

tetraploid, and 22 were hexaploid; there were no "mixed" samples among them.

The results of the chromosome counts are shown on *map 1*. No difference was made between population samples and seed samples. This map shows some interesting peculiarities. The ranges of the three levels of ploidy hardly overlap. Diploids are of frequent occurrence in the Massif Central, more particularly in the central and southern parts, in the Cévennes, and on the Montagne Noire. Farther to the S. diploids are also found on the Massif du Maure near Marseilles. It is noteworthy that the appreciable differences in climate between particularly the last-mentioned two regions (mediterranean) and large parts of the Massif Central (montane), and in consequence the differences in elevation: Le Môle (Var) 30 m, and, e.g., Mont Aigoual (Gard), 1500 m, do not seem to have any influence in the distribution of the ploidy level.

Another concentration of diploid populations is present in the Alpes Maritimes, in the Massif du Mercantour, and farther to the N. in the Val d'Entremont in Valais (Switzerland). In these areas hardly any other chromosome number was found.

In the parts of the Pyrenees that were explored only tetraploids were encountered. The locality of the population of Lannemezan (Dépt. Hte Pyrénées) no. 311 with  $2n = 42$  is not situated in the Pyrenees proper, but already in the flatter foreland, and that of the population of Canet-Plage (Pyrénées-Or.), no. 321, is also outside the mountains.

A number of tetraploid populations was found concentrated in the N. part of the Massif Central, roughly speaking in the upper reaches of the river Loire and its tributaries. A few localities lie in the French Alps, e.g., in the Massif du Champsaur.

In the whole of the W. and N. regions of France neither diploids nor tetraploids were encountered, but only hexaploids. The range of the diploids is adjoined at the W. & N. by the area of the hexaploids; in the N. border zone also a population complex of tetraploids occurs. In this part of France diploids, tetraploids, and hexaploids are found in close proximity of one another, and sometimes even partly sympatrically. In the W. "mixed" populations containing both diploids and hexaploids occur (Lacalm, Aveyron, no. 337, and Le Chastang, Corrèze no. 341). Compare *table 3*.

In the N. zone of overlap the situation is much more complicated: not only do we find "mixed" populations, but also hybridisation between the different ploidy levels. In consequence, seedlings reared from seed collected from such populations appear to exhibit a great diversity in their chromosome numbers. Such hybrid populations are indicated on *map 1* with an asterisk. These populations will be discussed in a subsequent chapter.

### 3.3. Angiocarpy and chromosome numbers

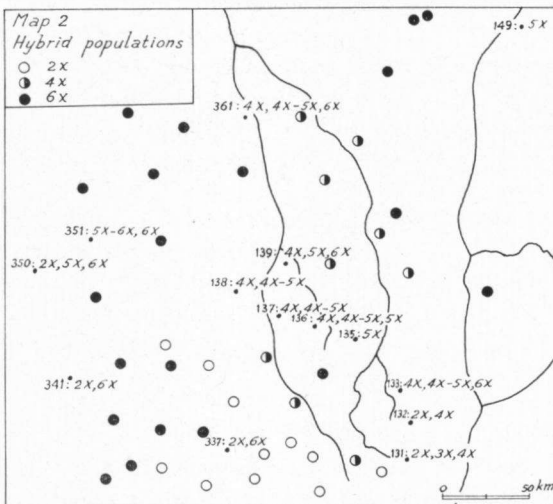
*Map 1* shows not only the chromosome numbers of the populations studied but also the distribution of angiocarpy and gymnocarpy among these populations. As reported before, angiocarpy is predominant in France, a part of the Alpine region excepted. It is evident (see *table 1*) that nearly all populations, irrespective

of their ploidy level, are angiocarpous; in other words, angiocarpy occurs in hexaploid, tetraploid, and diploid populations. It follows that angiocarpy is not a characteristic diagnostic character of the diploid taxon.

