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Biosystematic studies of the *Rumex acetosella* complex. IX. Cytogeography of the complex in the Iberian Peninsula and taxonomic discussion

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Abstract

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The *Rumex acetosella* complex was studied on the basis of herbarium material and field-collected population samples from the Iberian Peninsula. All plants investigated have non-multifid leaf-lobes and all females produce angiocarpous fruits.

Di-, tetra-, and hexaploids are more or less common, octoploids are decidedly of rare occurrence; diploids seem rather narrowly restricted to inland mountain areas, whereas the tetra- and hexaploids are distributed throughout the region studied; the majority of the populations contain two or three ploidy levels. There are many hybrids and back-cross individuals; this implicates a high frequency of cytological imbalance. Judging from the hybrid frequency one is forced to conclude that there are no serious crossing barriers between the various ploidy levels. The dynamic evolutionary (and cytogeographical) status of the complex is discussed in relation to a phylogenetic survey.

Recent alternative taxonomic treatments of the group by Á. Löve and A. Fernandes are critically discussed. The present authors hold the view that in the region studied only *A. acetosella* L. subsp. *angiocarpus* (Murb.) Murb. emend. den Nijs occurs. A subdivision into varieties is thought to be possible, but is not recommended.

Keywords: *Rumex acetosella* L. ssp. *angiocarpus* (Murb.) Murb. emend. den Nijs, distribution, cytotypes, hybrids, Iberian Peninsula, taxonomy.

Introduction

In the preceding series of studies of the *R. acetosella* complex populations from the greater part of Central and Southeastern Europe were investigated (den Nijs 1974, 1976, 1983, 1984, den Nijs & van der Hulst 1982).

On the basis of several hundreds of population samples, in which morphological and cytotaxonomical analyses were carried out, the senior author drew, *inter alia*, the following conclusions (den Nijs 1983):

Table 1. Cytogeographical data concerning the Iberian Peninsula compiled from records in the literature, with an indication (as far as known) of the number of provenances

Author	Cytogeography and number of provenances							
	2x		4x		6x		8x	
	Distribution	Number of provenances	Distribution	Number of provenances	Distribution	Number of provenances	Distribution	Number of provenances
Löve (1944)	Lisboa, P.	single one	-	-	-	-	-	-
Harris (1968)	-	-	-	Portugal	5	-	-	-
den Nijs (1974)	-	-	Pyrenees	many	N.E. Spain	3	-	-
Löve (1983)	Spain, Portugal: Lowlands	not indicated	North Spain	not indicated	Spain: mountains	not indicated	-	-
den Nijs (1983)	Serra d'Estrela, Portugal	single one	C. Spain	single one	C. Spain W.+C. Portugal	2	-	-
Fernandes (1983)	-	-	-	-	-	4	S. Portugal Spain: Malaga	many 6
Fernandes (1984a)*	Coastal Portugal	few	N. Portugal	many	all over Portugal	many	throughout Portugal	many

* Most of these data are based on measurements of the pollen diameters and apparently not on chromosome counts.

- Combinations of morphological and cytological characters permit the recognition of 11 taxa, the majority of which have rather clear-cut distribution areas. From a taxonomic standpoint most taxa appear to be cryptic because of the fact that the delimiting ploidy levels find their expression only weakly in quantitative morphological differences.
- In a phylogenetic survey the 11 taxa were grouped into two evolutionary lines representing two polyploid series, viz., a south-eastern (Central-North) European series morphologically characterised by the presence of so-called gymnocarpous fruits and by the high degree of multifidness of the basal leaf-lobes (especially in the SE. parts of its distribution area) and a second line (originally S. W. European) with consistently angiocarpous fruits; multifidy is mostly lacking in this series.
- In order to get the evolutionary data fitted in with a practical taxonomic approach, it has been proposed to divide the aggregate species *R. acetosella* L. into 4 subspecies, as follows: (1) ssp. *acetosella*: gymnocarpous fruits, non-multifid (= hastate) leaves; common in C. and N. Europe. (2) ssp. *acetoselloides* (Bal.) den Nijs: gymnocarpous fruits, multifid (palmate) basal leaf-lobes; common in S.E. Europe, Anatolia and elsewhere, e.g., in the Ukraine. (3) ssp. *angiocarpus* (Murb.) Murb emend. den Nijs: angiocarpous fruits, non-multifid leaves; common in S.W. and C. Europe. (4) ssp. *multifidus* (L.) Arc.: angiocarpous fruits, multifid leaf-lobes fairly common in (S.) Italy and S.W. Yugoslavia to Greece.

Each of the subspecies is known to comprise different ploidy levels. In the regions where the distribution areas overlap, the subspecies are synechic and hybridise freely, resulting in hybrid swarms, introgression, and a decline of discontinuities.

The proposed taxonomy is contrary to the proposals of Löve (1983), who recently restated his earlier findings (Löve 1941, 1944). Apart from the taxonomic status of units (*genus* and *species*, respectively against *species* and *subspecies*), the essential difference lies in Löve's conviction that each ploidy level should be given specific rank.

After the draft of the present paper had been completed, a study was published by Fernandes (1984a) on the distribution and taxonomy of the aggregate in Portugal. In the revisional part a divergent taxonomic view is presented. A more elaborated evaluation of these two views is given below in the discussion. For the time being the subspecies, as given above, are maintained.

Until recently only scanty information had been available from the Iberian Peninsula (den Nijs, 1983). From this information, together with the data of Löve (1983) and Harris (1968), only a restricted and mostly speculative picture could be drawn. The plants were morphologically thought to be all angiocarpous with non-multifid leaves. Up till now only the following cytological data are known, see Tab. 1. The data in this table do not always give an indication of the number of specimens counted per sampling site, so that the rate of representation of the samples is uncertain. The samples cited from den Nijs (1983) comprised only 1–3 individuals.

It is impossible to draw a clear picture from these data; and this suggests that a fairly complicated pattern of distribution of the ploidy levels may exist.

