Evaluation of the breeding behaviour of the triploid hybrids

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the functioning of polarized R and RA gametes in the 24chromosomic hybrids, individuals from the wild as well as those experimentally reconstructed behaving alike. Furthermore, the experiments indicate that diploid backcross plants may replace a genuine *C. rivularis* in crosses with the triploids.

4. Evaluation of the breeding behaviour of the triploid hybrids

The results obtained in the course of the present study strongly suggest a non-Mendelian segregation occurring in the 24chromosomic plants from Urnerboden. It is conceivable that two complementary phases i.e. a selective sporogenesis and a zygotic selection are involved, the former mechanism eliminating all aneuploid spores or most of them, whereas the latter one may favourize only some of euploid zygotes.

No positive proof was obtained as to the functioning of truly reduced, 12chromosomic gametes in the triploid hybrids; the 24chromosomic plants obtained in our experimental crosses might as well have arisen from an union of polarized gametes with the respective chromosome numbers 8 and 16. On the other hand, as much as 21 plants out of the total 25, might only have been formed with a part of one or both polarized gametes (Table 13).

Table 13. Plants obtained in various experimental crosses with triploid(s) used as one or both parents; the latter cases marked by a double asterisk (**).

Chromosome number	Genomic structure	Possible way of origin*	Number of plants
2n=16	RR	R + R	15
2n=24	RRA	RA + R	5
2n=24**	RRA	RA + R or R1/2A + R1/2A	5
2n=32**	RRRA	RRA + R	1
2n=32	RRRA	RRA + R	2
2n=40	RRRRA	RRA + RR	2

*putative gametes of triploids listed first.

It should be kept in mind that the sexual reproduction in the triploid hybrids is apparently limited; just these limitations, however, stress the importance of an anomalous breeding behaviour as a factor of stabilizing the hybridity, structural and numerical one alike.

Formation of gametes containing whole genomes and subsequently functioning in a complementary way might fortuitously appear in any sexual hybrid; by contrast, only a few well-documented cases are known where this mechanism represents a principal factor influencing patterns of variation and evolution. For the purpose of comparison, three classic examples are characterized below.

