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Genetics of apomixis in *Ranunculus auricomus*.

VI. Epilogue

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Abstract

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Details concerning parthenogenesis, collected during my cytogenetic analysis of apospory in apomictic *R. auricomus*, are compiled and discussed in the light of recent views and of the hypothesis of monogenic inheritance of gametophytic apomixis.

Key words: Apomixis, parthenogenesis, *Ranunculus auricomus*.

Introduction

Based on the new view of “checkpoints in the cell cycle” published in 1989 by Hartwell and Weinert, a very suggestive working hypothesis concerning “the events spanning female gametogenesis and embryogenesis in sexual systems” was discussed by Koltunow (1993): In sexual Angiosperms, the entire reproductive phase in ovules, from the ♀ archesporium to the embryo initiation, is conceived as “one coupled sequential event”. In gametophytic apomicts, this “sequential event” is somehow *uncoupled*, “for example by inducing mutations in the feedback controls that normally act on a checkpoint”, so “that a late event is induced to proceed without the completion of an earlier one” (Koltunow 1993 p. 1432).

The action of the allele *A* responsible for gametophytic apomixis* could simply lead to an *uncoupling* of this “sequential event” coupled in normal, sexual Angiosperms. This uncoupling can happen at 2 well defined points, namely at the transition points sporophyte/gametophyte and gametophyte/sporophyte, i.e. at the seams between the generations. Thus in gametophytic apomicts (1) a ♀ gametophyte (=embryo sac) may be initiated just as well without preceding meiosis, and (2) a sporophyte (=embryo) just as well without fertilization (=parthenogenesis). This allele *A*, however, does neither prevent meiosis nor fertilization, so that, in principle, a normal development can run parallel in the same ovule. Hence an appropriate *timing* of the different events involved

* This dominant allele *A* has been postulated by Savidan (1982) based on an analysis of apomixis in *Panicum maximum*, and by Nogler (1975–1984) based on an analysis of apospory in *R. auricomus*. The corresponding recessive wild allele *a*⁺ does not contribute to apomixis.

is decisive in order to attain a high degree of apomixis (= % of maternal offspring). In particular:

(1) A high degree of apospory/diplospory – often susceptible to environmental influences – can be achieved by mechanisms dealt with at large in the pertaining literature.

(2) The degree of parthenogenesis and its putative susceptibility to timing and other differences has been discussed recently by Martínez, Espinoza & Quarín (1994), and by Leblanc & Savidan (1994). Unfortunately, a cytogenetic approach is very difficult, due to the extreme rareness of apomeiotic individuals showing high proportions of B_{III} ($2n+n$) hybrids in their offspring (i.e. of apomeiotic individuals with low degrees of parthenogenesis). In my numerous crossing experiments with *R. auricomus*, for instance, I obtained – among hundreds of hybrids – only one single individual combining these characteristics, viz. the trisomic B_{II} hybrid T ($2n=17$). All relevant data on this plant T, and on parthenogenesis in particular, have been assembled in the following. (Many of them were provisionally presented in “Apomixis Newsletter” 1, 1989, but the interpretation given there needs reconsideration.)

Material and methods

The trisomic hybrid T (original designation $C(CM_3)_{13}$, Nogler 1982) with $2n=17$ chromosomes developed from a backcrossing (BC_1) using the F_1 hybrid CM_3 ($2n=3x=24$, $n=8$. . .16, Nogler 1973) as pollen parent. In the reciprocal backcrossing, CM_3 gave rise to two tetraploid ($2n=32$) B_{III} hybrids, CM_3C_5 and CM_3C_8 – among other offspring. In the genealogical tree (Nogler 1984 p. 412), these three hybrids figure under **d** and **k**, respectively.