Summarising, judging from these published data, one may expect a widespread occurrence of subspecies *angiocarpus*, whereas the distribution of the 3 (4) cytotypes, which may all be involved, had as yet been incompletely studied.

As to the overall distribution of the species *sensu lato* in the area, one has to reckon with both its calcifugous character and its rather temperate (more mesic to atlantic rather than mediterranean) climatic preferences (see, e.g., den Nijs 1983).

Flora Europaea (Rechinger 1964) mentions the widespread occurrence of 3 species (called *R. angiocarpus*, *R. acetosella*, and *R. tenuifolius*). The regional floras only mention *R. acetosella* s.l., but some distinguish infraspecific taxa: Willkomm & Lange (1861) in *Prodromus Florae Hispanicae*: 4 varieties (?), viz. *vulgaris* (Meissn. (distribution: North, East, and Central regions), *australis* WK, with original description (distribution: Southern region of Granada, from sea level up to about 2200 m), *integrifolia* Wallr. (distribution: Pyrenees), and *multifidus* DC. The occurrence of the latter is said to be only expected, especially in the southern provinces. A correlation is suggested with the occurrence of the multifid taxon in other southern European regions, such as Sicily, the vicinity of Naples, and Anatolia. Coutinho (1913) records *angiocarpus* as subspecies: common throughout the country (Portugal) subdivided into 3 varieties: *communis* (common), *australis* (common, like the typical variety), and *subintegrifolius* (rare). Polunin & Smithies (1973) mention the presence of *R. acetosella* s.l. in the alpine vegetation (grassy heaths and dwarf shrubs) of the northern Portuguese Serras up to about 1500 m.

Materials and Methods

Herbarium material (about 200 sheets in all) was kindly sent on loan by the following institutions: *Spain*: Instituto Botánico Cavanilles, Madrid (MA); Universidad Complutense de Madrid: Fac. Farmacia, Madrid (MAF); Departamento de Botánica, Fac. Farmacia, Barcelona (BCI); Herbario del Departamento de Botánica, Fac. de Ciencias, Sevilla (SEV); *Portugal*: Jardim e Museu Agrícola de Ultramar, Lisboa (LISJC).

Population samples (about 30) were collected in the field during the summer of 1982. For practical reasons the distribution of the herbarium sampling localities was used to a certain extent for the planning of the collecting itinerary. Consequently most of the larger calcareous and the low-lying mediterranean regions were not visited. One must bear in mind that the collection of population samples is a selective procedure. The present goal was to collect samples comprising about at least 50 individuals, but as a consequence of the relative scarcity of the species and the often small population sizes, this number of individuals could not often be attained.

A concomitant difficulty was the unequal phenological stage of the plants: due to the mediterranean summer heat and drought, at some sites the vegetative parts of the plants had often already become dry and shrivelled and thus become useless for morphological studies; and of necessity only seed samples were taken in such places. In the southernmost regions all fruits had already been shed, so that from these regions but scanty material became available.

The methods used in the cytological analysis and the assessment of angiocarpy were described earlier in den Nijs (1983). The leaf ratio calculations are based on the length of the lamina, including the lobes, and on the width of the lamina excluding that of the lobes. Leaves are recorded as "narrow" when the leaf ratio (l : w) is 10 or higher. All population samples and the voucher specimens are kept in the herbarium of the Hugo de Vries Laboratory (AMD).

Herbarium studies

About 200 sheets were studied. Most of the localities are shown in Fig. 1; in this figure the sites where population samples were taken are denoted by asterisks. The following conclusions could be drawn:

- all (female) plants studied had angiocarpous fruits
 - all plants studied had hastate leaves, i. e., multifidy is absent
 - there is a great variability in the leaf ratio: both broad and narrow leaves are present.
- No characteristic geographical distribution pattern could be detected.