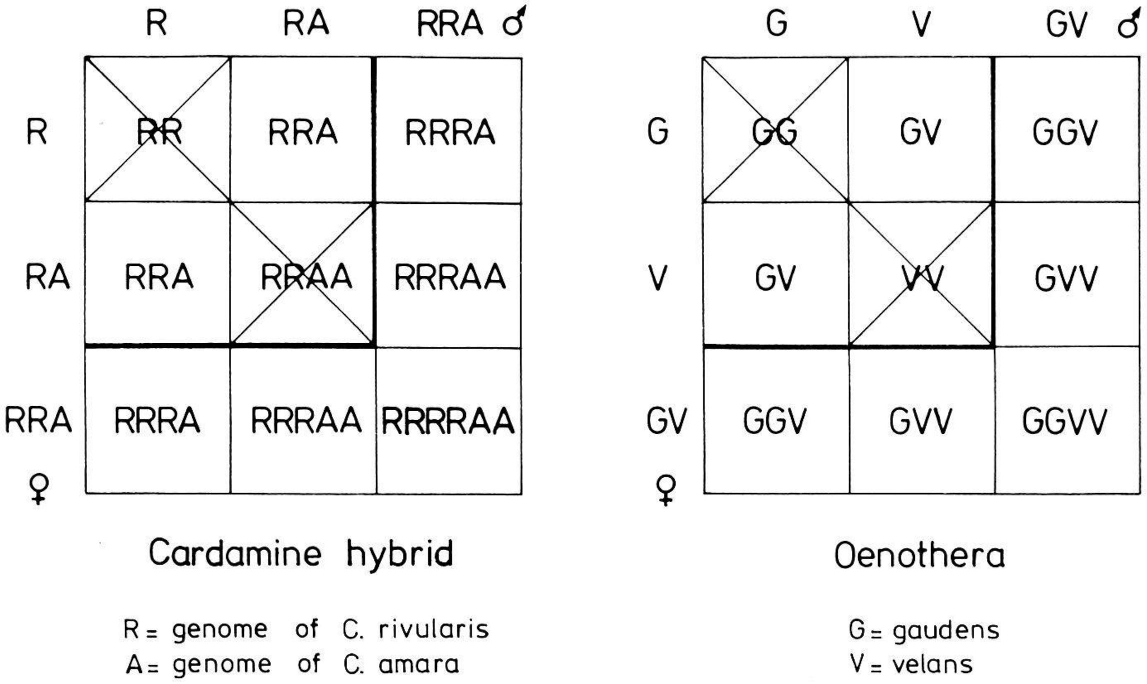
The anomalous breeding behaviour of the *Oenothera biennis* group (2n=14) and, in particular, that of *O. Lamarckiana* was extensively investigated (DE VRIES 1917, RENNER 1917, 1925 etc.; for detailed references see CLELAND 1972). These diploid taxa are permanent heterozygotes for successive translocations on all or nearly all chromosomes of the complement. The formation of chromosome rings followed by a polarized segregation results in two differentiated genomes ("the RENNER complexes") being reassembled intact at the end of meiosis; all spores produced by a given *Oenothera* taxon have accordingly the same reduced chromosome number n=7, but in fact represent two genetically distinct classes, both on the male and the female side. However, the plants breed true for their specific heterozygous structure, all other combinations being eliminated in selfings or sib crosses by a system of balanced lethals that operates either in gametes (e.g. *O. muricata*, DARLINGTON 1937) or zygotes (e.g. *O. Lamarckiana*). On the other hand, crosses between various true breeding lines often produce segregating progeny in the F_1; one, two or four classes of progeny may appear depending whether one or both parents produce one or two kinds of functional sperms and eggs (CLEVELAND 1962). A comparable behaviour was recorded in some *Oenothera* species of temperate South America (HAGEN 1950, HECHT 1950), in *Gayophytum heterozygum* (LEWIS et al. 1958, LEWIS and SZWEYKOWSKI 1964), *Gaura biennis* and *G. triangulata* (RAVEN and GREGORY 1972), *Rhoeo discolor* (SAX 1931), *Paeonia californica* and *P. Brownii* (STEBBINS and ELLERTON 1939, WALTERS 1942) and partly in *Isotoma petraea* (JAMES 1956, 1970); however, in most of these cases it is not known whether the translocation heterozygosity is associated with balanced lethals.

The *Rosa canina* group represents a different aspect. Most taxa are pentaploid (2n=35). At meiosis seven bivalents and twenty-one univalents occur both in PMCs and EMCs; however, the distribution of chromosomes at I anaphase is quite different in anthers and ovules. A random segregation of univalents occurring in PMCs results mostly in aneuploid, abortive microspores; the only functioning pollen grains are those with a basic set of 7 chromosomes derived from a normal distribution of bivalents. On the other hand, a polarized segregation occurring in the ovules results in the formation of two uneven groups comprising 7 and 28 chromosomes, respectively; the only functioning macrospores are 28chromosomic. Pentaploid chromosome number is subsequently restored through the fertilization of a 28chromosomic female gamete with 7chromosomic sperm. Thus, the heterogamic representatives of the *Rosa canina* group breed true for their odd polyploid condition (TäCKHOLM 1922, HURST 1931, DARLINGTON 1937, FAGERLIND 1940).

Leucopogon juniperinus is, to our knowledge, the only case comparable to the *Rosa canina* group although a random segregation does not occur; furthermore, the pattern of microspore selection being very special, there is no reduction in the total output of a good pollen. In this heterogamic allotriploid (2n=12, the genomic constitution AAB), both PMCs and EMCs form four bivalents and four univalents. As a result of a polarized segregation at I anaphase, 8 and 4 chromosomes occur in the respective groups. A subsequent elimination of some micro- and macrospores taking place, the embryo sacs in *Leucopogon* always carry eight chromosomes corresponding to a genomic constitution AB, whereas the functioning microspores contain only four chromosomes representing the genome A. Fertilization restores the original chromosome number and the proportion of the parent genomes (SMITH-WHITE 1948, 1955, 1959b).

