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How to obtain diploid apomictic *Ranunculus auricomus* plants not found in the wild state¹

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Abstract

In *Auricomi* the factor A^- causing aposporous embryo sac formation (the wild allele A^+ of which does not contribute to apospory) is transmissible by diploid (reduced or unreduced) gametes in the heterozygous state (A^+A^-) but not by haploid (monoploid) male or female gametes. Diploid apomicts are, therefore, formed only by parthenogenesis as dihaploids but not by hybridization.

The apospory factor A^- is rather closely linked with haploid parthenogenesis.

Some of the dihaploids are meiotic (sexual, genotype A^+A^+); the large majority are highly aposporous. All aposporous dihaploids are heterozygous (A^+A^-).

Aposporous dihaploids are partially apomictic, whereby the degree of apomixis (the relative amount of maternal offspring) may be dependent on the male parent.

Introduction

One hardly ever finds diploid apomicts in nature but practically only polyploid ones (e.g. the *Auricomi* in Switzerland are almost all tetraploid). The best known exceptions are certain diploid apomictic strains of *Potentilla argentea* (Müntzing and Müntzing 1945, Asker 1970). On the other hand diploid relatives of apomicts are generally purely sexual. The *Auricomi* are not an exception to this; *R. cassubicifolius*, too, is purely sexual (meiotic embryo sac formation) – see Rutishauser 1965, Nogler 1971, 1975 further the footnote on page 18.

Not being able to find diploid apomicts in the natural state I attempted to produce them experimentally, using reduced pollen ($n=x...2x$) of triploid, partially apomictic F_1 hybrids ($2n=24$) from crossings between diploid, sexual *R. cassubicifolius* and tetraploid, apomictic *R. megacarpus* (Rutishauser 1965, Nogler 1971 sqq.). By this means I expected to transmit the factor A^- causing aposporous embryo sac formation (Nogler 1975) to diploid backcross hybrids.

¹ This paper gives a summary with further details and a discussion of results presented in 1978 (unpublished, mimeographed «Habilitationsschrift ETH Zürich»).

The **terminology** concerning hybrids which is recommended for use in cytogenetics of apomixis is that introduced by Rutishauser in 1948. Facultative apomicts have four possible modes of reproduction: Fertilization of unreduced egg cells results in B_{III} hybrids, fertilization of reduced egg cells results in B_{II} hybrids. Parthenogenetic development of unreduced egg cells results in maternal offspring, parthenogenetic development of reduced egg cells results in polyhaploids, in the case of tetraploid mother plants in dihaploids.

Material and methods

The plant material was the same as described in previous publications (Rutishauser 1965, Nogler 1971 sqq.). In addition, two sexual diploid ($2x=16$) taxa of *R. auricomus* s.l. from the Massif Central, France (designated as R_2 and R_6) were used. I am grateful to Prof. Dr. E. Landolt, Zürich, for supplying these.

Embryological analyses were made on complete series of sections $12\ \mu\text{m}$ thick stained with iron haematoxylin Heidenhain. One to three buds per plant were sectioned, each giving about 30 to 50 analyzable ovules. The most suitable stage is shown in Fig. 1A in Nogler 1975.

Results

All the hybrids used in this investigation originated from the poorly compatible crossing between the sexual *R. cassubicifolius* (C in Fig. 1, diploid, $2n=16$, embryo sac formation purely meiotic) and the apomictic *R. megacarpus* (M, tetraploid, $2n=32$, embryo sac formation predominantly aposporous; occasional meiotic embryo sacs functionless – see Nogler 1971, 1972). This crossing resulted in 6 triploid B_{II} hybrids ($2n=24$) 4 of which ($CM_{1,2,3,6}$) were fertile and predominantly aposporous (Nogler 1971 sqq.) and produced reduced pollen ($n=x\dots 2x=8\dots 16$).

First backcross, using triploid, aposporous F_1 hybrids as male parents (Tab. 1)

All the 20 euploid *diploid* B_{II} hybrids ($2n=16$) were purely meiotic, without a trace of apospory, as were all but one of the 9 hyperploids ($2n=17, 18$). This exceptional case, designated as $C(CM_3)_{13}$ ($2n=17$), was highly aposporous (see below). All the diploids, including the aneuploid ones, were vigorous and fairly fertile – even the plant with 18 chromosomes.

In contrast to the diploid the *triploid* B_{II} hybrids ($2n=22, 23, 24$) were in the majority, at least 8 out of the 13, aposporous, and only 2 or 3 were meiotic. The single pentaploid B_{III} hybrid ($2n=40=16+24$) has not been embryologically investigated and is commented on in the footnote on p. 18.