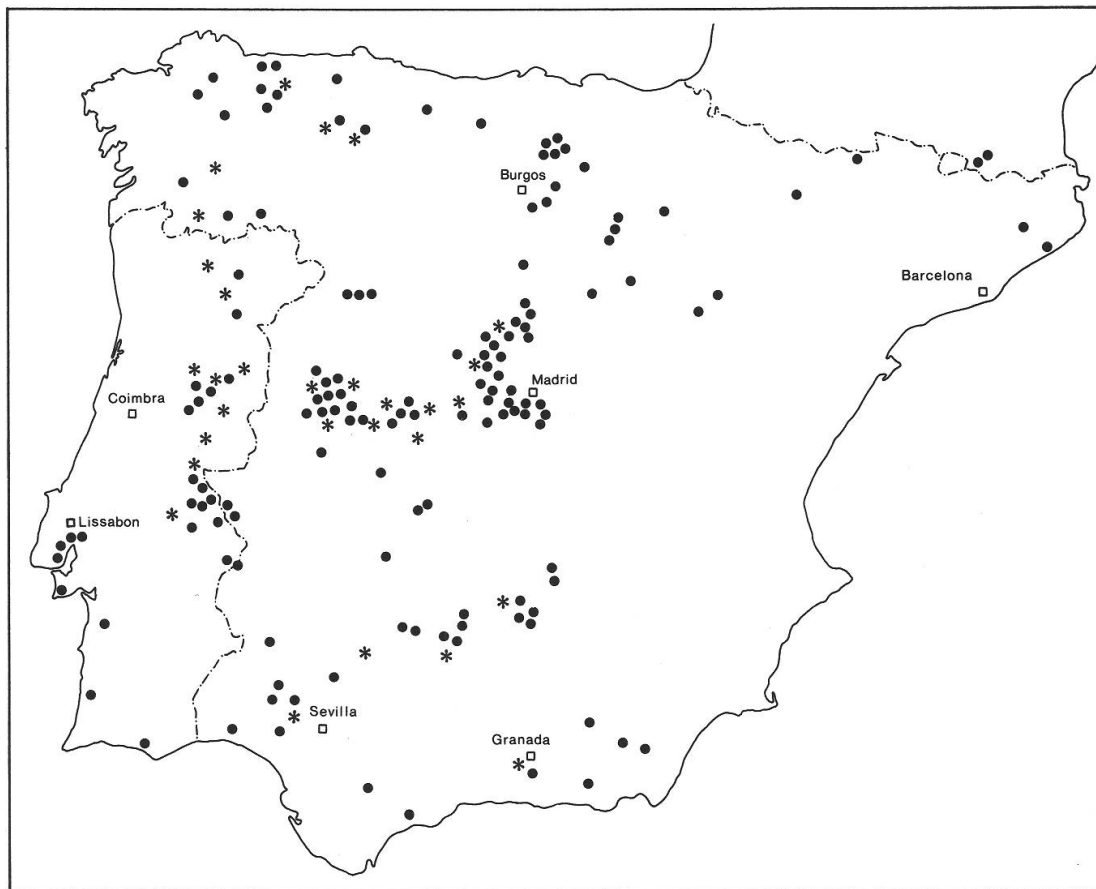


Fig. 1. Survey of the sampling sites of the herbarium specimens studied. All plants are angiocarpous and non-multifid. Asterisks denote the sampling sites of the population samples, as discussed in the next chapter.

The population samples

In Tab. 2 the series of sampling sites of the populations is presented. In addition some ecological information and data concerning the morpho- and cytological analyses are listed. Seedlings could be raised from 27 samples, the remainder appeared to be non-viable. (For the distribution, see the asterisks in Fig. 1.)

Angiocarpy and multifidy

All population samples contained only specimens producing angiocarpous fruits and non-multifid leaves, leading to the conclusion that only specimens of subspecies *angiocarpus* are present in the area.

Chromosome numbers

Variation at the individual and the population level. – The collection appeared to be rather singular in that a great deal of cytological variation at different levels is present. In many seedlings cells with different chromosome numbers were found, thus in-

Sampling locality	m.a.s.l. Material collected		Plants seed only	Leaf form	Ploidy levels recorded								Number seedlings studied				
	Broad/Narrow	X-2x			2x	2-3x	3x	3-4x	4x	4-5x	5x	5-6x		6x	6-7x	7x	7-8x
2. Granada-Pico Veleta, Sierra Nevada (roadside), (Granada, S.)			+	B													-
3. Vila del Río-Cardana, N420 (Córdoba, S.)			+	B	N				*								11
4. Villanueva del Duque-Penaroya (Córdoba, S.)			-	-					*								8
5. Arroyo de la Plata-Valdeflores (Sevilla, S.)			-	-				*									9
8. Castelo Branco-Covilha, roadside (Castelo Branco, P.)			+	B				*									10
9. Penhas da Suade, Sierra d'Estrela (Castello Branco, P.)			+		N			*									2
10. Penhas da Suade-Manteigas, Sra d'Estrela (Guarda, P.)			+		N	*											14
11. Aldeio do Mato-Vale d'Estrela, Sra d'Estrela (Guarda, P.)			-	-				*									12
12. Guarda-Trancoso, N102 (Guarda, P.)			+	B	N			*									11
13. Lamego-Vila Real, N2 (Vila Real, P.)			+	B	N			*									4
14. Vila Real-Chaves (Vila Real, P.)			+	B	N			*									12
15. Verin-Orense (Orense, S.)			+	B	N			*									22
16. Orense-Lugo, N540 (Lugo, S.)			+	B	N			*									15
17. Ribadeo-Navia (Oviedo, S.)			+	B	N			*									15
18. Trubia-San Emiliano (Leon, S.)			+	B	N			*									12
19. San Emiliano, near highway (Leon, S.)			-	-				*									8
20. Lozolueta-Pto de Lozolueta (Madrid, S.)			+	B				*									9
21. Rascarría-Pto de Navacerrada, C604, (Segovia, S.)			-	-				*									13
22. Robledo-St. Martin (Madrid, S.)			+		N			*									8
23. Piedralaves-Arenas de S. Pedro (Sra de Gredos, Avila, S.)			-	-				*									14
24. Pto del Pico (Sra de Gredos, Avila, S.)			+	B	N			*									5
25. Pto del Pico-El Barco (Sra de Gredos, Avila, S.)			-	-				*									11
26. El Barco-Bejar (Sra Candelaria, Salamanca, S.)			-	-				*									12
27. Bejar-Miranda del Castañar (Salamanca, S.)			+	B	N			*									15
28. La Alberca (Sra de Pena de Francia, Salamanca, S.)			+	-				*									7
29. Pena de Cabra-Vecinos (Salamanca, S.)			-	-				*									11
30. Penhas Douradas (Sra d'Estrela, Guarda, P.)			-	-				*									6
31. Lamas, near Viseu (Viseu, P.)			-	B				*									3

Table 2. Enumeration of the population samples and the results of some of the analyses. In addition to the sampling locality also the magisterial district and (in relevant cases) the mountain chain is mentioned. All specimens studied have nonmultifid leaves, all females produce angiocarpous fruits. Leaf narrowness has been calculated as explained in the text. The columns "Ploidy-levels" show the occurrence of the chromosome numbers as found in the number of seedlings studied per population sample.

dicating a karyologically unbalanced situation. Fig. 2 shows the relative frequency distribution based on 791 individual cells from 265 seedlings. Many aneuploid cells were present in the material studied, resulting in a combined relative frequency distribution showing high peaks at the 2x, 4x, and 6x levels and minor ones at the 3x and 5x ones, whereas the great majority of the intermediate numbers were also represented, albeit in lower percentages. In some individuals cells were found with $2n = 56$ chromosomes. In most cases at least also one other cell appeared to have $2n = 28$, which suggests that the octoploid cells are the result of endopolyploidy.

