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Apomixis versus sexuality in blackberries (*Rubus* subgen. *Rubus, Rosaceae*)

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Abstract: In *Rubus* L. a connection seems to exist between the degree of meiotic disturbances on the one hand, and the production of unreduced embryo sacs, pollen fertility and relative seed set on the other hand. Severe meiotic disturbances commonly encountered in apomictic taxa decrease pollen fertility and thereby seed set since pollen is necessary for endosperm development. By contrast interspecific hybrids between apomictic taxa appear to be sexual and exhibit high pollen fertilities, probably due to an improved meiosis. Thus, apomixis leads to a decreased fertility in *Rubus*, not the opposite, as often discussed.

In the genus *Rubus* apomixis (defined according to ASKER 1979: asexual reproduction through seed formation) was well documented by LIDFORSS (1905, 1907) on the basis of extensive crossing experiments. Additional crossing data as well as cytological and embryological studies have since been presented by e.g. CRANE (1940), GUSTAFSSON (1943), CHRISTEN (1950), PRATT & EINSET (1955), HASKELL (1960), JENNINGS & al. (1967) and CZAPIK (1983).

Among the 3 large and 9 small subgenera commonly recognized, apomixis seems to prevail mainly in subg. *Rubus*, and there only in the polyploid taxa (GUSTAFSSON 1943, NYBOM 1986 b). A rather small number of diploid, sexual species have been described from Europe and N. America; in contrast, polyploid apomictic taxa (for which species rank has been claimed) number at least 2000 in Europe alone (GUSTAFSSON 1943, HESLOP-HARRISON 1968), and include an additional large number from N. America. Polyploidy also dominates in another large subgenus, *Malachobatus*, here apparently in combination with sexuality (NYBOM 1986 b). Apomixis is rare in the third large subgenus, *Idaeobatus* (raspberries), where it is found only in the few triploid specimens encountered of otherwise diploid taxa (PETROV 1939, PRATT & al. 1958).

In *Rubus* apomixis is facultative and usually occurs by the formation of unreduced embryo sacs from sporogenous (diplospory) or other archesporal cells (apospory) (CHRISTEN 1950, BERGER 1953, PRATT & EINSET 1955, CZAPIK 1983). Apospory, diplospory, and reduced embryo sacs commonly occur together in the same species (CHRISTEN 1950). Apomictic *Rubus* spp. are pseudogamous, i.e. pollination is necessary for endosperm development. Normally, reduced embryo sacs do not develop until fertilized, while unreduced embryo sacs develop parthenogenetically. Exceptions to both however occur, thereby rendering reproduction in *Rubus* extremely versatile.

Here I shall present some results from crossing experiments with wild Swedish blackberries and discuss the regulatory role of meiotic disturbances in determining the balance between apomixis and sexuality.

Material and methods

In the Helsingborg Botanical Garden (Fredriksdal) a collection of indigenous blackberry species is grown together with a few European cultivars. In this study 20 species, including one member of the critical *R. corylifolius* agg. (*R. wahlbergii*) and one cultivar (*R. laciniatus*) were used (Table 1). Only one clone is grown of each species.

In 1983 artificial selfing as well as some interspecific pollinations were carried out on previously emasculated flowers (NYBOM 1985, 1987). Each inflorescence was pollinated once only. Only flowers terminating first-order laterals in the inflorescence were used, as also in all following parts of this study. The pollination was effectuated by brushing the donor flower against the recipient flower. Both types of flowers were isolated with glassine bags several days in advance. Seed set was estimated by counting the number of well-developed drupelets. An average of 59 flowers per species was used for the selfings and 45 for the interspecific pollinations.

The number of ovules was counted on 12 flowers per species (Table 1). Pollen fertility was assessed by staining with cotton blue (aniline blue lactophenol) as previously described (NYBOM 1985, 1987). Reduced pollen is formed but due to meiotic disturbances a proportion of the grains are small and empty. The percentage of well-developed (staining) pollen grains out of 200 was estimated on 2 sets of 10 flowers each, collected at an interval of 2 – 5 days (Table 1).

