Gametophytic apomixis: elements and genetic regulation

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Introduction

1. Definitions and control of apomictic phenomena

The classical definition of apomixis includes all kinds of asexual reproduction in higher plants that are able to replace sexuality more or less permanently in nature—asesexual seed formation (agamospermy) and vegetative reproduction (GUSTAFSSON 1946). In agamospermy, the embryos are either formed directly from somatic cells (nucellar embryony) or by parthenogenetic development of egg cells in unreduced embryo-sacs (gametophytic apomixis). In the latter case, the embryo-sacs are either formed from primary embryo-sac mother cells (EMC:s) by circumvention of meiosis (diplospory) or from somatic cells in the ovule (aposporo).

Apomixis may be obligate or facultative—in the latter case, egg cells in reduced embryo-sacs are usually fertilized, whereas egg cells in unreduced embryo-sacs develop parthenogenetically. Fertilization of the central nucleus (or polar nuclei) may be essential for seed formation (pseudogamy) or superfluous (autonomous apomixis). Pseudogamy is often combined with facultative apomixis.

According to the opinion of some authors, vegetative reproduction should not be included among the apomictic phenomena (cf. RUTISHAUSER 1967, p. 5–6). Even the inclusion of nucellar embryony has been questioned.

A functional gametophytic apomixis implies various changes of the sexual cycle. The most important ones are the predominant formation of unreduced embryo-sacs, and the highly developed capacity of their egg cells for parthenogenetic development. These two processes are under independent genetic control.

In angiosperms with sexual reproduction, unreduced embryo-sacs and egg cells are often formed, and parthenogenetic development of reduced egg cells sometimes gives rise to haploid offspring. These two phenomena may also be combined to give diploid offspring of maternal type. Studies of such processes in sexual plants are obviously within the scope of apomixis research. Also must be taken into consideration cases where all (androgenesis) or part of the offspring (semigamy) receives its genetic material only from the male parent.—The reproductive possibilities of sexual and apomictic plants are summarized in Table 1.

Gametophytic apomixis is strongly correlated with the occurrence of hybrid and polyploid complexes. It was formerly thought to be a direct result of hybridization or increased level of ploidy. Today, all scientists in this field agree that apomixis is to some extent genetically regulated. Obviously, apomictic phenomena are also under environmental control, being influenced by factors like light and temperature regimen, and by the choice of pollinator (in facultative apomicts).

Although interesting models have been pro-
Table 1. Modes of reproduction in sexual and apomictic plants

| Character | Sexual plants | Apomictic plants |
|-----------|---------------|------------------|
| **EMBRYO FORMATION** | | |
| Reduced egg cells | Usual case | Facultative apomicts |
| | Sporadic (frequent for instance after foreign pollination) | Sporadic (in Hieracium and Potentilla following chromosome doubling) |
| Parthenogenesis | | |
| Unreduced egg cells* | Sporadic (frequent in distant crosses and after meiotic disturbances) | Sporadic (giving rise to “autotriploids” and U-hybrids) |
| | Sporadic (i.e. “matromorphy” in Brassica) | Usual case in gametophytic apomixis (diplospory and apospory) |
| Both male and female nuclei (semigamy) | Occasional (spontaneous or induced) | Sporadic (Rudbeckia, Zephyranthes) |
| Male nuclei (androgenesis) | Occasional (after hybridization or inactivation of female nucleus) | ? |
| Somatic cells | Occasional | Usual case in nucellar embryony |
| **ENDOSPERM FORMATION** | | |
| Central nucleus (or polar nuclei) | Usual case | Pseudogamy |
| | Occasional | Autonomous apomixis |
| Parthenogenesis | | |
| **VEGETATIVE REPRODUCTION** | | |
| | Frequent | Frequent |

* Unreduced embryo-sacs are either formed by restitution after I or II division or by mitotization of meiosis—diplospory—or from embryo-sacs derived from somatic cells—apospory

posed, we don’t know with certainty the exact genetic regulation of apomixis in any case, with the possible exception of apospory. It is very important, in my opinion, to keep in mind that the different constituents, or elements (Petrov 1976) of apomixis, lie within the reproductive potentiality of sexual plants. Here, they play a greater part only when the normal sexual process with fusion of reduced gametes is impaired. Where they occur occasionally in sexual plants, such elements cannot be expected to be under simple genetic control.