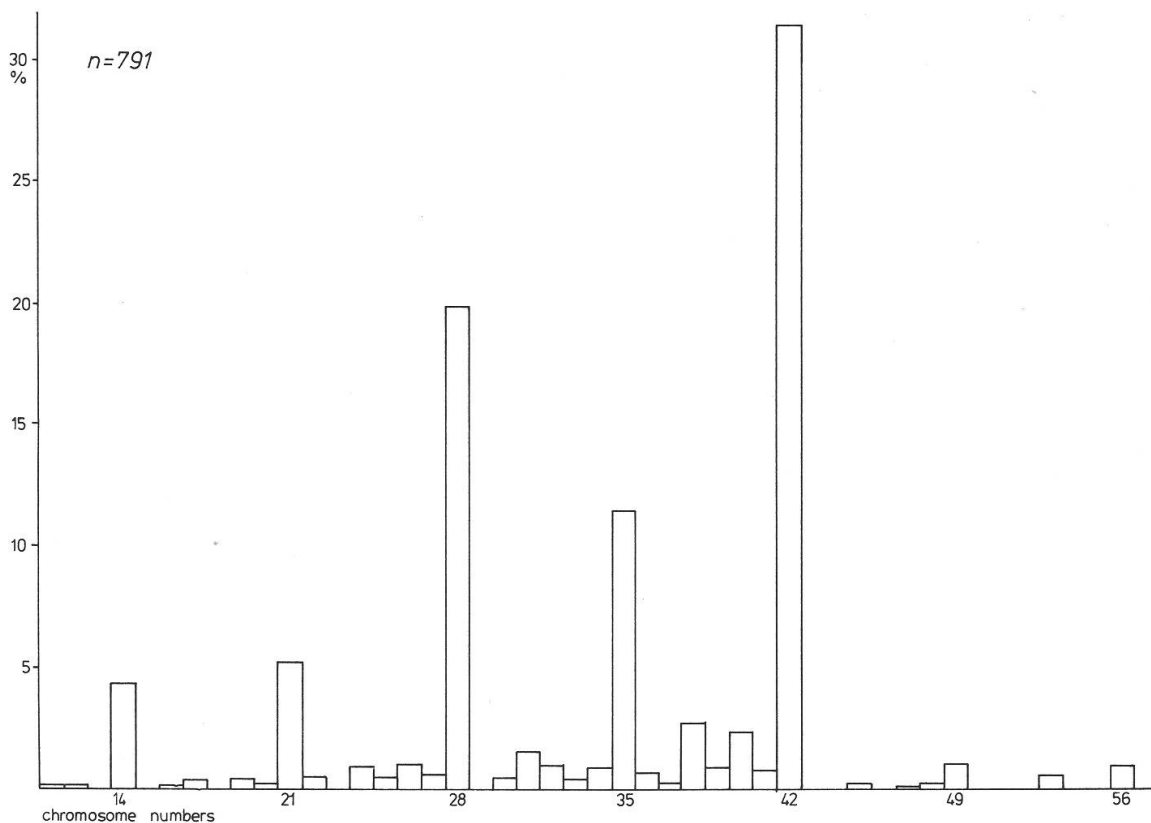


Fig. 2. Relative frequency distribution of the chromosome numbers of 791 individual cells from 279 seedlings.

The intra-individual variation caused some difficulties in assessing the actual chromosome number or the ploidy level of the individual seedlings, respectively, as exemplified by the series of cells in metaphase shown below.

Parent plant number: – seedlings: $2n =$

8 – 3: ($\pm 49, \pm 49$)(42, 42, $\pm 49, 49, 56$)

8 – 4: (31, 32)(36, 42, 47, 53–55)($\pm 28, \pm 28$)(37, ± 42)

12 – 9: (21, 35, 35, 35, 42, 42)(35, ± 35)($\pm 28, 35, 35, 35$)(28, 28)(21, 21)

15 – 3: (21, 21, 24)(28, 28, 28, 28)(30, 31, 35, 35)($\pm 40, \pm 42, 42$)(29)

On each line the cells from the same seedling individual are placed between brackets. There is obviously not only variation *within* a seedling, but also *between* the

seedlings from one offspring family: individual mother plants apparently often produce inhomogeneous offspring: unequal chromosome numbers occur in a series of seedlings.

Obviously, hybridisation processes do not only generate this diversity of chromosome number, but also cause practical problems when it comes to establishing the exact chromosome number of a given cell or seedling. The unbalanced karyological condition disturbs the mitotic processes which often results in the chromosomes' sticking together, in poor contraction, etc. As a consequence in a number of dividing cells in metaphase only the approximate number of chromosomes could be established. In spite of these difficulties it was possible to refer all seedlings to a ploidy level class, as recorded in Fig. 3. These diagnoses of ploidy levels of seedlings are listed in Tab. 2, resulting in an unweighted presence-matrix of the diverse cyto-types per population sample. Fig. 3 shows the relative frequency distribution of the chromosome numbers of the seedlings. Many seedlings had apparently arisen from hybridisation (31% of the grand total of 265 seedlings): triploids (7%) and pentaploids (12%), as well as aneuploids resulting from back-crosses (11% in all).

A single seedling (raised from sample 4) turned out to be an octoploid, other seedlings grown from that population had $2n = 28, 42, \text{ or } 35$.

The seedlings of course represent the F_1 offspring of the standing population in the field and thus only indicate the actual chromosome number of the *mother plants*. This causes hardly any difficulties in non-hybridogenous situations, but in many of the represented populations hybridisation is likely to have occurred. The F_1 generations of single individuals are for that reason to a high degree heterogeneous. The above-listed series of descendants shows examples of this heterogeneity.

Obviously, in some cases it is by no means easy to arrive at a definite conclusion as regards the chromosome number of the mother plant.

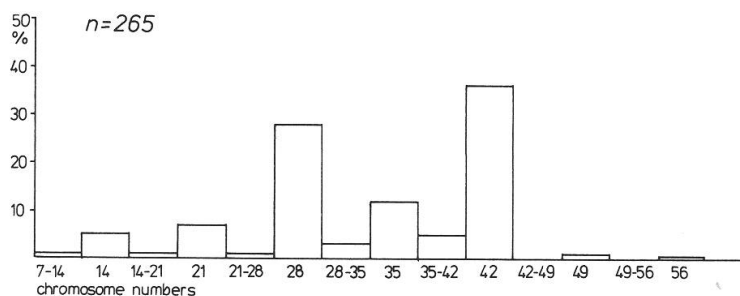


Fig. 3. Relative frequency distribution of the chromosome numbers of 279 seedlings hailing from 27 populations.