The seeds obtained from the interspecific pollinations were scarified with sulphuric acid as previously described (NYBOM 1980) in order to maximize germination. Germination occurred the following spring and seedlings were kept until they could with reasonable safety be ascribed to apomictic or sexual origin (Table 2). Voucher specimens are deposited at LD.

Except for the easily determined seedlings containing *R. laciniatus* (with deeply dissected leaves) in their pedigree, most plants were kept for 1.5 years, during which time unfortunately part of the material was destroyed by freezing in the intervening winter before being accurately determined. The degree of frost injuries was due mainly to the location of the plants in the garden and has probably not seriously affected the proportion of apomictic vs. sexually derived offspring. However, the number of offspring reported for each crossing (Table 2) is not relevant for the actual success of that crossing.

In 1986 almost all plants had been discarded except those resulting from pollinations within the fairly homogenous subsect. *Suberecti*. On some of these plants pollen stainability tests were performed on 3 – 10 flowers per plant (Table 4).

Results

Pollen stainability and sexuality. Ovule number, seed set after isolation, pollen stainability and mean percentage of hybrids in the offspring are given for each species in Table 1. Since hybrid percentages sometimes varied strongly with different pollen parents, the results from individual crossings are shown separately (Table 2).

Pollen stainability may be regarded as an estimate, albeit crude, of meiotic regularity. As this could in its turn affect the degree of sexuality, Spearman rank correlation coefficients were calculated on a relationship between pollen stainability

Table 1. Chromosome number (from Gustafsson 1943), number of ovules per flower, number of seeds per flower after isolation and pollen stainability for each *Rubus* species investigated. Also the average percentage of resulting hybrids when used as a seed, and a pollen parent, respectively as well as the number of determined offspring. *R. divaricatus* = *R. nitidus* Weihe & Nees pro parte, nom. illeg., *R. vigorosus* = *R. affinis* Weihe & Nees pro parte, nom. illeg., *R. grabowskii* = *R. thyrsanthus* Focke, nom. illeg., *R. pedemontanus* = *R. bellardii* Weihe pro parte, typo excl., *R. infestus* = *R. taeniarum* Lindeb., a later synonym (H. E. Weber, pers. comm.)

Species	Chrom. no.	Ovules/ flower	Seeds/ flower isolation	% Pollen stainability	% Hybrids seed parent	N	% Hybrids pollen parent	N
R. nessensis W. Hall	2n=28	46	9.6	41	22	18	29	35
R. scissus W. C. R. Watson	2n=28	67	7.1	34	34	35	0	3
R. plicatus Weihe & Nees	2n=28	75	13.7	33	18	77	28	25
R. sulcatus Tratt.	2n=28	103	6.8	33	21	38	22	92
R. divaricatus P. J. Mueller	2n=21	49	0.1	6	0	27	–	0
R. vigorosus P. J. Mueller & Wirtgren	2n=28	60	19.5	48	13	76	25	145
R. axillaris Lej.	2n=28	46	10.5	21	–	0	23	30
R. insularis F. Aresch.	2n=28	80	15.4	28	0	53	5	77
R. lindebergii P. J. Mueller	2n=28	56	3.2	14	17	23	0	5
R. laciniatus Willd.	2n=28	76	16.3	23	27	270	36	14
R. sprengelii Weihe	2n=28	66	7.2	25	28	28	35	20
R. pyramidalis Kaltenb.	2n=28	70	20.5	24	22	37	28	170
R. polyanthemus Lindeb.	2n=28	69	14.4	41	36	14	17	47
R. grabowskii Weihe ex Gunther & al.	2n=21	55	1.1	11	2	123	15	27
R. pedemontanus Pinkwart	2n=35	80	7.6	43	4	48	10	51
R. hartmanni Sudre	2n=28	45	9.0	49	–	0	0	25
R. radula Weihe & Nees	2n=28	67	2.4	30	20	74	0	18
R. infestus Weihe & Nees	2n=28	49	1.9	41	0	1	0	28
R. vestitus Weihe & Nees	2n=28	78	22.2	40	15	55	6	162
R. wahlbergii Arrh.	2n=35	46	2.1	53	20	30	15	53