Table 1. Offspring of backcrosses between diploid *R. cassubicifolius* (C) and triploid F_1 B_{II} hybrids ($CM_{1\dots 3}$)

	2n=16	17	18	3x	5x	total
C \times CM_1	4	2				6
C \times CM_2	12	2	1	7		22
C \times CM_3	4	4		6	1	15
	20	8	1	13	1	43

Reciprocal first backcross, using triploid, aposporous F₁ hybrids as female parents

As the 4 fertile F₁ hybrids CM_{1,2,3,6} were predominantly aposporous, only 4 of the 53 backcross offspring resulted from meiotic embryo sacs (Nogler 1975). Three of these 4 B_{II} hybrids were triploid and aposporous; only one (CM₆C₂, see Nogler 1973) was diploid (2n = 17) and meiotic. This was established from 10 buds, one endosperm (with 3n = 26 = 9 + 9 + 8 chromosomes), and 12 offspring (all B_{II} hybrids, none of them maternal). Of the 49 apomeiotically formed offspring 42 were maternal (triploid) and the remaining 7 B_{III} hybrids (tetraploid: CM₁C_{1,11,20}, CM₃C_{2,5,8}, CM₆C₇, see Nogler 1973, 1978). These 7 tetraploid F₂ B_{III} hybrids were all predominantly meiotic but produced aposporous embryo sacs to a variable extent. As both reduced and unreduced embryo sacs developed either parthenogenetically or after fertilization, these 7 tetraploid plants formed B_{III} hybrids, maternals, B_{II} hybrids, and dihaploids (for quantitative embryological and cytogenetical data, see Nogler 1973, 1975). In what follows only the dihaploids will be considered. (The reproduction of triploid B_{II} offspring will be discussed in a later publication.)

From backcrossing with diploid *R. cassubicifolius* 28 dihaploids resulted (see Fig. 1). In addition 12 dihaploids were obtained from different 4x × 4x crossings (including selfings). All dihaploids were analyzed together (Tab. 2) as the male parent has no genetic influence.

Embryology of dihaploids (Tab. 2)

The great majority of the dihaploids obtained were, contrary to expectation, aposporous (Tab. 2). Aposporous dihaploids have a much higher degree of apospory than the tetraploid wild form *R. megacarpus* – due to much earlier induction of apospory (see Fig. 1 in Nogler 1975).

Table 2. Embryology of dihaploids (enlarged from Nogler 1978)

Mother plant (all 4x = 16)	Dihaploids		2n =				total
	total	EMBRYOLOGY	15	16	17	18	
6 F ₂ B _{III} hybrids:							
CM ₁ C ₁	4	aposporous (vegetative)	–	2	–	–	2
			–	–	1	1	2
CM ₁ C ₁₁	11	aposporous meiotic	–	6	4	–	10
			–	1	–	–	1
CM ₁ C ₂₀	9	aposporous (vegetative)	–	3	2	1	6
			1	–	2	–	3
CM ₃ C ₅	1	aposporous	–	1	–	–	1
CM ₃ C ₈	2	aposporous	–	1	1	–	2
CM ₆ C ₇	6	aposporous meiotic (vegetative)	–	4	–	–	4
			–	1	–	–	1
			–	–	–	1	1
5 F ₃ B _{II} hybrids	7	aposporous meiotic (vegetative)	–	2	2	–	4
			–	2	–	–	2
			1	–	–	–	1
Total	40	aposporous meiotic (vegetative)	–	19	9	1	29
			–	4	–	–	4
			2	–	3	2	7

Aneuploid dihaploids ($2n = 17, 18$) were weak to sublethal, poorly fertile to sterile, in certain cases even purely vegetative – in contrast to the aneuploid dihaploid B_{II} hybrids ($2n = 12, 18$) mentioned. The euploid dihaploids, on the other hand, were all surprisingly vigorous and both male and female fertile, and it was easy to obtain the offspring necessary to confirm the embryological findings.

Offspring of aposporous dihaploids used as female parents (Tab. 3A)

Six aposporous dihaploids ($2n = 16$) were pollinated with pollen of different diploid and tetraploid plants (Tab. 3A). The proportions of B_{III} hybrids versus maternal offspring were much higher after $2x \times 4x$ crossings and, even more striking, after crossings with R_2 (one of the diploid taxa from the Massif Central) than after the other $2x \times 2x$ crossings.