Tab. 2 shows the occurrence of the ploidy levels in each of the population samples. The number of seedlings counted per population is too small to yield accurate information about the relative frequencies of the cytotypes.

Nevertheless, it is quite clear that the great majority of the populations is heterogeneous as regards their chromosome numbers. A single population may contain a mixture of diploids, tetraploids, and hexaploids, as well as several hybridogenous intermediates.

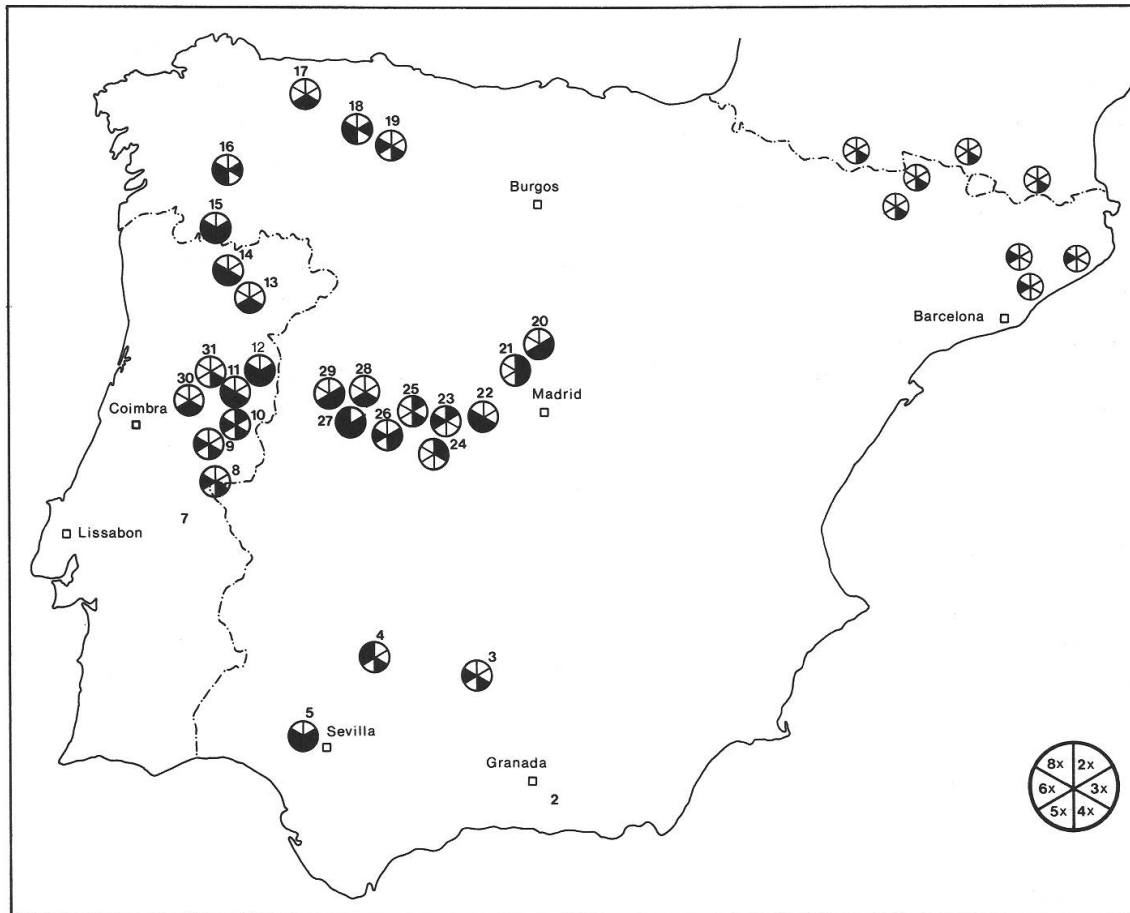


Fig. 4. Distribution of the population samples and the occurrence of ploidy levels. Dysploid numbers (see text and Tab. 2) are omitted. Data from N. E. Spain are borrowed from den Nijs (1974).

Cytogeography

Fig. 4 shows the distribution of the sampling localities and the ploidy levels found in the population samples (taken there). It appeared that the cytotypes do not exhibit distinctive distribution patterns.

The following comments can be made:

- Diploids: rather rare, only found in the inland mountainous regions of the Serra del Estrela (P) and in the Guadarrama and Gredos Ranges (SP). The Sierra Nevada sample was not viable; the Pyrenean populations had turned out to be tetraploid in an earlier study (den Nijs 1974).
- Triploids, in some samples in association with diploids: at some other sites the occurrence of triploids in the absence of diploids suggests that at least in the immediate vicinity of the sampled stand also diploids may have occurred. Compare, for example, the isolated localisation of sample 5 in the Sevilla area. Clearly one always has to reckon with the possible development of unreduced gametes in some diploids, also resulting in the incidence of triploids. The less probable, but not altogether to be precluded, incidence of *twice* reduced (i. e., haploid) gametes in tetraploid plants may conceivably also lead to the origin of triploids in a wholly tetraploid population.

- Tetraploids are widespread throughout the Peninsula but nowhere very common, except in the Eastern Pyrenees where they occur exclusively and abundantly (see den Nijs 1974).
- Pentaploids are apparently often produced in a great number of mixed populations.
- Hexaploids are widespread and of common occurrence throughout the Peninsula, except in the Pyrenees.
- Heptaploids were found in sample 8 from the Castela Branca district, P (2 seedlings). In this population also a 6x–7x intermediate was encountered. These heptaploids may be indicative of the occurrence of octoploids in the vicinity.
- Octoploids: some intra-individual octoploid cells were found, and in three cells of an individual seedling studied only $2n = 56$ was recorded. As shown in Tab. 2, population no. 4 (from the Córdoba district, Sp.) contains also 4x and 6x (and 5x) specimens. More detailed information about the presence and distribution of octoploids could not be obtained.

