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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 breed 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*

veris ($2n=22$) and *P. elatior* ($2n=22$), apparently formed with a part of an unreduced gamete of the latter species, belongs also to this rare category (VALENTINE 1966). However, in the above mentioned cases both diploid and triploid hybrids occurred within the populations, whereas diploid hybrids of *Cardamine* have so far been sought unsuccessfully among the hundreds of triploids at Urnerboden.

Unreduced pollen grains were previously observed in *Cardamine rivularis* from various parts of its distribution range, including Urnerboden (URBANSKA-WORYTKIEWICZ and LANDOLT 1972, 1974, 1977). They proved to be functioning in some crosses performed in the course of the present study: two pentaploid individuals ($2n=40$, RRRRA) obtained in backcrosses to *C. rivularis* could only have been formed through the union of unreduced gametes, RRA and RR respectively. Therefore a possibility cannot be ruled out that triploid plants with a genomic constitution RRA might occasionally appear in natural populations as a direct result of crosses between *C. rivularis* and *C. amara*.

It is generally believed that the sterility of hybrids depends most frequently either upon their genic balance or chromosomic structure; interesting remarks in this subject were presented among others by REUSCH (1960), AHL00WALIA (1965) as well as GYMER and WHITTINGTON (1975a) dealing with the triploid hybrids between *Lolium* and *Festuca*. A similar interpretation might apply to the *Cardamine* hybrids from Urnerboden: some rare triploids developed from crosses between *C. rivularis* and *C. amara* were more likely to contain a full series of complementary genes than their diploid siblings; it is also possible that small translocations and deficiencies that mainly account for chromosomic sterility might occur less frequently in triploids than in diploids. The particular genomic constitution of the 24chromosomic RRA hybrids might accordingly have conferred them some chance of reproduction and survival within the population whereas the diploid RA plants remained genetically passive and eventually disappeared.

The above presented hypothesis might explain an initial phase of development of the triploid hybrid population at Urnerboden; however, it is not very helpful when the characteristic abundance of the 24chromosomic plants with non-dehiscent anthers is being considered. To begin with, it is

rather difficult to accept a recurrent hybridization between the diploid *Cardamine rivularis* and *C. amara* always resulting solely in triploids. Secondly, sexually reproducing triploids of the F_1 generation should normally produce various intermediate, aneuploid segregates; however, all the 337 studied triploids have invariably represented an exactly euploid level and the same genomic constitution RRA, in spite of the fact that some slight morphological variation occurred and the rare pollen-producing individuals showed various degrees of the pollen fertility (26%-62%).

Observations on meiosis in the triploid hybrids as well as the results obtained in experimental crosses contribute to a better understanding of the unusual stabilization of the triploid hybrids from Urnerboden. Three different types of chromosome segregation were observed at I anaphase: 1/ a normal segregation 12 : 12 was rather infrequent; 2/ a random segregation, characteristic for the studied material and 3/ the most peculiar, polarized or preferential segregation i.e. $8_R 8_A$ vs 8_R rather frequently occurring both in anthers and ovules. The diversified meiosis followed by elimination of numerous micro- and macrospores and probably by a zygotic selection as well, proved to have a variety of effects upon the breeding behaviour.

An apparently normal sporogenesis should first be commented. It cannot be excluded that the triploid hybrids may sometimes segregate truly reduced viz. 12chromosomic micro- and macrospores. However, the functioning of such gametes seems rather doubtful given their unbalanced genomic constitution: they should carry one genome of *Cardamine rivularis* plus only a half the genome of *C. amara*. It should be emphasized that the results of our experimental crosses positively indicate three euploid gametic types i.e. R, RA and RRA functioning in the hybrids, no definite proof, however, has been obtained for the reduced, aneuploid gametes.

A random segregation during meiosis is a well-known feature of hybrids, often accounting for their reduced fertility and giving rise to aneuploid offspring in the F_2 . A noteworthy example represents the 35chromosomic hybrid between *Agrostis gigantea* ($2n=42$) and *A. tenuis* ($2n=28$): this low-fertile pentaploid forms 14 bivalents and 7 univalents, but an apparently random segregation results in aneuploid backcross- and F_2 -individuals, both in the wild as well as in experiments (STUCKEY and BANFIELD 1946, JONES

1956, WIDEN 1971). The random segregation mostly resulting in various abortive aneuploid spores in the *Cardamine* hybrids speaks well, on the one hand, for their status of interspecific hybrids; on the other hand, it represents an important evolutionary mechanism contributing to the gamete pool of hybrids, for it may lead to the formation of unreduced gametes. The autoallohexaploids ($2n=48$, RRRRAA) spontaneously formed at Urnerboden represent the best argument in favour of unreduced gametes functioning in triploid hybrids (URBANSKA-WORYTKIEWICZ and LANDOLT 1974, 1977, URBANSKA-WORYTKIEWICZ, in press).

Incidentally, balanced gametes of R and/or RA type might also be formed as a result of a random segregation. On this occasion, the 9chromosomic hybrid between *Hypochoeris radicata* ($2n=8$) and *H. glabra* ($2n=10$) should be mentioned. Viable gametes of this plant contain respectively four, five or rarely nine chromosomes; all these gametic types are functioning in ovules, as indicated by results of backcrosses to *H. radicata* (HOLMBERG 1930, SANDWITCH 1954, BENOIT 1959, PARKER 1971). In view of the fact that two classes of gametes viz. $n=4$ and $n=5$ correspond numerically to constituent genomes of the *Hypochoeris* hybrid, it would be very interesting to get still more data concerning mechanism of its segregation.