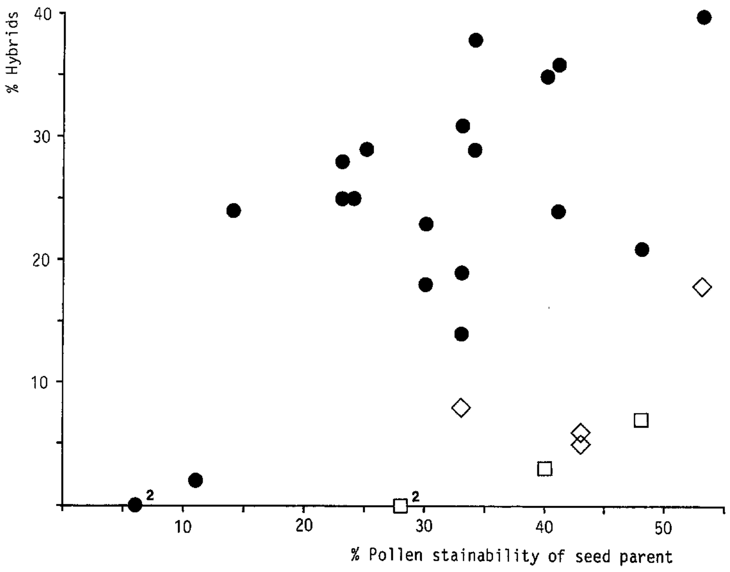

Fig. 1. Hybrid percentage of each crossing of *Rubus* spp. (determined offspring $\geqslant 10$) plotted against pollen stainability of the seed parent. "2" denotes 2 points in the same space. □ Crossings involving *R. insularis,* ◇ *R. pedemontanus,* ● other species only

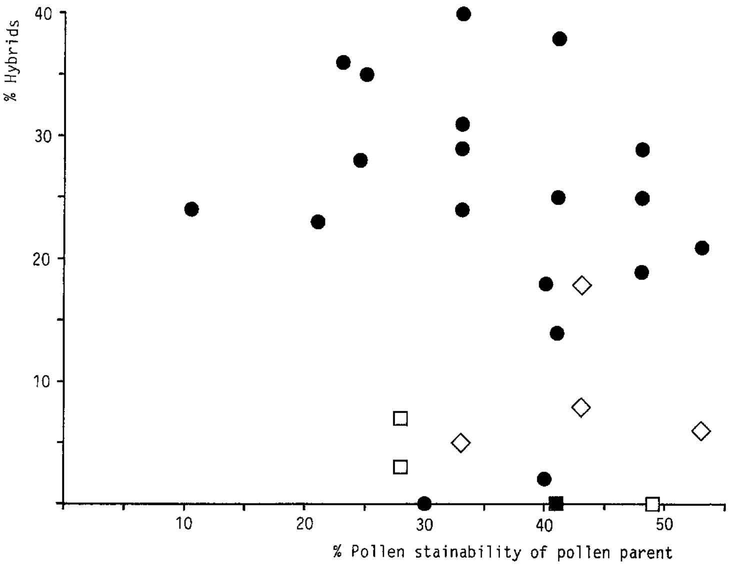

Fig. 2. Hybrid percentage of each crossing of *Rubus* spp. plotted against pollen stainability of the pollen parent. Symbols as in Fig. 1

of a certain species and the hybrid percentage in the offspring ($\geqslant$ 10 offspring) when used as seed parent; $r_s = 0.186$, and as pollen parent; $r_s = -0.335$, both non-significant. In Fig. 1 the hybrid percentage for each individual crossing ($\geqslant 10$ offspring) is plotted against the pollen stainability of the seed parent. Now an association is discerned and it may be noted that all serious outliers contain either *R. insularis* or *R. pedemontanus*, species that appear to yield consistently low hybrid