2. Origin and advantages of apomixis

A perfectly operating gametophytic apomixis is usually not likely to arise in one single step. Genes promoting effective apomictic reproduction are successively incorporated by mutation or recombination. According to a hypothesis developed for Parthenium by Powers (1945), apomixis depends upon homozygosity for recessive genes influencing its constituents. The sexual ancestors of apomicts are usually cross-fertilizers—preferably self-incompatible or dioecious, because a high level of outcrossing should be necessary to bring together the genes for apomixis. Certain intermediate combinations of such genes are, according to Powers, liable to reduce fertility. As the sexual plants giving rise to apomicts are also often more or less sterile due to hybrid structure or polyploidy, they should usually be perennial plants with good capacities for vegetative reproduction (Table 2).

What, if any, are then the evolutionary advantages of acquiring the capacity for apomictic reproduction? According to Mather (1943), each population has to find a compromise between immediate fitness—with genetic constancy but difficulties of adaptation to a changing environment—and flexibility—with high genetic variability but with formation of many individuals poorly adapted to the immediate environment. The facultative apomicts have exploited an extremely effective solution to these contrasting demands, one that “enables them to store interspecific variability and, nevertheless, remain constant for ages” (Clausen 1954).

Stebbins (1958) states that adaptations promoting immediate fitness occur in temporary habitats,
where populations fluctuate greatly in size and formation of several descendants is essential. Such adaptations are apomixis, self-fertilization, and low recombination index (low chromosome number combined with low chiasma frequency).

According to DARLINGTON (1939), agamic complexes have a limited evolutionary potential, losing their capacity for further evolution when the condition of obligate apomixis is finally reached. This is true to the extent that, obviously, apomictic groups have not given rise to new higher taxonomic categories such as families.

On the other extreme stands the view of KHOKHLOV (1976). He looks upon the development of apomixis as a regular step of progressive evolution. In his opinion, the reduction of the gametophyte in apomicts is only the end point of the successive reduction of the gametophyte during the development of higher plants.

According to the commonly adopted view, species with facultative apomixis retain their capacity for progressive evolution, whereas obligate apomixis should be an irreversible and regressive process. Recent work indicates that traces of sexuality occur even in groups judged to be obligately apomictic (ASKER 1979).

Apomixis obviously involves fixation of heterosis. It is not surprising, then, that induction of apomixis in sexual crops has been considered by breeders. According to SOLNTSEVA (1978), this possibility was discussed by Navashin and Karpechenko as early as in the thirties. During later years, work of this type has been carried out in different materials.

In this paper, especially the constituents (elements) of apomixis are discussed. Their occurrence in sexual taxa is reviewed, and our knowledge concerning their genetic regulation is surveyed.

### The elements of apomixis

#### 1. Modifications of the meiosis

##### A. Sexual species

Several mutant genes are known that influence the course of meiosis in sexual species. Such mutations were first described by BEADLE (1930, 1932, 1933) in maize and by SATINA and BLAKESLEE (1935) in *Datura*. Some examples are given in Table 3.

Many of these mutations affect synopsis. According to CATCHESIDE (1977), true **asynapsis**—failure of synopsis at zygotene and failure of chiasma formation—is a rare case. More common are **desynaptic mutants**, where synopsis occurs but no or few chiasmata are formed.

Especially well known is the genetic control of the cytologically diploid behaviour of hexaploid wheat. A gene on chromosome 5B suppresses homoeologous or at the other extreme, promotes homologous pairing (RILEY and CHAPMAN 1958).

The gene elongate (*el*) in maize causes a high frequency of unreduced egg cells (RHOADES 1956) and has been used for various experimental purposes. It omits the second division, which should lead to the onset and conservation of a high level of homozygosity.

Mutants are also known that affect post-meiotic development of spores. Especially in fungi, mutations are known that influence recombination in various ways other than meiotic changes.