Nearly all B_{II} hybrids originated from a single dihaploid (designated as $CM_1C_{11}M_4$) which produced 13.3 % B_{II} hybrids after $2x \times 2x$ crosses and 13.5 % after $2x \times 4x$ crosses whereas the other 5 dihaploids produced very few if any B_{II} hybrids. This does not become evident from Tab. 3A.

The aneuploid dihaploids ($2n = 17, 18$) were embryologically just as highly aposporous as the euploid ones, but were so weak and poorly fertile that only two (both $2n = 17$) set some seeds after backcrossing with *R. cassubicifolius*. From 5 crossings a total of 15 hybrids resulted (included in Fig. 1 but not in Tab. 3A) of which, contrary to expectation, only 3 were maternal ($2n = 17$), not one a B_{III} hybrid, and 12 B_{II} hybrids (all $2n = 16$). Ten of these B_{II} hybrids could be investigated embryologically: all turned out to be purely meiotic. The same applies to the 6 investigated diploid B_{II} hybrids obtained from euploid dihaploids as mother plants.

Table 3. Offspring of aposporous dihaploids ($2n=16$)

	B_{II} hybrids 2x 3x	maternal (2x)	B_{III} hybrids 3x 4x	TOTAL plants
A. Dihaploids as ♀				
<i>2x × 2x crosses</i>				
DH × C, DH, R_6 , S	3.9 %	83.8 %	12.3 %	154
DH × R_2	1.6 %	21.9 %	76.5 %	64
<i>2x × 4x crosses</i>				
DH × A, M	8.5 %	48.0 %	43.5 %	177
TOTAL plants	22	228	145	395
B. Dihaploids as ♂				
C × DH	63 plants		(1)	64 (+ 3 lethals)

Abbreviations :

A : *R. argoviensis*, $2n = 32$

C : *R. cassubicifolius*, $2n = 16$

DH : 6 different aposporous dihaploids, all $2n = 16$

M : *R. megacarpus*, $2n = 32$

R_2/R_6 : 2 different taxa of *R. auricomus* s.l. from the Massif Central, France ; both $2n = 16$

S : Selfing of aposporous dihaploids

Offspring of aposporous dihaploids used as male parents (Tab. 3B)

Backcrossings of *R. cassubicifolius* (♀) with 6 different euploid aposporous dihaploids (see Nogler 1978, p. 31) resulted in 67 offspring of which 3 were lethal. Of the 63 B_{II} hybrids obtained (Tab. 3B) 61 were analyzed embryologically: all were purely meiotic. Although I investigated a large amount of material, I could not find any trace of apospory typical for the male parents.

Discussion

In *Auricomi* the induction of aposporous embryo sacs from somatic nucellar cells is made possible by an apospory factor A^- the wild allele of which does not contribute to apospory but may have a function in the normal, meiotic embryo sac formation (Nogler 1975). The apospory factor A^- cannot be recessive to the wild allele A^+ as was previously assumed (Nogler 1971). This was shown by independent methods (Nogler 1973, 1975, 1978, and the present results). The diploid, sexual parent *R. cassubicifolius* with purely meiotic embryo sac formation² is homozygous A^+A^+ , the apomictic (aposporous) parent *R. megacarpus* heterozygous (Nogler 1975, 1978). There are no known hybrids homozygous for A^- .

The attempt to synthesize diploid aposporous plants by transmission of the apospory factor A^- by haploid (monoploid) gametes of triploid, predominantly aposporous F₁ plants failed (Tab. 1). Apospory was only transmitted by heterozygous A^+A^- gametes, to triploid B_{II} hybrids as well as to one single trisomic B_{II} hybrid, designated as C(CM₃)₁₃ ($2n = 17$, genotype $A^+A^+A^-$). This plant unfortunately has died, but both the reciprocal backcrosses were successful (publication in preparation). The fact that the apospory factor A^- is not transmitted by haploid gametes is confirmed by the diploid B_{II} hybrid offspring of aposporous dihaploids. This applies regardless of the sex of the gametes: 16 B_{II} hybrids arose from female, 61 from male gametes. All were meiotic.

The aposporous dihaploids reported here (Tab. 2) originated from tetraploid, partially aposporous F₂ and F₃ hybrids with the genotype $A^+A^+A^+A^-$ (Nogler 1975); all aposporous dihaploids must, therefore, be heterozygous A^+A^- . (Indications from investigations made hitherto let it seem doubtful that homozygous A^-A^- gametes function at all.) Surprisingly enough the large majority of the dihaploids are aposporous (Tab. 2): of the 33 analyzed only 4 are meiotic. Obviously the tendency for haploid parthenogenesis is much more pronounced in heterozygous A^+A^- egg cells, in other words the two components of apomixis (apospory and parthenogenesis) seem to be rather closely linked in *Auricomi*.