Table 2. For each crossing of *Rubus* spp. seed set, expressed per flower and per ovule, are given, as also hybrid percentage and number of determined offspring. For species abbreviations see Table 1

Crossing	Seed set per flower	Relative seed set %	% Hybrids	No. offspring
nes × *sci*	9.9	21.5	0	1
nes × *sul*	9.0	19.6	24	17
sci × *nes*	6.5	9.7	38	21
sci × *sul*	7.7	11.5	29	14
pli × *sul*	7.8	10.4	31	35
pli × *ped*	3.1	4.1	8	40
pli × *wah*	0.4	0.5	0	2
sul × *nes*	3.0	2.9	14	14
sul × *sci*	6.1	5.9	0	2
sul × *pli*	14.8	14.4	50	6
sul × *vig*	10.4	10.1	19	16
sul × *ped*	2.8	2.7	–	0
sul × *wah*	0.5	0.5	–	0
div × *pol*	1.5	3.0	0	15
div × *rad*	1.3	2.7	0	12
vig × *pli*	17.3	28.8	–	0
vig × *ins*	17.8	29.7	7	42
vig × *inf*	12.5	20.8	–	0
vig × *wah*	2.9	4.8	21	34
axi × *div*	0.9	2.0	–	0
ins × *inf*	18.1	22.6	0	28
ins × *har*	16.5	20.6	0	25
lin × *gra*	1.2	2.1	24	17
lin × *rad*	1.7	3.0	0	6
lac × *vig*	14.5	19.0	25	100
lac × *pyr*	16.5	21.7	28	170
spr × *vig*	9.6	14.5	29	28
pyr × *pol*	16.7	23.9	25	32
pyr × *gra*	1.3	1.9	0	5
pol × *pyr*	8.0	11.6	–	0
pol × *lac*	2.7	3.9	36	14
gra × *lin*	0.6	1.1	0	5
gra × *ves*	13.1	16.8	2	118
ped × *pli*	5.3	6.6	0	9
ped × *sul*	5.6	7.0	5	22
ped × *wah*	3.5	4.4	6	17
rad × *div*	0.6	0.9	–	0
rad × *axi*	6.4	9.6	23	30
rad × *ves*	4.8	7.2	18	44
inf × *vig*	1.1	2.2	0	1
ves × *div*	2.3	2.9	–	0
ves × *spr*	14.2	18.2	35	20
ves × *ins*	17.5	22.4	3	30
ves × *gra*	3.2	4.1	0	5
wah × *pli*	4.0	8.7	40	10
wah × *sul*	3.0	6.5	0	4
wah × *ins*	5.6	12.2	0	5
wah × *ped*	2.3	5.0	18	11

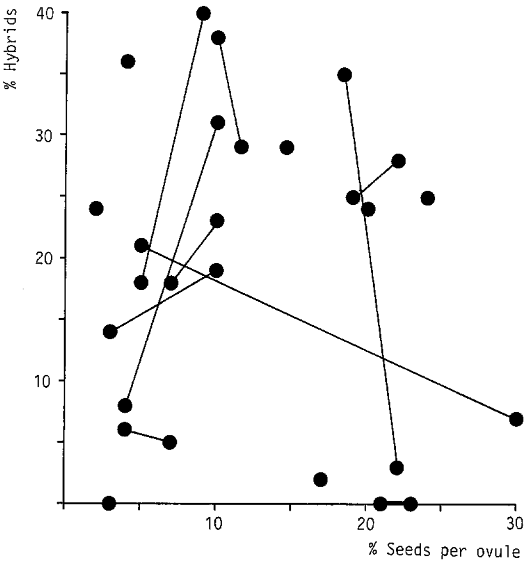

Fig. 3. Hybrid percentage of each crossing of *Rubus* spp. (determined offspring ⩾10) plotted against average percentage seeds per ovule. Points representing the same seed parent are joined