Unreduced egg cells are fairly frequent in sexual plants (HARLAN and DE WET 1975; FRANKE 1975). The formation of unreduced gametes in plants is usually thought to depend on restitution following the first or second meiotic division. But unreduced egg cells may also be derived from embryo-sac mother cells with twice the somatic number, or from occasional aposporous embryo-sacs.
Table 3. Examples of meiotic mutants in sexual angiosperms

| Type of anomaly                  | Genus         | References        |
|----------------------------------|---------------|-------------------|
| Total inhibition of meiosis      | Zea           | PALMER 1971       |
| Asynapsis/desynapsis            | Several genera| BEADLE 1930 a.o.  |
| Control of pairing               | Triticum      | RILEY and CHAPMAN 1958 |
| Precocious centromere division   | Lycopersicum  | CLAYBERG 1960     |
| Lack of cytokinesis following    | Several genera| SATINA and BLAKESLEE 1935 a.o. |
| first or second division         |               |                   |

Meiotic disturbances, such as in species hybrids and autotriploids, greatly increase the formation of unreduced gametes through restitution. Often all functional egg cells are unreduced in such cases.—In wide crosses, even where meiosis is not disturbed, sometimes only unreduced egg cells give rise to hybrids. The function of unreduced egg cells is thus dependent on the type of pollination.

Autotriploids—sometimes, perhaps, “future apomicts”—originate by fertilizations of unreduced egg cells. Their occurrence reveals the presence of unreduced gametes even in diploids with perfectly regular meiosis. Function of unreduced gametes is, on the whole, the most important mechanism in the formation of polyploid series.

B. Apomictic species

We now turn to the modifications of meiosis in apomictic plants. In diplospory, the course of the first nuclear division in the EMC:s may take three different forms, according to GUSTAFSSON (1946). These are a formation of restitution nuclei, pseudohomeotypic division, and mitotic division. The distinction of the pseudohomeotypic division was, however, questioned by RUTISHAUSER (1967).

In Taraxacum, for instance, stages similar to a normal first division of meiosis are observed, but most chromosomes occur as univalents. The distribution of homologous chromosomes at the end of the first division is interrupted, and all chromosomes are enclosed within a common nuclear membrane. But the second division proceeds normally, giving a dyad of cells one of which gives rise to the embryo-sac.—In Antennaria and Eupatorium on the other hand, the EMC grows out directly into a gametophyte without cell divisions. Thus, the first division of the EMC is here of mitotic type.

In all diplosporous apomicts with restitution nuclei so far studied, restitution takes place after the first meiotic division (FDR). However, in occasional formation of unreduced egg cells in sexual plants, both FDR and SDR (restitution after the second division) occur.

As suggested earlier, mutations are also known that induce either FDR or SDR. SDR should lead to homozygosity, whereas FDR preserves heterozygosity and fixes heterosis. These statements are quite true, however, only if no bivalent formation or at least no crossing-over between homologues takes place. The suppression of chromosome pairing, which has been observed in diplosporous plants with restitution nuclei, is maybe another genetically determined meiotic adaption.

Inhibition of meiosis in primary EMC:s sometimes occurs even in the case of apospory. In certain Potentilla biotypes, meiosis seems to be initiated in primary EMC:s and proceeds to a pachytene-like stage. Here, the divisions stop and the EMC:s gradually degenerate. Meiosis on the male side is much less disturbed in these pseudogamous forms. By inhibition of meiosis in primary EMC:s the competition between reduced and unreduced embryo-sacs might be eliminated. Constancy of offspring is ensured at the expense of evolutionary rigidity.

In plants with autonomous apomixis, various degrees of degeneration of the male meiosis are observed (some species even lack pollen mother cells). The breakdown of meiosis must depend on the uselessness of pollen for reproduction. The degenerative phenomena are more pronounced in diplosporous apomicts. This may simply be due to the fact that autonomous apomixis is common here, whereas apospory is combined with pseudogamy to a much higher extent.