The gymnocarpous populations of the Alpes Maritimes, and the two gymnocarpous seed samples received from the Val d'Entremont (Valais) appeared to yield exclusively diploid plants ( $2n = 14$ ) when examined cytologically. This seems to be the first record of this combination of characters in Europe. The occurrence, in France, of both angiocarpous and gymnocarpous diploids has thus been established. The possible indicative value of the incidence of gymnocarpous diploids for the elucidation of, among other things, the (convergent) evolution of the complex will be assessed in the Discussion (see p. 669).

### 3.4. Hybrid populations

*Map 2* is a more detailed map of the region in central France where the areas of distribution of diploid, tetraploid, and/or hexaploid populations meet or overlap. In some of the populations sampled in this area a great diversity of chromosome numbers was recorded (see *table 3*: the sequence is determined by the degrees of polyploidy found per population, starting from the  $2n = 14$  diploid level.) In this table a number between brackets means that only a few seedlings examined (or only a single one) possessed this number, whereas an entry such as "21-23" indicates that the chromosome numbers of *all* seedlings fell within this range. The addition "ca" signifies that the chromosome number varied within a single root tip to such an extent that the variation could not be blamed upon inaccuracies during the counting (and must be explained as intra-individual somatic variation).



Map 2: The populations in the N.-E. part of the Massif Central: distribution of ploidy levels and occurrence of hybrids.

Table 3: Mixed and Hybrid Populations: Origin, Percentage of angiocarpy and Chromosome numbers.

Locality	Magisterial department	Population number	Population samples		Individual plants			
			Number of ♀ plants	% Angioc. plants	Number of seedlings counted	Number of parent plants	2n number of chromosomes	Plant: ang. + gym.-
St.-Martin-de-Valamas	625 m Ardèche	132	26	100	1	1	14	+
Lacalm	1050 m Aveyron	337	46	100	4	2	28	+
Le Chastang	540 m Corrèze	341	50	100	3	1	14	+
Laviolle	600 m Ardèche	131	16	100	9	3	42	+
					5	2	14	+
					5	2	42	+
					2	1	14	+
					3	1	14(21)	+
					5	1	21-23(28)	+
St.-Léonard	350 m Hte-Vienne	350	51	100	3	1	14	+
					3	1	14(35)	+
					3	1	42	+
Labruyère	180 m Côte-d'Or	149	76	100	1	1	c. 35	+
Usson-en-Forez	900 m Loire	135	46	100	13	3	c. 35	+
Pontaret	400 m Puy-de-Dôme	139	34	100	2	1	28	+
					3	1	c. 30	+
					2	1	42(35)	+
St.-Menoux	250 m Allier	361	70	100	3	1	28	+
					5	1	28(c. 32)	+
					1	1	35	+
St.-Bonnet-le-Chastel	870 m Puy-de-Dôme	136	66	100	4	1	28(30)	+
					3	1	30(31)	+
					3	1	c. 35	+
Chazaux	880 m Hte-Loire	133	56	100	6	1	42(28)(35)	+
					3	1	43(35)	+
					2	1	c. 32	+
Rouillas-haut	940 m Puy-de-Dôme	138	68	100	3	1	28	+
					2	1	28(c. 30)	+
					4	2	c. 30	+
Chauvaye	680 m Puy-de-Dôme	137	43	100	3	1	28	+
					3	1	28(29)	+
					3	1	28(c. 31)	+
St.-Hilaire-le-Chateau	460 m Creuse	351	55	100	2	2	42	+
					1	1	c. 37	+
					3	1	c. 39	+

In a number of populations two discrete levels of ploidy were noted: in the W. (no. 341, La Chastang, Corrèze, and no. 337, Lacalm, Aveyron) the plants had either  $2n = 14$  or  $2n = 42$ , and in the S. (population no. 132 from St.-

Martin-de-Valamas, Ardèche) either  $2n = 14$  or  $2n = 28$ . Intermediate or otherwise deviating chromosome numbers were not noted, so that the conclusion can be drawn that in these "mixed" populations no hybridisation takes place. In the other samples the great variety of chromosome numbers points to the incidence of crosses between plants with different ploidy levels. The following cases will be discussed:

– Pop. 131 from Laviolle (Ardèche) yielded in the progeny seedlings with  $2x$  and other ones with  $4x$  chromosome sets, but also one with  $2n = 21$  and two (from another parent plant) with  $2n = 21-22$  and  $2n = 21-23$ , respectively, while in the same progeny also  $2n = 28$  was found. Most probably hybridisation took place between di- and tetraploids resulting in offspring with  $2n = 7 + 14 = 21$ . However, the possibility of a combination of an unreduced gamete mother cell functioning as a gamete and a haploid  $n = 7$  gamete resulting in viable seed cannot be ruled out.