Table 3. For each *Rubus* species the hybrid percentage it yielded (determined offspring ⩾10) is given for each combination with the partner within parentheses, when used as a seed, and as a pollen parent respectively. χ^2-tests were performed for deviations in hybrid percentage between the offspring emanating from one species. *** $p<0.001$

Species	% Hybrids, seed parent	% Hybrids, pollen parent
R. nessensis	24 (*sul*)	14 (*sul*) 36 (*sci*)
R. scissus	36 (*nes*) 29 (*sul*) $\chi^2=0.33$ ns	
R. plicatus	31 (*sul*) 8 (*ped*) $\chi^2=7.04$***	40 (*wah*)
R. sulcatus	14 (*nes*) 19 (*vig*)	24 (*nes*) 29 (*sci*) 31 (*pli*) 5 (*ped*) $\chi^2=5.93$ ns
R. divaricatus	0 (*pol*) 0 (*rad*)	
R. vigorosus	7 (*ins*) 21 (*wah*) $\chi^2=2.99$ ns	19 (*sul*) 29 (*spr*) 25 (*lac*)
R. axillaris		23 (*rad*)
R. insularis	0 (*har*) 0 (*inf*)	7 (*vig*) 3 (*ves*)
R. lindebergii	24 (*gra*)	
R. laciniatus	25 (*vig*) 28 (*pyr*) $\chi^2=0.22$ ns	36 (*pol*)
R. sprengelii	29 (*vig*)	35 (*ves*)
R. pyramidalis	25 (*pol*)	28 (*lac*)
R. polyanthemus	36 (*lac*)	0 (*div*) 25 (*pyr*)
R. grabowskii	2 (*ves*)	24 (*lin*)
R. pedemontanus	5 (*sul*) 6 (*wah*)	8 (*pli*) 18 (*wah*)
R. hartmanii		0 (*ins*)
R. radula	23 (*axi*) 18 (*ves*) $\chi^2=0.29$ ns	0 (*div*)
R. infestus		0 (*ins*)
R. vestitus	3 (*ins*) 35 (*spr*)	2 (*gra*) 18 (*rad*)
R. wahlbergii	40 (*pli*) 18 (*ped*)	21 (*vig*) 6 (*ped*)

Table 4. Average pollen stainability and standard deviations, within parentheses, for each investigated plant. As no plants of *R. nessensis* were available in this material, 3 plants resulting from selfing in another material were investigated (top line). For species abbreviations see Table 1

Crossing	Apomictically derived offspring	Sexually derived offspring
nes × *nes*	35.8 (6.2) 40.1 (4.7) 37.8 (3.5)	
nes × *sul*		63.7 (4.9)
sci × *nes*	54.4 (4.9) 50.9 (5.5) 54.8 (5.2) 52.0 (6.3)	89.5 (2.8) 80.9 (8.9) 87.5 (7.1) 90.6 (2.4) 90.6 (2.6)
sci × *sul*	54.3 (4.7) 50.4 (5.2) 54.9 (4.4) 53.8 (4.4)	69.1 (7.3) 73.9 (8.3)
pli × *sul*	38.6 (4.2) 40.4 (4.2) 41.6 (5.4) 35.4 (6.1) 41.6 (6.6)	62.8 (4.2) 53.8 (9.5) 63.9 (9.9)
sul × *nes*	28.6 (4.7) 22.8 (3.3) 29.1 (4.9)	54.8 (7.3)
sul × *pli*	32.3 (3.8)	59.8 (5.4)
sul × *vig*	27.3 (3.7) 27.2 (5.1)	41.1 (2.7) 36.8 (11.8)

percentages when used as seed or pollen parents (Table 2). By contrast, the hybrid percentages show no relationship at all with the pollen stainability values of the pollen parents (Fig. 2).

Sexuality and seed set. To find out whether seed set is affected by the degree of sexuality, the percentage of hybrids in the offspring was plotted against relative seet set (Fig. 3). No association seems to exist. Some species show an increase in seed set with percentage of hybrids while others show the opposite trend.