The occurrence of these meiotic changes in connection with the transition from sexuality to apomixis makes it difficult to conclude to what
Table 4. Meiotic disturbances in apomicts

| Kind of apomixis | Sex showing disturbances | Changes of meiosis |
|------------------|--------------------------|-------------------|
| Diplospory       | ♂                       | Restitution after 1st meiotic division or substitution of mitotic for meiotic divisions |
|                   |                          | Suppression of chromosome pairing and chiasma formation (in the case of restitution) |
| Apospory         | ♂                       | Meiosis sometimes arrested at a pachytene-like stage |
| Autonomous apomixis (either diplo- or apospory) | ♂ and ♀ | Various degrees of inhibition |
| All types        | ♂ and ♀                 | Meiotic irregularities due to hybrid or polyploid structure |

extent meiotic disturbances were present in the sexual population giving rise to the apomicts (see Table 4). We know almost nothing about the genetic background of the secondary changes of meiosis. The genetics of permanent and casual diplospory is discussed later in this paper.

The course of meiosis in sexuals and facultative apomicts depends also upon environmental influences. These affect in apospory the frequency of reduced egg cells formed after completed meiosis and, in diplospory, the balance between reduction and restitution.

2. Aposporous embryo-sacs

In apospory, one or more somatic cells in the ovule usually enlarge considerably and become vacuolated, giving rise to a uninuclear embryo-sac. If their development is completed, usually 8-nucleated embryo-sacs of the common Polygonum-type are formed, which are morphologically similar to the meiotic embryo-sacs. In Gramineae (Poaceae), subfamily Panicoideae, the aposporous sacs are usually four-nucleated and monopolar, which facilitates their separation from sexual embryo-sacs and the estimation of the degree of apospory in squash preparations. — In certain genera of Rosaceae, the complex structure of the archespore makes the distinction between embryo-sacs with diplosporous and aposporous origin difficult.

Aposporous embryo-sacs have been observed in several sexual species. Especially, they have been found within Compositae (Asteraceae)—a list of species is given by Davis (1967). For instance, they occur in Cirsium arvense and other Cirsium species (Zabinska 1977). Aposporous sacs occur in the intergeneric hybrid Raphanobrassica (Ellerstrom and Zagorcheva 1977) and in certain hybrids of Sanguisorba (Nordborg 1967). Sometimes, aposporous initials or embryo-sacs degenerate without giving any offspring. Their formation and function is enhanced by, if not caused by, defective functioning of the meiotic sacs.

Apospory, meaning the presence of aposporous embryo-sacs (as contrasted to sexuality = absence of aposporous sacs) is a phenomenon quite independent of the course of meiosis and the disposition to parthenogenetic development of egg cells. As discussed later, it seems to have a simple genetic regulation in certain cases.

3. Parthenogenesis

A. Haploid formation

Parthenogenetic development of egg cells takes place occasionally in sexual plants, whereas in plants with regular gametophytic apomixis, it is a necessity. The latent tendency towards parthenogenesis in sexual plants is explicitly displayed by the production of haploids in a multitude of plant species. Reviews in this field have been written by, e.g., Kimber and Riley (1963) and—concerning maize—by Chase (1969). The parthenogenetic development of a reduced gamete from a diploid plant by definition gives rise to a monoploid (Langlet 1927) or simply a haploid, whereas a polyploid plant under the same conditions gives rise to a polyhaploid (Katayama 1934).

Haploids arise by spontaneous parthenogenesis, but their formation is promoted by various cir-
cumstances. They are known to occur at increased frequency among twin plants, resulting from polyembryonic seeds. In this case, the haploid embryos may develop from synergids. Special types of pollination can induce parthenogenesis: wide crosses, delayed pollination, use of pollen treated with X-rays, ultraviolet light, or toluidine blue (Kimber and Riley 1963). Haploids have also been obtained after treatments designed to give polyploids, viz. colchicine treatment and temperature shocks (Table 5). It is usually not possible here to decide if the egg cell or some other cell in the embryo-sac has given rise to the embryo.

Studies of meiotic chromosome behaviour in haploids have revealed paired affinities not observed in the “diploid” plants, and, thus, contributed to our cytogenetic knowledge of certain groups. By doubling the chromosome number of monohaploids, completely homozygous (“autodiploid”) lines for breeding and experimental purposes are obtained.

Cultivated alfalfa (Medicago sativa) behaves as an autotetraploid, and dihaploids are produced from certain 4x x 2x crosses. Primary haploids are rather infertile. By crossing them as females with 2x Medicago falcata and repeated back-crosses with dihaploids combined with selection, stable and vigorous diploids containing more than 98% cultivated germ-plasm have been obtained (Bingham and McCoy 1979).