– Pop. 350 from St.-Léonard (Hte-Vienne): the progenies of three parent plants appeared to have  $2n = 14$ ,  $2n = 42$ , and  $2n = 14$  with one descendant with  $2n = 35$ , respectively. Since in a wide area around this site no tetraploids were encountered (the nearest locality being Rouillas-Haut, Puy-de-Dôme at a distance of about 170 km), one must conclude that in this case an unreduced gamete mother cell with  $2n = 14$  became a functional gamete and fused with a haploid ( $n = 21$ ) gametic cell of a hexaploid plant to form a viable seed with  $2n = 14 + 21 = 35$ .

– Pop. 149 from Labruyère (Côte-d'Or) and Pop. 135 from Usson-en-Forez (Loire) yielded only seedlings with  $2n = c. 35$ . In Pop. 149 this number could only be counted in one root tip (33–36), three plants of Pop. 135 yielded 13 seedlings in all of which  $2n = 35$ . There can be very little doubt that in this population hybridisation between tetraploids and hexaploids must take place on a large scale.

– In the offsprings of Pop. 139 from Pontaret (Puy-de-Dôme), Pop. 361 from St.-Menoux (Allier), 136 from St.-Bonnet-le-Chastel (Puy-de-Dôme) and 133 from Chazaux (Hte-Loire) tetraploids, hexaploids, and their hybrids (pentaploids) were recorded. In a number of seedlings the chromosome number lay between 28 and 35, and when this was the case, the variation in number between individuals of the same progeny, and the somatic aneuploidy was appreciable. In one seedling raised from a parent plant from Pop. 136 the counts were, e.g.,  $2n = 32$  (recorded three times),  $2n = 33$  (twice), and  $2n = 34$  (once); two other seedlings of the same progeny yielded  $2n = 32-36$  and  $2n = 34-35$ , respectively. It is highly probable that in such cases, apart from hybridogenous irregularities in the mitoses, back-crosses have occurred between a pentaploid ( $2n = 35$ ) of hybrid origin and a tetraploid ( $2n = 28$ ), which resulted in the above-mentioned variation in number of chromosomes owing to an irregular distribution of the chromosomes during their meiotic separation. SINGH (1964) reports this phenomenon in progenies of crosses between *Rumex acetosella* ( $2n = 42$ ) and *R. hastatulus* ( $2n = 4x = 16$ ).

– Pop. 137 from Chauvaye (Puy-de-Dôme) and Pop. 138 from Rouillas-Haut

(Puy-de-Dôme) yielded progenies with the following counts (each number between brackets representing the number in a single root tip):

137:  $2n = (28) (28) (29)$ ;  $2n = (28) (28-29) (28-33)$ ;

$2n = (28) (28) (28)$ .

138:  $2n = (28) (28) (28)$ ;  $2n = (27-32)$ ;  $2n = (25-30)$ ;

$2n = (27-29) (28) (27-30)$ .

The variation within individual seedlings and the large number of aneuploid cells (with, in this case, numbers which are "too high") suggests that a number of generations back pentaploids must have been present and that subsequent, repeated back-crossing with tetraploid individuals again lowered the number to nearly the tetraploid level. The possible incidence of chromosome drop as a consequence of instability must also be reckoned with.

– Pop. 351 (St. Hilaire-le-Chateau, Creuse) yielded the following results:  $2n = (42)$ ;  $2n = (42)$ ;  $2n = (35-42)$ ;  $2n = (35-41)$ . Conceivably back-crossing between pentaploid individuals with hexaploids took place here. If pentaploids were present at one time, this implies that tetraploids must have been present (at least in the vicinity) or may still be present in the area. The pentaploid seedling raised from a seed of Pop. 350 (St.-Léonard, Hte-Vienne), situated in the neighbourhood of Pop. 351, may also have originated from an unreduced tetraploid pregametic cell (with  $2n = 28$ ) and a normal gametic cell with  $n = 7$  from a diploid parent plant (see p. 668).