Degree of sexuality. A compilation of all crossings that yielded at least 10 determined offspring is shown in Table 3. Outstandingly low hybrid percentages are shown by the triploid species *R. divaricatus* and *R. grabowskii*, by the tetraploid *R. insularis*, and by the pentaploid *R. pedemontanus* when used as seed parents. Apart from crossings including these, most species yielded 20–30% hybrids. χ^2-tests for deviations in hybrid percentage between the different offspring involving the same seed or pollen parent were performed where permissible (no expected frequency <5) (Table 3).

Pollen stainability in the offspring. In Table 4 the results from the pollen stainability tests on the offspring are given. Clearly hybrids have higher pollen stainabilities than their apomictically derived counterparts.

Discussion

Embryo sac development. In *Rosaceae* the archespore is multicellular, thus multiple embryos may be formed. However, in diploid blackberries usually only one, reduced embryo sac occurs per ovule (Christen 1950, Kerr 1954, Pratt & Einset 1955). In polyploid species meiosis is often attempted and sometimes succeeds so that reduced, apparently functional embryo sacs are formed. However, unreduced embryo sacs may subsequently develop, suppressing possible reduced ones, especially if these are weak and slow to develop, as might be expected if meiotic disturbances occur (CHRISTEN 1950, PRATT & EINSET 1955, CZAPIK 1983). At anthesis the ovules of polyploid species often lack viable embryo sacs or have multiple ones (THOMAS 1940, KERR 1954, PRATT & EINSET 1955, CZAPIK 1983). The origin of embryo sacs present at this stage cannot be determined, as possible tetrad remnants have already disintegrated. Since unreduced embryo sacs are common in earlier stages one may assume that the majority of functional embryo sacs at anthesis are unreduced in most polyploid species (PRATT & EINSET 1955).

Similarly triploid plants of *R. idaeus* (subg. *Idaeobatus*), sometimes encountered in nature, produced mainly unreduced embryo sacs (PRATT & al. 1958) as did also a triploid cultivar (PETROV 1939). The sexual but polyploid species *R. saxatilis* (4 x, subgenus *Cylactis*) and *R. chamaemorus* (8 x, subg. *Chamaemorus*) produce a considerable number of apomeiotic initials, which however usually degenerate at an early stage (CZAPIK 1983). Even diploid blackberries and raspberries occasionally produce unreduced embryo sacs that may develop after fertilization (CRANE & DARLINGTON 1932, ROZANOVA 1938, CRANE 1940)

Regulation. A high degree of disturbances in pollen meiosis has frequently been reported for polyploid blackberries in the form of multivalents, univalents and sometimes inversion bridges (THOMAS 1940, GUSTAFSSON 1943, BERGER 1953, CRAIG 1960, BAMMI & OLMO 1966). Similarly, a disturbed meiosis can be expected to decrease the production of reduced embryo sacs. THOMAS (1940) suggested a connection between cytology and the degree of sexuality; the less similar the homologous genomes of an alloploid species, the more regular the meiosis and the higher the degree of sexuality. The association, although weak, found in the present study between pollen stainability of the seed parent and the percentage of hybrids in the offspring points in the same direction. In line are also the highly polyploid but still comparatively sexual taxa (see below, Paternal influence) of the N. American sect. *Ursini* which are characterized by a regular meiosis (DARROW & LONGLEY 1933) and a high pollen stainability (GUSTAFSSON 1943). On the other hand the European dewberry, *R. caesius* (4 x, apomict) usually placed in a subsection or even section of its own, *Caesii*, is highly apomictic in spite of a regular meiosis (GUSTAFSSON 1943, CHRISTEN 1950), a high pollen stainability (LIDFORSS 1905) and accordingly a high production of reduced embryo sacs (CHRISTEN 1950, CZAPIK 1983). However, GERLACH (1965) showed that a mitotic restitution of the egg cell sometimes occurs, in combination with parthenogenesis. In sect. *Rubus* (proper blackberries) restitution has not been reported, except as inferred by DOWRICK (1966) in a paper which needs further confirmation since the discussion is based on incorrect citations of other authors.