R. cassubicifolius was used as mother plant in 318 cases so far, viz. 254 hybrids and 64 endosperms. Only 2 of these 318 originated from unreduced egg cells, one was a pentaploid hybrid ($2n = 40 = 16 + 24$ Tab. 1), the other a tetraploid hybrid ($2n = 32 = 16 + 16$, Tab. 3B). It is striking that in both cases the fertilizing pollen was also unreduced. As unreduced pollen is in general very rare in this material, it can be assumed that combination of an unreduced egg cell with a reduced male gamete is more likely to be incompatible, in other words that *R. cassubicifolius* presumably produces rather more unreduced embryo sacs than the 0.6% observed. Since degrees of apospory of about 1% would be easily detectable in embryological routine investigations it can be concluded that occasional unreduced embryo sacs originate in *R. cassubicifolius* – as in many other normal, sexual plants (Harlan and deWet 1975) – due to failure of meiosis in certain megaspore mother cells, but certainly not from aposporous initials.

The apospory of dihaploids is very pronounced — although only one of the two genomes has A^- . This is the definite proof that apospory cannot be recessive in *Auricomi*. (Recently Savidan — 1981 — proved dominant inheritance of apospory and close linkage with parthenogenesis in apomictic *Panicum maximum*.) My embryological findings were confirmed by analyses of offspring: Most of the investigated dihaploids produced very few B_{II} hybrids, if any; nearly all their offspring arose from aposporous egg cells, viz. B_{III} hybrids and, above all, maternal plants (Tab. 3A). The aposporous dihaploids are, therefore, to a large extent *apomictic*. The degree of apomixis, the proportion of parthenogenetically developed unreduced egg cells, i.e. maternal versus aberrant (B_{III} hybrid) offspring, may be dependent on the male parent. This was strikingly shown by a single diploid biotype (designated above as R_2) the pollen of which had a tendency to fertilize which was at least four times greater than that of the pollen of the other diploid male parents used. A slightly less pronounced increase, as compared to the diploid male parents, was found after crossing with tetraploids.

Since the apospory of the two poorly fertile *aneuploid* dihaploids investigated (both $2n = 17$) was as pronounced as that of the 6 fertile euploid dihaploids, one would expect development of meiotic egg cells to be just as unlikely. But the meagre offspring of these two aneuploids was composed quite differently: the majority were B_{II} hybrids, and only a few were maternal plants. Contrary to expectations these two highly aposporous aneuploid dihaploids were only slightly apomictic. The reason for this unusual feature is no doubt that, in contrast to the vigorous euploid dihaploids, the chances of development of B_{II} embryos were nevertheless greater than those of the even weaker maternal ones.

*

The apomictic dihaploids reported here prove that apomixis is, in principle, quite possible on the diploid level and by no means limited to polyploidy. Some of the dihaploids are no doubt sufficiently vigorous and fertile both on the male and female side to be able to compete, at least for a time, in natural surroundings. However, *Auricomi* seem to be an exceptional case as, in general, dihaploids are either sexual or sterile and very often more or less weak. DeWet (1965) supposes that «sterility of certain dihaploids may be due to apomixis» [apospory]; but in my opinion it is just as possible that diploid apomicts occurring exceptionally in nature originated as dihaploids from tetraploid apomicts.

The fact that diploid apomicts are hardly ever found in nature can be plausibly explained by the above results in *Auricomi*: As A^- is not transmissible via haploid but only via diploid (heterozygous) gametes, diploid apomicts may only originate, if at all, parthenogenetically as dihaploids, but not as diploid B_{II} hybrids. As apomictic dihaploids are normally so weak and poorly fertile they no doubt die out in spite of possible maternal reproduction. Or, at best, they may give rise to B_{III} hybrids. Tetraploid B_{III} hybrids may be formed as $2n+2n$ hybrids after selfing or crossing with other dihaploids or, more likely, as $2n+n$ hybrids within tetraploid populations — a variation of the «diploid-tetraploid-di(ha)ploid cycles», the well known model for evolutionary possibilities within apomictic (agamic) species complexes (compare Savidan and Pernès 1982).