Leaf shape variation

When still alive at the time of collecting the basal stem- or central rosette leaves were harvested and measured so as to assess the leaf lamina ratios. Tab. 2 shows the data: B(road) represents leaves with ratios < 10 , N(arrow) represents ratios > 10 .

In discussions on the foliar characteristics of *R. acetosella* ratios higher than 10 are said to be of the *tenuifolius* type, so the table quite clearly shows that (1) *tenuifolius* and non-*tenuifolius* plant types are widespread in the region studied and that (2) both plant types often occur together in the same population.

Discussion

Present data

Although the set of cytological data from about 40 populations (including those previously studied: den Nijs 1974) is still rather limited in number, it is fairly safe to conclude that, as in other parts of southern Europe (den Nijs 1983), also in the Iberian Peninsula the three different ploidy levels are represented. The relative frequencies are as yet not known in greater detail, but it seems as if diploids were in the minority and more or less restricted to certain refugial, mountainous areas such as parts of the inland Sierras. This distribution pattern differs from that of the closely related diploid angiocarpous taxon which is very common and widespread in S.E. France (den Nijs 1974, 1983).

The newly found distribution patterns are partly at variance with those recently published by Löve (1983) and Fernandes (1984a). The first author describes the occurrence of diploids as “spread throughout the lowland areas of Spain and Portugal”. The second records, for Portugal only, “coastal regions” as the distributional optimum for one of the species he distinguishes in his study, viz. *R. angiocarpus* (and also for the supposedly rare species *R. multifidus*, known to him from a single locality in Portugal). Fernandes (1984a) also recognises the taxon *R. tenuifolius* at the specific level – we shall return to that point later – and mentions the occurrence of 4 different ploidy levels, viz., $2n = 2x, 4x, 6x,$ and $8x$.

The diploid specimens cited are from the Serra da Marofa, Guarda district; this is a part of the Serra Estrela. These sampling sites coincide with some of our present records of the occurrence of diploids in Portugal.

Tetraploids are found throughout the Peninsula, including the southern part. It seems as if this cytotype is very widespread over a vast range of habitats. A comparison with the overall distribution of the tetraploids in Europe shows that the Iberian situation is rather similar to the Balcan situation, where the tetraploids also show a very broad ecological amplitude, whereas in the northern regions there is a greater ecological restriction to certain habitats (den Nijs 1983).

Hexaploids, in contrast, are far more common and widespread in the Iberian Peninsula than in the Balkan region. However, pure hexaploid populations only seem to occur in the n.e. parts of Spain. It can, therefore, be posed that hexaploid populations arose only recently and that a cytologically stable situation has still not been attained. In this connection two arguments emerge from the data, viz.,

- the relative rareness of pure populations, and
- the common occurrence of hybrid specimens, recognizable, among other things, from the cytological instability within single individuals.

The recorded data show quite clearly that the diverse ploidy levels hybridise rather freely *inter se*, especially the 4x and 6x cytotypes. The large numbers of $2n = \pm 35$ specimens as well as the frequent incidence of products of back-crossings ($2n = 28-35$ and $35-42$) are indicative of this process (see Fig. 3). An attempt to evaluate this situation leads to the conclusion that one has to reckon with unequal colonizing and competitive capacities of the different cytotypes. The hexaploid may be expected to be able to oust the tetraploid form. It follows that the present introgressive hybridisation may ultimately lead to a dominance of hexaploids to the detriment of, in particular, the 4x cytotype (compare den Nijs 1983).

As regards the answer to the question why the karyo-typical distribution is still so unbalanced one only can speculate:

- Hexaploids must, relatively speaking, only rather recently have reached the Peninsula and spread there. If this would be the case, the (angiocarpous) 6x type must have hailed from, e.g., S.E. France. The centre of origin and distribution of the angiocarpous S.W. European polyploid complex *sensu* den Nijs (1983) must lie in the s.e. parts of France. Being given as basic data the very intensive and already long-lasting anthropogenic influences in the region as a whole, the present authors hesitate to accept such a recent introduction of hexaploids into Spain and Portugal.
- The ecological and colonizing capacities differ to a lesser extent than they do elsewhere (to the North of the Pyrenees). As in the Balkan region, also in the Iberian Peninsula 6x cytotypes with a relatively minor capacity of vegetative reproduction (and the correlated, restricting ecological amplitudes?) may have developed. In this train of thought also the plausible xerothermic adaptation of the Balkan 4x cytotype may again be brought to mind. As in the Balkans, the ecological circumstances prevailing in Iberia may especially favour the 4x cytotype, thus bringing about a strong competitive power against the hexploids.

As regards the single octoploid seedling from sample 4, the following points are to be considered: this 8x specimen originated from a collective seed sample from which also individuals with $2n = 28$, $2n = 42$ and $2n = 35$ somatic chromosome numbers have been raised. It is difficult to decide whether octoploids do occur as adults in this population, because conceivably the incidental occurrence of an unreduced ($2n = 42$) gamete that fused with a diploid ($n = 14$) (from a tetraploid) would also produce an occasional octoploid. Still, the variability and fertility of such a *de novo* formed octoploid remains

to be proven. Furthermore, some $2n = 56$ cells were recorded in a series of 6 more seedlings, but there were always tetraploid (or hexaploid) cells in the same root-tip as well, a clear indication of endopolyploidy.

It is, however, of considerable interest to refer to the studies of Fernandes (1983, 1984a) on this topic. This author reports a fairly common occurrence of octoploids distributed almost throughout Portugal, including some of the regions studied by us. According to Fernandes there are two octoploid plant types: – specimens belonging to “*R. tenuifolius*”: dwarf individuals with very narrow leaf blades, and representatives of the species “*R. australis*”, the tallest morph of the complex with glaucous, broad leaves. The status of these taxa will be discussed in the next chapter.