From tetraploid Solanum tuberosum (2n = 48), it has even been possible to produce monohaploids with 12 chromosomes by two successive cycles of female parthenogenesis, obtained by pollination with S. phureja (Breukelen et al. 1975). Such a repeated halving of the chromosome number (or “subhaploid” formation) has earlier been observed in apomictic Poa species (Kiellander 1942; Akerberg and Bingefors 1953).

Table 5. Origin of maternal haploids from seeds of sexual plants

| Type of Origin | Author |
|----------------|--------|
| Spontaneous    |        |
| From polyembryonic seeds (twin plants) |        |
| After exceptional types of pollination |        |
| Intergeneric, interspecific, or intervarietal pollination |        |
| Delayed pollination |        |
| Use of irradiated pollen |        |
| Use of pollen inactivated with compounds like toluidine blue |        |
| After treatments designed to give polyploids |        |
| Colchicine treatment |        |
| Temperature shock |        |

B. Matromorphy and related phenomena in sexuals

Diploid as well as haploid parthenogenesis occurs in sexual plants. Especially after intergeneric or interspecific crosses, so-called matromorphic plants are sometimes obtained, even where self-pollination after incomplete castration or contamination with foreign pollen can be excluded. According to Eenink (1974a), matromorphy, being synonymous with diploid parthenogenesis, should not be confused with matrocliny, meaning the formation of true hybrids which resemble the mother much more than the father.

We still know too little about the origin, occurrence and frequency of matromorphic plants. Possibly, the formation of such plants is a common phenomenon. Their presence after open pollination is likely to be overlooked. Matromorphy can be more common than haploid parthenogenesis, as especially monoploids are often inviable. The origin of matromorphic plants can be indicated by the use of suitable markers in crosses.

Matromorphy is best known from Brassica, where it has been extensively studied by Eenink (1974a, b, c, d, e, 1975a, b). References to other genera are given in Table 6.

Plants of maternal type are derived by asexual seed formation: (1) from EMC:s with twice the somatic chromosome number (pre-meiotic endomitosis has been observed in Brassica according to Eenink 1975b), giving rise after meiosis to “unreduced” macrospores and embryo-sacs; (2) by parthenogenetic development of egg cells in embryo-sacs, formed as a result of restitution after 1st or 2nd meiotic division; (3) by parthenogenetic development of reduced egg cells followed by reduplication or fusion.

The last possibility is interesting from the breeder’s point of view; it would give rise directly
to homozygous diploids. The formation of such diploids has been presupposed by several authors. It seems, however, that we still need a definitive genetical and embryological proof of their origin.

Automixis, fusion of two haploid nuclei in a meiotic embryo-sac to give diploid and homozygous progeny, has been claimed to occur in *Rubus* (Thomas 1940). In any case, such an automictic parthenogenesis does not at all play the same role in the plant as in the animal kingdom.

In *Brassica*, formation on unreduced embryo-sacs has been demonstrated, as well as the capacity for parthenogenetic development of their egg cells. Thus, not only the part processes of apomixis, but also their combination to a kind functional diplspory lie within the scope of reproductive behaviour in sexual plants.

In this connection, a question of terminology should be touched upon. Often plants which have originated by haploid or diploid parthenogenesis are designated as “apomictic haploids, parthogenetic diploids” and so on, irrespective of their own mode of reproduction. This can be misleading, in my opinion. One has to speak of such plants as (poly-)haploids or matromorphic, or else use the more laborious designation “plants that have arisen by . . .”.

C. Chemical treatments

Various chemical treatments have been tried in order to induce parthenogenesis in plants, but generally without success. On the other hand, parthenocarpy is easily induced by treatment by plant hormones. Deanon (1957) reported a significantly increased frequency of monoploids in maize after treatment with 50 ppm maleic hydrazide. Vermel and Solovova (1973a, b) claimed to have induced diploid parthenogenesis in some plant species by treatment with dimethyl sulphoxide (DMSO). According to their opinion, the diploids were homozygous, resulting from haploid parthenogenesis followed by chromosome doubling. The present author (unpublished work) performed DMSO treatments on *Ranunculus* material, furnished with genetic markers to judge if resulting diploids were homozygous. However, in this self-incompatible material there was no significant increase of seed set after isolation following DMSO treatment.