Wild species:

A = *R. argoviensis* W. Koch ($2n=4x=32$), apomictic;

C = *R. cassubicifolius* W. Koch ($2n=2x=16$), sexual parent;

M = *R. megacarpus* W. Koch ($2n=4x=32$), apomictic parent;

R₂ and **R₆** = two sexual taxa of *R. auricomus* s.l. ($2n=2x=16$) from the Massif Central (France).

For the description of the methods see Nogler 1984 and 1990.

Results, discussion

The trisomic hybrid T ($2n=17$) was highly aposporous (Nogler 1984) but, most unexpectedly, gave rise mainly to aberrant offspring when used as ♀ parent. All aberrants were B_{III} hybrids; not one was a B_{II} hybrid. The crossing $T \times A$ resulted in 18 tetraploid B_{III} hybrids. On the basis of a first series of backcrossings $T \times C$ (A in Tab. 1) the hybrid T was originally classified as “highly aposporic but lacking parthenogenesis”, and was – at first sight – interpreted as a recombinant, thus seemingly proving our initial working hypothesis which assumed two most closely linked genetic factors, one for aposporous embryo sac, the second for parthenogenetic embryo initiation. Later on, in three further small BC_2 series $T \times C$ (Tab. 1 B, C, D), a few maternal plants were detected, besides the B_{III} hybrids. Thus the trisomic hybrid T must have been latently parthenogenetic, with a low degree of parthenogenesis varying from 0 to 23%. This finding points to susceptibility to environmental influences but, unfortunately, no exact data are available to prove this. Be it as it may, T was not a recombinant as initially suspected, and there is no reason to insist any longer on a separate gene for parthenogenesis.

The high tendency to form B_{III} hybrids typical of the hybrid T has been inherited from its pollen parent CM_3 . When compared to the other triploid F_1 hybrids, CM_3 showed

Tab. 1. BC₂ offspring from backcrossing the trisomic, aposporous BC₁ hybrid T (2n=17) × C = *Ranunculus cassubicifolius* (sexual parent, 2n=16).

| Crossing series T × C | Total offspring T × C | Maternal plants 2n=17* | B _{III} hybrids | | Degree of parthenogenesis |
|--------------------------|--------------------------|---------------------------|--------------------------|----|---------------------------|
| | | | 2n=25 | 33 | |
| A | 36 | – | 36 | – | 0% |
| B | 14 | 1 | 12 | 1 | 7% |
| C | 13 | 3 | 10 | – | 23% |
| D | 14 | 1 | 13 | – | 7% |
| Total | 77 | 5 | 71 | 1 | 6.5% |

* Due to a certain tendency to somatic chromosome elimination in the hybrid T two diploid offspring were at first considered to be euploid (2n=16, see Nogler 1982). A reinvestigation then showed that both were trisomic and maternal.

Tab. 2. Offspring of 25 T × C hybrids (BC₂, 2n=25) inter se.

| Mother plants | Total offspring | B _{II} hybrids | Maternal plants | B _{III} hybrids | | Degree of parthenogenesis |
|---------------|-----------------|-------------------------|-----------------|--------------------------|----|---------------------------|
| | | | | 5x | 6x | |
| 8 T × C | 150 | 19=13% | 99=66% | 30+2=21% | | 76% |
| 12 T × C | 290 | 35=12% | 130=45% | 119+6=43% | | 51% |
| 5 T × C | 155 | 26=17% | 43=28% | 85+1=55% | | 33% |
| 25 T × C | 595 | 80=14% | 272=46% | 234+9=41% | | 53% |

definitely an increased tendency (2–3x) to form B_{III} hybrids (Nogler 1973). Of its two tetraploid (4x=32) B_{III} offspring in BC₁, one, viz. CM₃C₅, showed an equally high tendency to form again higher polyploid (5x, 6x) B_{III} hybrids, whereas the other, viz. CM₃C₈, did not form any B_{III} offspring (Nogler 1978 Tab. 3; note, however, the small number of progenies).