On the basis of the phylogenetic survey by den Nijs (1983) as a reference, the present cytogeographical and morphological data can be seen as a fair confirmation of the main line of development as hypothesized earlier:

- Not three, but up to four cytotypes are present: the $2x$ type in refugial areas, the $4x$, $6x$ and, accordingly to Fernandes (1983, 1984a) also the $8x$ types in a broad range of habitats. These types appeared to be sympatric and in many sites also synevic, they hybridise and obviously have unequal competing capacities.
- Only specimens producing angiocarpous fruits occur, although according to Fernandes (1984a) a minority of the plants produce some fruits with less firmly adnate perigone lobes.
- Only non-multifid leaf shapes are met with, with the exception of a single specimen – multifid and angiocarpous – from the northern part of Portugal (in Fernandes 1984a).

It is to be regretted that Fernandes (1984a) presents ploidy diagnoses that in most cases are based on supposedly different pollen diameters and not substantiated by chromosome counts. He claims to be able to distinguish, on the basis of clear-cut pollen size discontinuities, between the different ($2x$ – $4x$ – $6x$ – $8x$) ploidy levels. Data are presented on the euploid levels only, no intermediate numbers being mentioned. Our present study clearly shows the incidence of numerous hybridogenous individuals, and it would have been of considerable interest to study the pollen production of such hybrids in relation to the claim of the reported clear-cut pollen size differences of supposedly euploid cytotypes. In an earlier study the senior author was forced to conclude that the mean pollen diameters of different ploidy levels overlap to an appreciable extent (den Nijs et al. 1980), and Löve (1983) also concluded that the polyploidy levels are insufficiently correlated with pollen diameters. In other studies Fernandes (1984b) and Fernandes and Leitão (1984) intensively studied the pollen dimensions of a large series of specimens in order to clarify the origin of the polyploid forms and to understand possible blocs in the meiotic processes. From a number of the frequency distribution curves presented it is quite clear that some cytological disturbances are present: unreduced PMC's, as Fernandes stated; presumably attributable to the hybridogenous nature of the plant specimens, the present authors would like to comment. Some of the figures show normal distribution curves, resulting in an incongruent or inconsistent mean diameter, but instead of splitting the collected pollen sample into two categories (reduced *versus* unreduced) as Fernandes does, the present authors think it much more likely that the plants concerned were of hybridogenous origin and, therefore, producing pollen with an intermediate mean diameter and an (approximately) normal frequency distribution.

The occurrence of so many populations of mixed ploidy levels renders it very difficult to arrive at generalizations as stated by Fernandes (1984 a, b) and Fernandes and Leitão (1984). Studies of artificially produced hybrids (pentaploids) revealed the fairly normal production of pollen grains possessing 17/18 chromosomes (Aris 1978). In the opinion of the present authors this point still deserves a more thorough enquiry in order to obtain more cogent information both from biometrical as well as from cytological studies.

Taxonomic evaluation

With reference to the revision of the *acetosella* complex by the senior author (den Nijs 1984), the present data permit the conclusion that subspecies *angiocarpus* (Murb.) Murb. emend. den Nijs is indeed widely distributed throughout the Iberian Peninsula. The supposition that this subspecies is the only one occurring in this region is only defeated by one herbarium record by Fernandes (1984 a): a multifold and angiocarpous specimen from Vila Real in the northern part of Portugal. This may well be an incidental (anthropochorous) occurrence of subspecies *multifidus* (L.) Arc.. More recently, however, both Fernandes (1984 a) and Löve (1983) presented different views regarding the systematics of the (Portuguese) *acetosella*'s, to be discussed here in greater detail.

The revision of the Portuguese acetosellas by Fernandes (1984 a)

According to Fernandes, who recognises 4 species, all with angiocarpous fruits, the following characteristics are essential for the systematic classification:

- R. tenuifolius* (Wallr.) Löve: narrow leaves, (0.5)1–3(5) mm broad, with inrolled margins; pollen diameter variable; chromosome number: $2n = 14, 28, 42, \text{ or } 56$.
- R. angiocarpus* Murb.: broad and flat leaves; pollen diameter 20, 247–21, 354 μ ; chromosome number: $2n = 14$.
- R. acetosella* L.: broad and flat leaves; pollen diameter 23, 269–27, 284 μ ; chromosome number: $2n = 42$.
- R. australis* (Willk.) Fernandes: broad and flat leaves; plant glaucous; pollen diameter 27, 960–31, 194 μ ; chromosome number: $2n = 56$.

Apart from the above-mentioned characters there are several others that, according to the descriptions and the key, more or less overlap, among others, the mode of branching of the flowering stem, the height of the plants, and the dimensions of the perigone lobes of the male flowers.

According to Fernandes there are two separate polyploid series in Portugal: one series of $2x-8x$, all representatives having narrow leaves (*R. tenuifolius*), and a second with the numbers $2n = 14, 42, \text{ and } 56$ in which each ploidy level coincides with the species boundaries as given above.

There are some points of criticism:

- Fernandes himself already mentions the sympatric and even synecic occurrence of and possible interbreeding between the species he recognises. The rate of introgression into the populations found in the present study reveals that most populations studied were cytologically quite inhomogeneous and that apparently gene flow is of frequent occurrence.
- Judging from Tab. 2, the character of narrow leaf blades, i. e., the *tenuifolius* type of habitat form, frequently occurs together with broad-leaved specimens in one and the same population. In an earlier study the phenotypical plasticity of the lamina in *R.*

acetosella s.l. was mentioned (den Nijs & Sangster 1980), which results in forms with narrow leaves in dry, warm habitats. These may constitute a (genetically defined) ecotype with narrow leaf blades, but both phenotypical and genotypical phenomena are operative in the populations (see also den Nijs 1983).