It was often difficult to determine the chromosome number in the natural hybrids under discussion, the more so in the plants with the highest numbers. The percentage of germination of the seeds was frequently low and seedling development poor. Mitotic divisions were of infrequent occurrence and the chromosomes did not spread very well but tended to remain grouped in clusters, so that for these reasons sometimes results were obtained from only a few seedlings of a certain parent plant.

#### 4. DISCUSSION

The presence of a narrow zone of transition between (almost) completely gymnocarpous populations in the N. to angiocarpous ones in the S. of Belgium previously established (STERK & DEN NIJS 1971) has been confirmed at least as far as the region of W. Europe discussed in the present publication is concerned, and may be accepted as a definite border-line between them. As we have seen, angiocarpous populations occur everywhere except in a part of the Alps. This characteristic distribution of this feature agrees with the map published by LÖVE (1944) supposed to show the distribution of *R. angiocarpus* Murb. (said to have  $2n = 14$ ) in this area. The presence of gymnocarpy in the French Alps Maritimes agrees with the ditribution maps of *R. tenuifolius* (Wallr.). Löve (supposed to have  $2n = 28$ ) and *R. acetosella* L. s.s. (sensu Löve:  $2n = 42$ ) published by the same author and supposed by him to be consistently gymnocarpous. The detailed analysis proves this agreement to be restricted to the fruit character, the chromosome numbers being combined with either fruit form at

all ploidy levels. Angiocarpy is certainly not strictly associated with diploidy, and gymnocarpy occurs in diploid populations as well (e.g., in the Alpes Maritimes and the Valais). Publications reporting the presence of angiocarpy in tetra- and hexaploid populations (see STERK & DEN NIJS 1971) consequently do not relate to incidental cases, but most probably indicate the rarity or the absence of diploids in the areas studied, angiocarpy in tetraploid and hexaploid populations being of common occurrence in these regions.

SINGH (1964) reported angiocarpy in hexaploids from the U.S.A. (N. Carolina, Tennessee, Arkansas, Colorado, Montana), the Argentine, and Chile. The present author found this condition in material from the Portuguese coast (Figueira) and from a number of localities in Eire and Gt. Britain.

Gymnocarpous diploids have also been recorded in the literature. ZHUKOVA (1968) reported their occurrence in populations of *R. graminifolius* Lamb. s.l. from N.E. Siberia, and PADZURKOVA (1966) studied gymnocarpous diploids without giving the exact locality of origin. The present author received Siberian material from Drs. Zhukova and Yurtsev (Leningrad), and also counted  $2n = 14$ . A gymnocarpous seed sample from Bohemia (Czechoslovakia), obtained through the intermediary of Professor H. Meusel (Halle), also proved to be diploid. It is quite clear that the idea of an exclusive association between angiocarpy and the diploid chromosome number must be completely abandoned.

In the area discussed in the present publication no correlation was found between the incidence of angiocarpy and either a fine-grained type of soil, or soil fertility, as previously recorded in Belgium (STERK & DEN NIJS 1971), where the gymnocarpous populations occur mostly on the poorer sandy soils, and the angiocarpous ones on loamy soil types. Unpublished studies of German populations (SPRENGER & DEN NIJS, in preparation) revealed that the coupling of gymnocarpy with a poorer soil type, and of angiocarpy with a more fertile substrate is also manifest in W. Germany. Such data may indicate that in N.W. Europe the "marginal" angiocarpous populations exhibit other requirements as far as their habitat is concerned than they do in the central part of the distributional range (i.e., in S.W. Europe), so that in the bordering zone certain ecologically discriminating factors present on loamy soil types have replaced originally not so strictly habitat-bound factors prevailing in the central part of the distributional area. The rather distinct line of separation delimits both angiocarpy and gymnocarpy: to the S. of that line gymnocarpy is almost completely absent, which need not have been the case if there is only a limiting factor preventing the dispersal of angiocarpy in a northward direction. Conceivably, the responsible factor (or factors) may exert an influence on both angiocarpy and gymnocarpy and thus precludes the sympatric occurrence of both types of plants. If angiocarpy and gymnocarpy have a genetical association, such a dual action needs not be present. It is not very probable that the phenotypical plasticity is important in this connection, although it is manifestly present particularly in angiocarpous lines, as demonstrated by culturing experiments.