B_{III} hybrids from the BC₂ backcrossing T × C with 2n=25 (=17+16/2) chromosomes were expected to present an even lower degree of parthenogenesis than T, since C, being a normal, sexual wild species, certainly has no tendencies towards parthenogenesis. Most surprisingly, however, all 25 cytogenetically investigated T × C hybrids (viz. the most vigorous out of the 71 B_{III} hybrids) showed considerably increased degrees of parthenogenesis (up to 76%: Tab. 2 – whereby the 25 plants, growing simultaneously in the same phytotrone and crossed inter se or selfed, have differed quantitatively, allowing to range them roughly into 3 groups). Addition of one genome of the sexual parent C restores parthenogenesis – only latently present in the aposporous T – to a large extent!

In the trisomic hybrid T, unreduced egg cells maintain obviously their receptivity far longer than the unreduced egg cells in all other plants investigated, be they dihaploids, B_{II}, or B_{III} hybrids, so that, at best, a very delayed and scarce pollination may increase the chances for a parthenogenetic development. In this respect, T represents the extreme opposite to “precocious embryony” (not known, however, in *R. auricomus*: Rutishauser 1954). Unfortunately, crossings with controlled pollination failed due to the weakness of

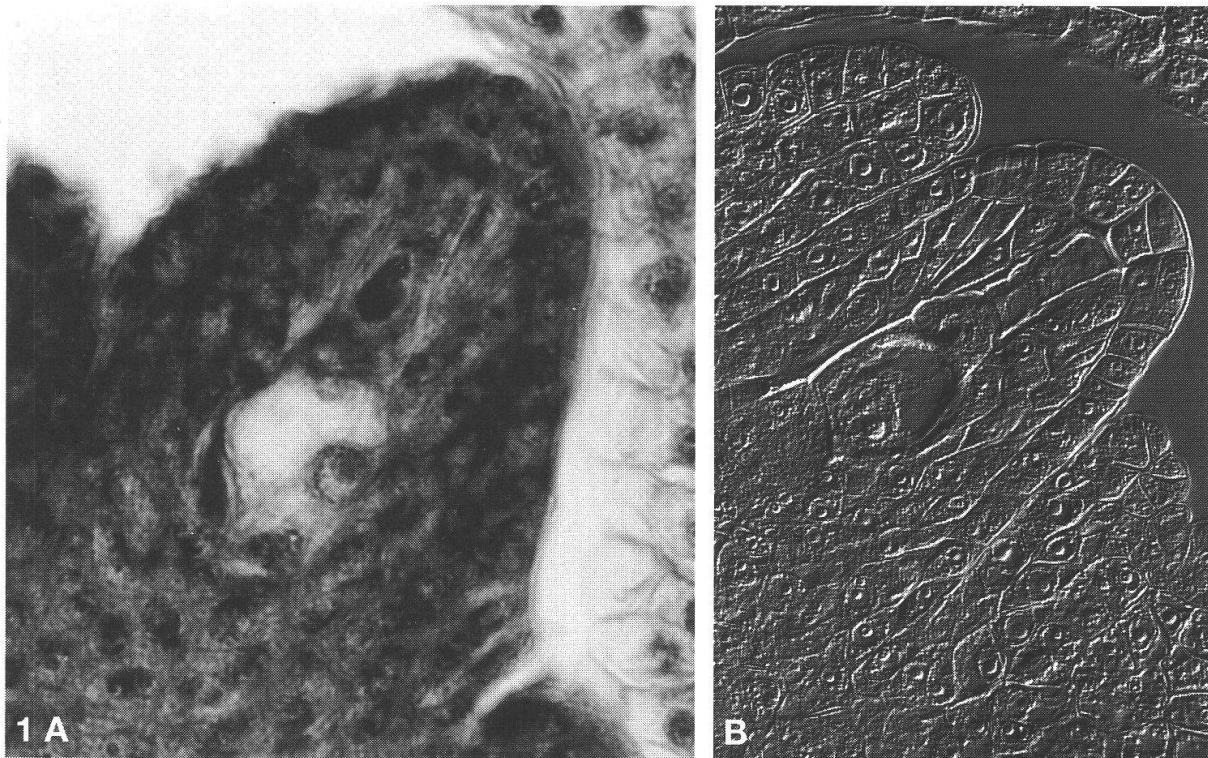


Fig. 1. Longitudinal sections of ovules with 1-nucleate aposporous embryo sacs in *Ranunculus auricomus* with advanced vacuolation. A. Premature aposporous development typical of the trisomic hybrid T ($2n = 17$), EMC in early prophase. B. Normal development with megaspore tetrad (3 degenerated) typical of T \times C hybrids ($2n = 25$) and other tri- and tetraploid aposporous hybrids. A. stained with Hematoxylin Heidenhain; B. unstained, interference contrast image (cf. Nogler 1990). Note the state of micropyle and integuments.

T and its poor maternal offspring, and are no longer possible, since the plants died long ago.

The embryological analysis of T and its maternal offspring (Nogler 1982) showed that the average induction of apospory takes place very early (compared with the meiotic development in the same bud) – bringing to mind the situation in aposporous dihaploids (Nogler 1975). Fig. 1 A shows an ovule with early aposporous induction typical of T, Fig. 1 B the normalized situation typical of T \times C B_{III} hybrids and of other triploid and tetraploid aposporous hybrids. In this way, in the trisomic hybrid T the time span between aposporous induction and the final loss of receptivity of the unreduced egg cells – presumably days after anthesis – becomes extremely long. In *R. auricomus* this time span varies far more than expected, probably with M (apomictic parent) and T as extremes.