Based on these data one can imagine that the proposed species "*tenuifolius*" is nothing but an assembly of the xerothermic morph of each of the other ploidy levels, instead of representing a separate evolutionary line of polyploidy. As a consequence, one is then forced to conclude that only one (angiocarpous) polyploid series is present.

- When raising the variety *tenuifolius* of Wallroth to specific level, Löve clearly indicated that this "species" is gymnocarpous.

Although Wallroth (1822) was not aware of the significance of this character, the present authors regard the amplification by Fernandes of the description of Löve (1941), who depicted the species as exclusively gymnocarpous, as undesirable.

More recently Löve (1983) also re-appraised the taxonomy of the *acetosella* aggregate. He proposed a change: *R. tenuifolius* would now have to be called *R. multifidus*. However, the latter species is angiocarpous, according to the typification by den Nijs (1984) with the iconotype, as given by Boccone as early as 1697.

- As regards the pollen diameters the reader is referred to the discussion in the preceding chapter.

The clear-cut gross-geographical distribution of angiocarpy and gymnocarpy and the rates of multifidy strongly suggest a diagnostic value just at the subspecies level. The present authors wish to retain and restate the division of the (European part of the) complex into 4 subspecies:

R. acetosella L. ssp. *acetosella*

R. acetosella ssp. *angiocarpus* (Murb.) Murb. emend. den Nijs

R. acetosella ssp. *acetoselloides* (Bal.) den Nijs

R. acetosella ssp. *multifidus* (L.) Arc.

Owing to the great variability and ecotypical differentiation it is to be expected that within each of these subspecies more or less discontinuous taxa can be distinguished. These taxa ought to have no more than a *varietas* or *forma* status. In this train of thought, but beyond the scope of this study, one might conceivably distinguish within the all-Iberian material of subspecies *angiocarpus* several varieties; for example a var. *australis* Willk. and a variety "*tenuifolius*". For reasons of synonymy and typification the valid name of this variety is to be carefully studied, because this morph is also represented in subspecies *acetosella*. One may assume that Wallroth (1822) based his original description of *tenuifolius* on gymnocarpous material, although at that time this character was not yet considered to be important.

It is to be expected that some of the varieties coincide with earlier designated, basic evolutionary taxa, or that they even may have to be newly described, to be added to the eleven recognised in den Nijs (1983) in his phylogenetic survey of the complex.

A comment on Löve's (1983) taxonomic treatment

When the previous studies in the present series were in press, an important article on the taxonomy of *Acetosella* by Löve (1983) appeared in which he gave a number of divergent viewpoints as regards the evolution and taxonomy of the complex. It is beyond the scope of the present study to discuss all these points exhaustively, but some selected topics may be dealt with here:

- Like Fernandes (1984a), Löve queries the value of angiocarpy and of the rate of multifidy. Nevertheless he accepts a genetical background for both of them. In the present authors' opinion most difficulties arise from the phenotypical plasticity, which under certain conditions may result in less firmly adnate perigone lobes in angiocarpous fruits. It never happens that a gymnocarpous plant changes into one producing angiocarpous fruits. Phenotypic responses are also responsible for the decrease of multifidy in colder and wetter habitats. The genetical basis of both angiocarpy and multifidy constitutes a good argument in the explanation of some aspects of the distribution patterns. Especially in the regions where the distribution areas of the characters adjoin or overlap one has to reckon with the effects of hybridogenous introgression. This has been exemplified earlier, for e.g., the area of Czechoslovakia and some of the Balkan countries. It is admittedly rather awkward that precisely in the floristically so well studied Central European region such introgressions are of very common occurrence and result in a certain blurring of the character correlations. These effects do not seriously affect the overall geographical distribution patterns, nor do they change the fact that the morphological differentiation is superimposed on all three ploidy levels.
- There is still a controversy regarding the incidence of hybridisation between the ploidy levels in the field. In contrast to the study of Löve, the present study shows that especially in certain regions introgressive hybridisation occurs most frequently. There must be an appreciable gene flow between the ploidy levels, especially between the 4x and 6x ones.
- The use of quantitative characters, such as pollen diameters, is considered doubtful by the present authors, because of considerable overlap. Statistically significant differences seem to be clear-cut, but they are to be based on a series of measurements from an adequate range of plants. It is therefore questionable whether quantitative characters of pollen (or perigone lobes, etc.) of a single individual could be properly determined in a reasonable majority of the cases (which ought to be high at the species level) to assess the actual ploidy level.
- This latter point is of special interest because Löve considers each ploidy level as absolutely species-delimiting. After ample discussions in the literature concerning this moot point it now seems to be accepted, at least as regards series of plants with racial polyploidy, that within a species several cytotypes (i.e., different chromosome numbers) may occur (compare, for example, Lewis 1980, and Tyrl 1975). It is partly a matter of personal appraisal to what extent more or less cryptic characters by themselves should define species boundaries within the ambit of a flora. This does not diminish the value of data pointing to the presence of evolutionary units within any taxon.

There still remains, in some cases, a controversy between our detailed knowledge about the evolutionary units within a taxon and the division of that taxon into subunits (species, subspecies, or whatever infra-specific taxon one distinguishes) sufficiently practicable from a taxonomic point of view. It is undesirable to apply a rigid interpretation of the so-called biological species concept to taxa which show such fine-meshed and partly unstabilized evolutionary patterns.
- It is regrettable that Löve (1983) does not give any useful cytogeographical data. The distribution pattern of the cytotypes is given only on a rough scale, without substantial indications of regional differentiations and/or correlations of the ploidy levels. A comparison with the fine-meshed geographical differentiation as met with in earlier studies thus becomes difficult.

In conclusion: the present authors assign great value to the geographical distribution pattern of the morphological characters, as discussed above and earlier in this series, in their direct relationship to the polyploidy development of the complex. We still are of the opinion that Löve's interpretation of the data does not give a plausible alternative for the postulated development of two evolutionary lines into two ploidy complexes: a (primary) S.E. European and W. Asiatic one and a (secondary) S.W. European one (see den Nijs 1983).

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