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SEXUAL REPRODUCTION AND HYBRIDIZATION IN SEDUM TELEPHIUM (CRASSULAEA)

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SUMMARY

In central Europe the diploid, triploid and tetraploid cytotypes of the morphologically extremely variable *S. telephium* L. (X = 12) are sympatric. The triploid plants are semisterile and most probably of hybrid origin. In mixed populations the triploid plants may give rise to an offspring consisting of aneuploid as well as diploid and/or tetraploid plants. Because the diploid and tetraploid cytotype each show almost the complete spectrum of morphological variation present within the *S. telephium* complex it is concluded that all taxa within this complex should be regarded as different expressions of a single though variable species.

1. INTRODUCTION

Sedum telephium L. is found in the temperate zone of the Old World, in an area ranging from Western Europe (Great Britain) to Japan (OHBA 1977). It is widely naturalized in the eastern part of North America where it has spread mostly by means of vegetative reproduction (CLAUSEN 1975). In Europe it is quite common and widely distributed in mesic habitats which, however, are often much influenced by human activities. Especially in the western part of its area *S. telephium* is extremely variable in habit, size, shape and arrangement of the leaves, size of the inflorescences and colour of the petals. Although some forms of *S. telephium* are very conspicuous, the infraspecific variation presents an almost continuous series (compare JALAS 1954 and GRULICH 1984) and consequently most attempts to delimit these forms properly are frustrated by the wide ranges of overlap in the discriminating characters. So far taxonomists have been concerned almost exclusively with the description and classification of the immense wealth of variation within *S. telephium,* and from the time of Linnaeus onwards large numbers of infraspecific taxa and several closely related species have been described. On the other hand, apart from some chromosome number reports and a few casual remarks about vegetative propagation and pollen sterility, very little is known yet about the origin of the variation in *S. telephium* s.l. and the way this variation is maintained.

For *S. telephium* s.l. the chromosome numbers 2n = 24, 36 and 48 have been reported (for references see OHBA 1977). In addition to this euploid series GRULICH (1984) reported two plants with the aneuploid chromosome number 2n = 30 from Moravia (Czechoslovakia). The plants with the chromosome number

2n = 36 are generally considered to be triploid (UHL & MORAN 1972, CLAUSEN 1975, GRULICH 1984) and consequently the basic chromosome number of *S. telephium* should be X = 12. CLAUSEN (1975) and GRULICH (1984) observed that plants with the chromosome number 2n = 36 have highly defective pollen. This observation supports the general assumption that these plants are triploid. According to Clausen the triploid plants produce no seeds although they flower profusely. However, the triploid plants studied by Grulich did produce viable seeds.

RESULTS AND DISCUSSION

PRAEGER (1921) reported that most forms of *S. telephium* s.l. hybridize freely when grown together. The resulting hybrid swarms "show every combination of the characters of the two species (i.e. *S. maximum* and *S. telephium*) as regards colour of flower, size, shape and arrangement of leaf..." (l.c.). Experimentally the different forms of *S. telephium* can be very easily hybridized and also the cytotypes with the chromosome numbers 2n = 24 and 2n = 48 can easily be crossed. The hybrids resulting from the latter cross had the chromosome number 2n = 36. The plants were vigorous and flowered abundantly. They had semi-sterile pollen (less than 50% fertile) like the plants with the chromosome number 2n = 36 from nature and did not produce seeds in the crossing experiments.

In the experimental garden in Utrecht all three cytotypes of *S. telephium* s.l. were grown together in a random arrangement and some of the plants with the chromosome number 2n = 36 produced seeds. The offspring of five Dutch plants with the chromosome number 2n = 36 proved to be almost completely aneuploid, the chromosome numbers ranging from 2n = 27 to 2n = 48 (*table 1*). This indicates that meiosis in the 2n = 36 cytotype is highly irregular and that this cytotype is indeed triploid.

However, the frequencies of the chromosome numbers observed in 30 plants of the progeny of these five triploid plants differed largely from the expected frequencies (*table 1*). The expected frequencies are based on the assumptions that in this experiment pollination and fertilization of the flowers with pollen of one of the three cytotypes was determined by chance alone, that in the triploid plants during meiosis the univalents were randomly distributed and that there had been no selection against aneuploid gametes, zygotes or embryos and seedlings. In the class of plants with the chromosome numbers 2n = 34 to 2n = 38, 95% of which are expected to have only triploid parents, some 8 plants were expected. However, only 2 plants were observed in this class, indicating that, though the dense, many-flowered inflorescences of *S. telephium* favour geitonogamy, selfing is almost negligible in the triploid plants, probably because of the reduced fertility of the pollen. In the class of plants with the chromosome numbers 2n = 39 to 2n = 48, 86.5% of which are expected to have a tetraploid male parent, some 10 plants were expected. Instead, 24 plants were observed in this class, which indicates that the pollen of the tetraploid plants has been more abundant and/or successful. The frequencies of the chromosome numbers

Table 1. Observed and expected frequencies of the chromosome numbers in the progeny of 5 triploid plants of *Sedum telephium* of Dutch origin. (N – number of plants)

2n =	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	N
I																	1		1	1					2	5
II												1											1		1	3
III								2			1						1	1		2	1					8
IV				1																	2	2	1			6
V								1								1	1		2		1	1	1			8
Observed				1				3			1	1				1	3	1	3	3	4	3	3		3	30
Expected	0	0	0	1	1	2	2	2	2	1	1	2	2	2	1	1	2	2	2	2	1	1	0	0	0	30
Expected													0	0	0	1	3	5	6	5	3	1	0	0	0	24

of the 24 plants which most probably all had a tetraploid male parent by and large agree with the expected frequencies, wich indicates that, during meiosis, at least in the ovules of the triploid plants the univalents are randomly distributed. The unexpected presence in the offspring of 3 plants with the chromosome number 2n = 48 and the over-representation of plants with the chromosome numbers 2n = 44, 45 and 46 may indicate that there is some form of selection against aneuploids.

Although in this experiment only a small number of plants have been studied some conclusions can be drawn about the reproduction of *S. telephium* in nature. In central Europe the diploid and tetraploid cytotype of *S. telephium* are sympatric and most probably hybridize on a large scale. The triploid hybrids are widely distributed, occurring in Czechoslovakia, Germany, northern France, Belgium and The Netherlands (GRULICH 1984, 'T HART unpubl.). Since *S. telephium* quite easily propagates vegetatively the triploid hybrids may live for a long time and also spread. For example, in The Netherlands only the triploid cytotype of *S. telephium* occurs, but there are a few tetraploid populations in the "fluviatile district" ('T HART unpubl.). In pure stands the triploid plants most probably do not reproduce generatively (see also CLAUSEN 1975). On the other hand in mixed populations the triploid plants may give rise to an offspring consisting of aneuploid and euploid plants (diploids and/or tetraploids). In this way the triploid plants may occasionally serve to bridge the gap between the diploid and tetraploid cytotypes of *S. telephium*, which are otherwise reproductively isolated.

Morphologically the diploid and tetraploid cytotypes of *S. telephium* s.l. cannot be separated because each cytotype comprises almost the complete spectrum of morphological variation present within the species. Moreover, since the diploid and tetraploid cytotype of *S. telephium* hybridize on a large scale and because reproductive isolation is not complete, it must be concluded that all taxa that have been distinguished within the *S. telephium* complex merely represent different expressions of a single though variable species. Concerning the classifi-

cation of the morphological variation within *S. telephium*: whenever it is necessary to name one of the numerous forms or local races of *S. telephium* the rank of "variety" seems to be the most appropriate.

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