As far as the *Cardamine* hybrids are concerned, eight bivalents and eight univalents occurred rather frequently during meiosis; it may be supposed that the bivalents corresponded to the two genomes RR of *C. rivularis*, whereas the univalents represented the only genome A of *C. amara*. A polarized segregation at I anaphase resulted in two uneven groups comprising respectively eight and sixteen chromosomes; the meiotic behaviour observed in some part of the studied material seems thus comparable both to *Leucopogon* as well as the *Rosa canina* group. However, gametes of either sex formed in the above mentioned taxa are of a single kind, whereas both polarized types of sperms and eggs i.e. R and RA apparently occur in the *Cardamine* hybrids; in this respect, the studied plants correspond to the *Oenothera Lamarckiana* group.

Recurrent patterns appearing in experimental crosses strongly suggest three categories of gametes operating in the 24chromosomic hybrids from Urnerboden: apart from the polarized gametes, unreduced RRA ones are functional. However, not all theoretically possible combinations were realized.



♀ \ ♂	R	RA	RRA ♂
R	~~RR~~	RRA	RRRA
RA	RRA	~~RRAA~~	RRRAA
RRA ♀	RRRA	RRRAA	RRRRAA

Cardamine hybrid

R = genome of C. rivularis
A = genome of C. amara

♀ \ ♂	G	V	GV ♂
G	~~GG~~	GV	GGV
V	GV	~~VV~~	GVV
GV ♀	GGV	GVV	GGVV

Oenothera

G = gaudens
V = velans

Fig. 41. Breeding behaviour of the triploid *Cardamine* hybrids compared to the *Oenothera Lamarckiana* type. RRRA - tetraploid found in the wild as well as obtained experimentally; RRRAA = pentaploid obtained from crosses between triploid hybrids and autoallohexaploids (URBANSKA-WORYTKIEWICZ, in press); RRRRAA = natural autoallohexaploid (URBANSKA-WORYTKIEWICZ and LANDOLT 1974, 1977, URBANSKA-WORYTKIEWICZ 1976, op. cit.). GGV and GVV = *O. semigigas* (STOMPS 1912, DE VRIES and BOEDIJN 1924, RENNER fide EMERSON 1935); GGVV = *O. gigas* (LUTZ 1907, 1908, EMERSON 1935).

Crosses between various triploid individuals resulted mostly in likewise triploid RRA plant; in addition, a single tetraploid of RRRA type was obtained. We are inclined to think that the triploid offspring derived from polarized gametes R and RA functioning in a complementary way; on the other hand, the tetraploid plant might have been issued from the union of an unreduced RRA gamete and a polarized R one. The triploid hybrids from Urnerboden appear thus to breed true for their particular genomic constitution, bar the cases where unreduced gametes occasionally contribute to some new combinations. This unusual breeding behaviour might be double-controlled by a gametophytic and a zygotic selection, the latter mechanism comparable to the balanced lethals system operating in *Oenothera Lamarckiana* (Fig. 41). It seems therefore that several ordinarily deleterious mechanisms add up in the *Cardamine* hybrids to a system with high survival value in which plants are able not only to bred true but also to profit from maximum hybrid vigour and to multiply prolifically.

5. Discussion

The rarity of hybrids between *Cardamine rivularis* and *C. amara* in the wild apparently is a measure of an isolation occurring between the two species (URBANSKA-WORYTKIEWICZ and LANDOLT 1972). The present investigations revealed that internal barriers of the reproductive isolation play the main rôle, strong incompatibility blocks operating both at pre- and postmating stages.

Natural hybrids born from crosses at the homoploid level between sexual species usually have the same chromosome number as their parents, particularly in diploid taxa. The large triploid population at Urnerboden issued from the diploid parents represents thus an exceptional case. To some extent comparable are the peculiar "lolioid" and "festucoid" hybrids (2n=21, the genomic constitution LLF and FFL, respectively) between *Lolium perenne* (2n=14) and *Festuca pratensis* (2n=14), studied by a succession of authors (e.g. PETO 1934, JENKIN 1933, 1955, WIT 1959, 1963, 1964, WHITTINGTON and HILL 1961, ESSAD 1962, 1964, 1966, 1968, GYMER and WHITTINGTON 1973a, 1973b, 1975a, 1975b). A single triploid hybrid (2n=33) between *Primula*