The question arises whether an obviously convergent evolution of angiocarpy has taken place in all three cytodemes. It is clearly necessary to collect informa-



tion about the phylogenetic sequence of the elements of the complex. Such a sharp geographical dividing line as found in Belgium in any event suggests a strong selective pressure, or a great adaptive significance of (dependent on the geographical region) angiocarpy or gymnocarpy. This is the more cogent since the dividing line holds for all levels of ploidy.

The genetical background of angiocarpy and gymnocarpy is at present under investigation in all three cytological races, more specially the question of possible dominance or recessivity, and of a monofactorial or polygenic control of the character. In either case a sharp separation may take place, provided the selective pressure is high enough (FORD 1971). These genetical studies may throw more light on the ecological relations and on the adaptive significance of the alternative features, and, furthermore, on the nature and intensity of selective pressure leading to the distinct geographical separation of the two phenotypes. In contrast to previous reports (e.g., LÖVE 1944, *Flora Europaea* I, 1964) the diploid cytodeme is decidedly rare in France, whereas the hexaploid form is by far the most common. Diploids are only common in the S.E. of France, and tetraploids are upon the whole also rare and almost restricted to only two areas. These results confirm the results previously obtained by STERK & DEN NIJS (1971) after having studied populations in Belgium: the hexaploids seem to have the broadest ecological amplitude and are of wide-spread occurrence, whereas tetraploids are much more limited in their habitats and in their distribution. This is a general characteristic of polyploid complexes (see, e.g., STEBBINS 1971). Such a restriction is exemplified by the fact that although tetraploids are common in the Pyrenees, they have not been capable of penetrating and colonising the adjoining territories (the coastal zones, the foreland of the mountains) where only hexaploids are present. The areas inhabited by the diploid populations are also distinctly restricted to almost exclusively mountainous regions (S. part of the Massif Central, Montagne Noire, Alpes Maritimes), where they are not strictly limited to certain zones, as is evident from the altitude records: they occur at low (about 200 m) to high (1600–1700 m) elevations. It is possible that such regions represent relict areas where the hexaploids did not, or not yet, penetrate after the Ice Ages, whereas the diploids could not enlarge their distributional area owing to their relatively low colonising ability (EHRENDORFER 1965, STEBBINS 1971). The fact that the areas occupied by the diploids are relatively little disturbed by human interference may be an additional explanation for the absence of the hexaploid race which is clearly better adapted to pioneer (and disturbed) habitats. The occurrence of introduced hexaploid populations in many countries outside Europe (N. America, Australia, New Zealand, Tristan da Cunha) presumably has something to do with a greater colonising capacity of this form by means of vegetative propagation.

LÖVE (1944) has already pointed to the possible correlation between the level of ploidy and the capacity of vegetative propagation in *R. acetosella*, but HARRIS (1970) disagreed because he did not find indications of an increased production of underground runners at the higher ploidy levels. Harris assumed that Löve's faulty conclusion is explicable by the fact that the latter's diploid

plant material came by chance from S. Europe (Portugal); in this region the day length and certain climatic factors might be favourable for flowering in the first year and also the capacity of vegetative multiplication might be less pronounced. The present information clearly shows that diploid populations are limited in their occurrence to certain restricted areas in France (and elsewhere in Europe?). The very reason for this limitation is undoubtedly not a matter of chance but rather the incapacity of this race to colonise larger (and more northerly situated) regions. The question in how far flowering in the first or in the second year, coupled with an increased rate of vegetative propagation by means of root runners, plays a part is being studied by growing the various cytodemes in an experimental garden.