Of course, the question remains how far this non-transmissibility of A^- via haploid gametes applies also to other apomicts. In this connection the following cases from the literature may be pointed out.

In a phenotypically sexual strain of *Dichanthium aristatum* ($2n = 20$), crossed with diploid *D. caricosum* ($2n = 20$), apospory is not transmitted by reduced male gametes but only by unreduced female gametes (d'Cruz and Reddy 1971). Contrary to *Auricomi*, however, apospory does not become manifest in the diploid strains which are, according to the authors, probably of dihaploid origin.

Similarly in *Taraxacum* diplospory is transmitted only by diploid but not by haploid male gametes, as shown by crossings made by Richards (1970) and Müller (1972) between triploid diplosporous and diploid sexual species. In this way Müller obtained 269 F_1 hybrids, 9 of which were triploid ($2n = 24$), all partly apomictic, and 260 diploid ($2n = 16$), all sexual (meiotic).

A single hyperdiploid *Parthenium argentatum* plant (trisomic, $2n = 37$, partially diplosporous) originated as a dihaploid from an apomictic strain ($2n = 4x = 72$; x being relatively high, as usual in the Heliantheae). By crossing this plant with the diploid, sexual *P. argentatum*, Gerstel et al. (1950, 1953) obtained 15 diploid F_1 B_{II} hybrids. By inbreeding, these F_1 plants produced 52 surviving diploid F_2 B_{II} hybrids out of 53. By pollinating these with diploid, sexual *P. stramonium* a total of 950 F_3 hybrids and not one maternal plant resulted. Only 306 of these were analysed: 300 were diploid and 6 triploid, formed as $n + 2n$ (!) hybrids. All these 306 F_3 plants thus were B_{II} hybrids and not one a B_{III} hybrid; it follows that all the 52 F_2 plants were meiotic and free of diplospory. As it was not possible to apply the hypothetical model with 3 recessive apomixis genes, postulated by Powers (1945) for the same *Parthenium* material, Gerstel et al. (1953) suggested «that apomixis in guayule is based on at least four recessive genes: a minimum of two being concerned with the process of meiotic reduction» [diplospory, Antennaria type] «and two more with the requirement for fertilization». But it is difficult to understand why diplospory should never become manifest amongst this large amount of material. However, assuming analogous conditions to those found in *Auricomi* one would naturally expect such results: Diplospory would not be recessive but simply not transmitted to the F_2 hybrids.

In sexual *Leontodon hispidus* ($2n = 14$) Bergman (1935) found a single abnormal plant with 10-20% aposporous (but functionless) embryo sacs. The roughly 20 F_1 hybrids from free flowering were normal (only meiotic embryo sacs). Inbreeding resulted in two F_2 hybrids, one meiotic, the other with disturbances in both male and female meiosis and various abnormalities in the chalaza, viz. free somatic and meiotic (!) divisions, irregularities in cell wall formation, nuclear fusions, and possibly, formation of restitution nuclei. Finally degeneration takes place, often preceded by vacuolation, which the author interprets as «apospory», although it is fundamentally different to the apospory of the original plant. Vacuolation is the first step in the normal formation of both aposporous and meiotic embryo sacs, which is also the case for the original plant, but is totally missing in the chalazal disturbances of the F_2 plant in which vacuolation accompanies degeneration. Therefore, I cannot agree with Bergman's conclusion; it is quite possible that apospory was not transmitted at all but only other recessive disturbances. Yet, the latter case is less evident than the others.

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Zusammenfassung

Der apospore Embryosackentwicklung bedingende Faktor A^- (dessen Wildallel A^+ nicht zur Aposporie beiträgt) ist bei *R. auricomus* wohl durch diploide (reduzierte oder unreduzierte), heterozygote Gameten (A^+A^-) übertragbar, nicht aber durch haploide (monoploide) männliche oder weibliche. Diploide apomiktische *Auricomi* können infolgedessen nur parthenogenetisch als Dihaploide, nicht aber als B_{II} -Bastarde entstehen.

Der Aposporiefaktor A^- scheint mit haploider Parthenogenese verhältnismäßig eng gekoppelt zu sein.

Nur wenige Dihaploide sind meiotisch (sexuell, Genotyp A^+A^+), die meisten hingegen hochgradig apospor. Alle aposporen Dihaplonten sind heterozygot (A^+A^-).

Apospore Dihaploide sind partielle Apomikten, wobei der Apomixisgrad, der Anteil materneller Nachkommen, vom Pollenelter mitbeeinflusst sein kann.

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