The polarized segregation occurring in triploid hybrids resulted in the formation of euploid gametes, respectively carrying a single genome of *C. rivularis* (R) and two genomes, one from either parent species (RA). The functioning of such gametes was confirmed in various experimental crosses.

Diploid and triploid backcross plants deserve a special attention, for they show striking affinities to the plants found in the wild. The 16-chromosomic RR plants resembled *Cardamine rivularis* in a spectacular way. The only distinct difference was their pronounced pollen sterility ranging with a single exception from 84 to 94 per cent, whereas a genuine *C. rivularis* produced on average only 13 per cent of abortive pollen. In view of these results, some highly sterile diploid plants of a *C. rivularis* type, recently found at Urnerboden are of a special interest (URBANSKA-WORYTKIEWICZ and LANDOLT 1977). Triploid backcross individuals, apparently resulting from polarized RA gametes of the hybrids fertilized by normal sperms of

C. rivularis corresponded exactly to the 24chromosomic plants predominating at Urnerboden, both in their morphology as well as the complete male-sterility.

Three tetraploids ($2n=32$, RRRR) obtained in the course of the present study apparently were formed with a part of unreduced gametes of the hybrids, fertilized either by normal sperms of *Cardamine rivularis* or polarized R gamete operating in the 24chromosomic plant. It is interesting to note that a single plant of the same kind was recently found at Urnerboden.

In conclusion, an attempt may be undertaken to explain the origin of plants forming the population at Urnerboden. It can be assumed that the rare triploids producing pollen in a frequency higher than 2-3%, represent the first hybrid generation i.e. a direct product of crosses between *Cardamine rivularis* and *C. amara*. On the other hand, hundreds of the male-sterile plants occurring at Urnerboden might correspond to further generations issued from backcrosses to *Cardamine rivularis* as well as the sexual reproduction of triploid hybrids themselves. The same could be said for the tetraploid RRRR plants, very seldom appearing within the population. Diploid plants of *C. rivularis* morphology might in turn represent not only the genuine parent taxon but also backcross individuals. The seed production in triploid plants is, admittedly, very limited, but might be partly compensated by the great total number of flowering shoots; recurrent backcrosses and allogamy of the hybrids might accordingly contribute to the development of the population, effects of the sexual reproduction with little or no segregation being reinforced by an extremely strong vegetative multiplication.

The two aspects of the reproduction of triploid hybrids apparently have a bearing upon the population structure. Demographical studies carried out at Urnerboden revealed a diversified density of population: some sectors situated within cut manured meadows were particularly dense, whereas hybrid stands within open pastures and drainage canals were much less compact (URBANSKA-WORYTKIEWICZ and LANDOLT, in press). Vegetative multiplication, promoted by the cutting of the meadows, apparently represents an optimal adaptation of triploid hybrids to this biotope. Reproduction by seeds seems there rather difficult for two reasons: 1/ some meadows may be cut before the seed devel-

opment is completed; 2/ establishment of seedlings might anyway be problematic in some densely inhabited stands. On the contrary, open pastures offer more favourable conditions for seed setting and their dispersion, for 1/ grazing is not very intensive and 2/ light conditions are better for young plants. One might accordingly suppose that triploid hybrids use a different reproductive strategy in different ecological niches, vegetative multiplication being the only mechanism acting within some cut, manured meadows, whereas both sexual and vegetative reproduction are occurring within the pastures and drainage canals.

The question remains of what changes in the variation pattern might be expected within the population at Urnerboden. The reproductive behaviour of the triploid hybrids is characterized by an exceedingly reduced recombination potential. In this way, adaptively valuable properties of F_1 are not lost in later generations. On the other hand, it might be expected that a production of essentially new variants will be critically hampered in the long run. However, the 24chromosomic hybrids have already generated an apparently successful variant through doubling of the chromosome number: the autoallohexaploids ($2n=48$, RRRRAA), recently found at Urnerboden, are fertile, vigorous and actually expanding within the population. Further investigations in this most interesting subject are continued.

Summary

Reproduction of the triploid *Cardamine* hybrids from Urnerboden comprises 1/ strong vegetative multiplication and 2/ sexual reproduction characterized by an extremely reduced recombination potential. The two mechanisms add up to an unusual system in which adaptive properties of the first hybrid generation become stabilized, the plants being thus able to profit from maximum hybrid vigour. Structure of the population from Urnerboden as well as its possible evolutionary trends are discussed.

Résumé

Reproduction des hybrides triploïdes de *Cardamine* d'Urnerboden comprend 1/ multiplication végétative très importante et 2/ reproduction sexuée caractérisée par un potentiel de recombinaison très réduit. Il en résulte un système étonnant stabilisateur des propriétés adaptives de la première génération des hybrides, les plantes pouvant ainsi profiter d'une vigueur hybride maximale. Sont discutés la structure de la population d'Urnerboden et ses changements évolutifs possibles.

Zusammenfassung

Die Fortpflanzung der triploiden *Cardamine*-Bastarde vom Urnerboden umfasst: 1. eine sehr erfolgreiche vegetative Vermehrung und 2. eine sexuelle Fortpflanzung, die durch stark reduzierte Rekombinationsmöglichkeiten charakterisiert ist. Daraus ergibt sich ein erstaunlich stabiles System von adaptiven Merkmalen der ersten Bastardgeneration, die den Pflanzen ein ausserordentlich üppiges Wachstum erlaubt. Die Populationsstruktur der Pflanzen vom Urnerboden und deren Entwicklungsmöglichkeiten werden diskutiert.

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