According to Martínez, Espinoza & Quarín (1994) in aposporous *Paspalum notatum* mere early pollination, viz. 2–3 days prior to anthesis, allegedly suffices to produce rather high proportions of B_{III} hybrids, whereas under normal conditions *P. notatum* is purely apomictic. The authors postulate that the “pollen tube penetration into the pistils is synchronized with meiotic embryo sac maturity”; this may “be too late for fertilization” of aposporous egg cells which, at that time, have already initiated embryo development. “In this way, parthenogenesis may take place as a consequence of failure of fertilization.” This hypothesis may indirectly be corroborated by the results with T, in which early apospory is combined with extremely prolonged maintenance of egg cell receptivity, a

constellation which, under normal circumstances, results in B_{III} hybridization. Another point, however, just touched by Martínez et al. (1994), deserves special consideration: In certain crossings, the degree of parthenogenesis may greatly be influenced by the degree of polyploidy of the pollen parent. This has already been established in the classical publication of Noack (1939). In my own material (Nogler 1982 Tab. 3), I found such great differences even at the same (diploid) level, in crossings between aposporous dihaploids ($2n=16$) and diploid pollen parents, above all two sexual taxa of *R. auricomus* s.l. from the Massif Central (France), designated as R₂ and R₆ ($2n=16$). Pollinations with R₆ gave rise to similar high proportions of maternal offspring as pollinations with other diploids (viz. roughly 80%), whereas pollinations with R₂ mainly resulted in B_{III} hybrids (little more than 20% of maternal offspring). The aposporous dihaploid CM₁C₁M₁ ($2n=16$), for instance, when pollinated in a greenhouse with R₆, gave rise to 5 offspring, all maternal; but when pollinated, under the same conditions, with R₂, issued in 7 offspring, 5 B_{III} hybrids and only 2 maternal (not expressly specified in the table mentioned). The control of parthenogenesis and the prevention of fertilization, no doubt, is more than a question of timing and coordination of processes involved in embryogenesis. In many normal, sexual plants unreduced egg cells may be occasionally formed from meiotic restitution nuclei – in certain biotypes with increased frequency. A thorough knowledge of the fate of such unreduced egg cells in cases of non-fertilization would greatly promote our understanding of parthenogenesis in gametophytic apomicts.

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