Fertilization. Triploids. Interspecific crossing experiments between apomictic taxa involving triploids as seed parents normally yield apomictically derived offspring (LIDFORSS 1907, GUSTAFSSON 1943, EINSET 1951), the few hybrids obtained probably mainly resulting from the fertilization of unreduced embryo sacs (EINSET 1951).

Similarly very low hybrid percentages were obtained for the triploid species in the present study.

Tetraploids. Tetraploid species as seed parents usually yield 10 – 40% hybrids (DARROW & WALDO 1933, CRANE 1940, GUSTAFSSON 1943, EINSET 1951, DOWRICK

1966, JENNINGS & al. 1967), apparently formed mainly from reduced embryo sacs (JENNINGS & al. 1967). Interesting exceptions are *R. insularis* which produced no hybrids and *R. vigorosus* and *R. lindebergii* with 1% or less, and *R. polyanthemus*, on the other hand, with up to 75% hybrids (LIDFORSS 1905).

In the present study the tetraploid species yielded an average of 21% hybrid offspring. Among these *R. insularis* again appears strongly apomictic. Contrary to earlier finds, *R. vigorosus, R. lindebergii,* and *R. polyanthemus* are well in line with other tetraploids even if the first-mentioned are among the more apomictic and the last one among the least.

Pentaploids. The pentaploid *R. pedemontanus* yielded no hybrids when used as a seed parent in an earlier investigation (GUSTAFSSON 1943) and comparatively few in the present study.

The other pentaploid, *R. wahlbergii,* produced 29% hybrids. This species belongs to the *R. corylifolius* agg., a hybrid aggregate involving *R. caesius,* the proper blackberries and, partly, *R. idaeus* (GUSTAFSSON 1943). It deviates from sect. *Rubus* by an increased proportion of 5 x and 6 x taxa, a higher pollen fertility, and a higher degree of sexuality, probably sometimes due to the fertilization of unreduced embryo sacs (GUSTAFSSON 1943).

Paternal influence. BERGER (1953) concludes his embryological work on *Rubus* hybrids by stating that species affinity and genetical composition of the pollen parent is the most important factor in determining whether an egg cell becomes fertilized or not. Evidence of this is given by *R. vitifolius* (8 x, sect. *Ursini*) which yields hybrids when pollen from diploid raspberries is applied, but a mixed offspring with pollen from autotetraploid raspberries (CRANE 1940). Similar results have been reported also for tetraploid blackberries with an increased proportion of apomictically derived offspring with increasing chromosome level of the pollen parent (DOWRICK 1966, JENNINGS & al. 1967), interpreted by the latter as a hormonal dosage effect.

Opposite trends are found in triploid species. Thus CRAIG (1960) obtained only triploid, apparently apomictically derived offspring after selfing the blackberry *R. canadensis* but 36% hybrids, all pentaploid, when pollinating with a set of tetraploid cultivars. PETROV (1939) and PRATT & al. (1958) obtained similar results when investigating triploid specimens of *R. idaeus.*

In the present study tetraploid seed parents yielded 15% hybrids with triploid pollen, 23% with tetraploid pollen, 8% with the pentaploid *R. pedemontanus,* and 19% with the pentaploid *R. wahlbergii* belonging to *R. corylifolius* agg.

Large differences in hybrid yield may exist also within ploidy levels. Thus *R. insularis* in the present study yielded only 7% and 3% hybrids when pollinating *R. vigorosus* and *R. vestitus,* two species that in other combinations produced far more hybrids. It should be noted that *R. insularis* also as a seed parent is highly apomictic.

From all these investigations a general pattern emerges. Pollen derived from species with severe meiotic disturbances seems less apt to produce hybrids than pollen from species with a more regular meiosis. Thus autotetraploid raspberries and polyploid blackberries that have a lower pollen stainability than their diploid counterparts produced fewer hybrids. Pollen of cultivars which usually exhibit a high stainability due mainly to their hybrid origin (NYBOM 1986 a) as also *R.*

corylifolius agg., on the other hand, produced comparatively many hybrids. It seems quite logical that somewhat unbalanced pollen could participate in endosperm formation but not in the production of viable embryos. However, no association was found in the present study between pollen stainability of the pollen parents and the percentage of hybrids in the offspring. This is probably due to the varying amounts of reduced embryo sacs in the seed parents, this being an even more important factor in determining reproductive mode.