The presence of gymnocarpous diploids in the western Alps is most interesting, gymnocarpy being a more primitive condition than angiocarpy, a character not found in any other representative of the genus *Rumex*. The gymnocarpous diploid cytodeme is presumably the most primitive of the *R. acetosella*-complex. Its presence in the W. Alpine region agrees with the theory that this area provided a refugium during the Ice Ages. A number of polyploid complexes are known whose most primitive representatives (usually diploids) are still restricted in their occurrence to the western Alps (FAVARGER 1964, 1967). Similar distributional patterns are also exhibited by such species as *Galium anisophyllum* (EHRENDORFER 1964).

In order to obtain a better insight into this aspect of the complex under investigation, and in view of incidental reports of diploids from elsewhere in Europe, it appears necessary to include the whole Alpine area and the surrounding territories in our studies. The results will be published in a forthcoming contribution.

As far as can be ascertained, and in broad outline, the distribution of the three cytodemes is typical of a "young" polyploid complex, with S.E. France as the centre of origin from which it migrated. The diploids are only found in mountainous country. Tetraploids apparently originated as several independent population complexes. The occurrence of tetraploids in the Pyrenees is known in a considerable number of taxa: e.g., *Draba subnivalis*, *Anthyllis montana*, *Tanacetum alpinum*, and *Bupleurum ranunculooides* all have tetraploid forms in the Pyrenees and diploid ones in the Alps, and the last species also has a hexaploid race N. of the Alps (FAVARGER & KÜPFER 1968).

As pointed out before, the hexaploids occupy by far the largest area in a whole range of climates and habitats.

Hybrid populations are restricted in their occurrence to a zone where diploids, tetraploids and/or hexaploids grow sympatrically (see *map 2*), namely in the N.E. part of the Massif Central. In the W. part, where hexaploids and diploids are found, no hybrids were observed, not even in mixed populations. An exception is Pop. 350 where  $2n = 35$  was found as we have seen, but in this case it is highly probable that an unreduced pregametic cell (functioning as an egg cell) was fertilised by a haploid pollen grain ( $n = 21$ ). (N.B. The incidence of such unreduced pregametic cells functioning as egg cells has actually been observed

by the present author during the continuation of his investigations).

From these data the preliminary conclusion can be drawn that in the field spontaneous crosses between diploids and tetraploids, and between tetraploids and hexaploids occur, but, as far as the field observations indicate, never viable hybrids between di- and hexaploids.

The aneuploid numbers of chromosomes found in a number of progenies (table 3) may have originated in one or several ways. Seedlings often exhibit abnormalities which disappear again during the subsequent development. Hybrids may "revert" to the original ploidy level of one of the parents by abnormal mitoses (EHRENDORFER 1959). Another cause of aneuploidy may be chromosomal drop as the result of chromosomal instability. Nevertheless it is more probable that repeated back-crossing between different ploidy levels is responsible for the greater deviations (EHRENDORFER 1964). This phenomenon is also known from various other taxa. JONES (1958) found after open pollination of diverse chromosome races of *Holcus mollis* ( $2n = 28, 35, 42$ ) in the progenies an appreciable range of chromosome numbers (a  $2n = 35$  parent plant produced offspring with  $2n = 21-44$ , and a  $2n = 42$  plant  $2n = \pm 28$  and  $2n = 40-49$ ). KÜPFER (1971) also found aneuploidy in *Viola spec.* in the Pyrenees attributable to backcrossing after crossing of different ploidy levels. SINGH (1964) studied hybrids between *Rumex hastatulus* ( $2n = 4x = 16$ ) and *R. acetosella* ( $2n = 42$ ) and found an appreciable diversity of the chromosome numbers in the back-crosses. The investigations are still in progress and it will be attempted, among other things, to reproduce the natural hybridisations in the experimental garden.

The final conclusion to be drawn is that the available data are still too incomplete to explain all observed phenomena. The studies are being continued and extended, both by expanding the area studied to include Central Europe, and by a program of breeding and crossing experiments, with as the ultimate goal a reconstruction of the origin and the subsequent development of the *Rumex acetosella* complex.

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