Unfortunately, no information exists on the levels of sexuality after intraspecific pollinations. Due to paternal influence this may be rather different from that obtained after interspecific pollination.

In some genera the amount of apomictically derived offspring in interspecific crossings rises with increasing genetic distance between the parental species (Asker 1979). No such tendency was found within subg. *Rubus* (Lidforss 1907, Haskell 1960).

Evidence of paternal influence is given also for other subgenera by Rozanova (1938) who reports that the ability of *R. caesius* to fertilize unreduced egg cells of *R. idaeus* depends on the geographic race of the pollen donor plants.

The influence of the pollinator on the hybrid yield has been reported also in the pseudogamous grass *Poa,* for which it has been suggested that vitality of the sexually formed embryo might influence its ability to successfully compete with asexually formed ones in the same ovule (Grazi & al. 1961). A similar competition might be visualized in *Rubus* also between the developing drupelets within a berry.

Hybrids. Sect. *Rubus.* Primary hybrids between apomictic species seem to be completely sexual, as deduced from the extensive crossing experiments carried out by Lidforss (1905, 1907). In the present study the hybrids always surpassed the parental species in pollen stainability. Similar results have been presented by Lidforss (1905) and Peitersen (1921). The rise in pollen fertility is probably due to a more regular meiosis, as previously reported for polyploid *Rubus* hybrids (Crane & Darlington 1927, Rozanova 1938, Bammi & Olmo 1966) which may increase the production of reduced embryo sacs and thus also the level of sexuality. On the other hand Thomas (1940) reports of a hybrid which had as much meiotic disturbances and accordingly as low pollen fertility as the parental species. Unfortunately the reproductive mode of this hybrid was not investigated.

R. corylifolius. High levels of sexuality are found also in *R. corylifolius* with 17 – 100% hybrids after crossing experiments (Lidforss 1905, 1907). Very variable progeny was sometimes obtained from naturally occurring specimens, also indicating high levels of sexuality (Lidforss 1905, 1907). Berger (1953) found almost no reduced embryo sacs in tetraploid specimens but a considerable number in a hexaploid. This is consistent with the increase in pollen stainability with ploidy level reported by Gustafsson (1943).

Also in some graminiferous genera high levels of sexuality have been reported for hybrids between apomictic taxa (Åkerberg 1942, Clausen 1954, Williamson 1981).

Escape from sterility. The "escape from sterility" has been advocated as the main reason for apomixis developing in polyploid hybrid complexes (De Wet & Stalker 1974). In subg. *Rubus* diploid hybrids are seldom formed and appear to be highly sterile (Crane 1940, Gustafsson 1943). On the other hand hybrids on the polyploid level are quite fertile (except for triploids), sometimes producing more seeds than their apomictic parents (LIDFORSS 1905, 1907, BAMMI & OLMO 1966). This is probably due to the improved meiosis leading to a higher pollen fertility and thus an increased seed set (NYBOM 1985, 1987). Improved meiosis could also result in an increased total production of viable embryo sacs and thus raise seed set (NYBOM 1987). However, natural hybrids between apomictic taxa are very scarce in nature (GUSTAFSSON 1943, WEBER 1973, NEWTON 1975). Thus sexuality, even though combined with an increased fertility, appears not to be more successful than apomixis, but rather the opposite.

Apomixis in *Rubus* should thus involve benefits large enough to counter-balance the decrease in fertility caused by the meiotic disturbances that seem necessary for a successful production of unreduced embryo sacs. However, since blackberries are long-lived perennials with vigorous vegetative reproduction through tip-rooting of stem apices or through root-suckering, such reduction in seed set may not be very serious.

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