D. Pseudogamy and parthenogenesis in apomicts

Haploid and diploid parthenogenesis in sexual plants seem to be combined with pseudogamy. The central nucleus must be fertilized to secure endosperm and seed formation. It is not known if, in this case, the egg cell divides before fertilization.

In pseudogamous animals, the entrance of the sperm initiates parthenogenetic development. Similarly in certain plant species, for instance *Ranunculus auricomus*, the egg cell does not divide until after fertilization of the central nucleus (Rutishauser 1967).

This seems, however, to be an exception among higher plants. In apomictic angiosperms, the parthenogenetic development is usually initiated well before the opening of flowers. At anthesis, the embryo-sacs contain multicellular embryos, instead of egg cells capable of fertilization (Podubnaja-Arnoldi 1939 in Gustafsson 1946). A regular formation of maternal offspring is secured by an early division of the egg cells. In the case of pseudogamy, however, without fertilization and endosperm formation, the embryo eventually degenerates.

According to Gustafsson (1947b) “this new rhythm often gets accentuated by the mere increase in chromosome number. Superficially seen, this early egg cell division does not tally with the general effect of polyploidy, which is to delay mitosis". In sexual plants, a prolonged resting stage of the egg cell is desirable to secure fertilization. Polyploidy is thought to eliminate this long resting stage, which would be useful in an apomict.

Bennett (1977 a.o.) has shown that polyploids have a shorter duration of meiotic divisions than diploids with corresponding DNA amounts. The shorter meiotic divisions may be one cause of early egg cell division in polyploids, and this effect may remain even in diplsporous apomicts where meiosis is mitotisized.

Even in autonomous apomicts, the development of the embryo is sometimes independent of that of the endosperm (*Taraxacum*), whereas in other cases the egg cells divide after endosperm formation (Doll 1971).

Fertilization of unreduced egg cells in apomicts—possible, where egg cells do not divide prior to pollination—may add to the formation of polyploid complexes. However, it interferes with the preservation of heterosis and is not desirable to occur in higher frequencies. Powers (1945) described a *Parthenium* strain which “polyploidized itself out of existence” by repeated fertilization of unreduced egg cells in the offspring. A similar
behaviour was observed by me in offspring from a biotype hybrid in *Potentilla argentea* (Asker 1970b).

In apomicts where meiosis is not wholly suppressed, polyhaploids are sometimes formed by parthenogenetic development of reduced egg cells. In grasses belonging to the *Bothriochloa-Dichanthium*-complex diploids are regularly formed from apomictic tetraploids in this way (De Wet 1968).

**E. Androgenesis and semigamy**

In special cases, offspring obtained by parthenogenesis has the genotype of the male gamete nucleus. In the case of androgenesis, or male parthenogenesis, the early stages of fertilization take place normally. After the male nucleus has entered the egg cell, the nucleus of the latter degenerates. The pollen nucleus divides in the cytoplasm of the egg cell and finally gives rise to a haploid embryo.

Androgenesis was first observed after a cross *Nicotiana digluta* × *N. tabacum* (Claussen and Lammerts 1929). In *Crepis*, Gerassimova (1936) demonstrated the occurrence of androgenesis by X-ray treatment of plants homozygous for a dominant marker and pollination from untreated plants homozygous for the corresponding recessive genes. Ehrensberger (1948) obtained paternal haploids in *Antirrhinum* from crosses irradiated egg cells × normal pollen. The reverse combination normal egg cells × irradiated pollen gave rise to maternal haploids. In maize, androgenetic haploid formation occurs spontaneously at a rate about $1 \times 10^{-5}$ (Chase 1969).

Semigamy was first described by Battaglia (1945) in *Rudbeckia*. Here, sometimes the sperm nucleus does not fuse with the egg nucleus, and they begin to divide independently and simultaneously. In *Rudbeckia*, the embryo-sac nuclei are unreduced, and in this way chimaeric embryos with both the somatic and half the somatic number arise. In *Zephyranthes* (Solntzeva 1978) male nuclei have been observed to give rise to diploid tissue after restitutional division.

In a semigamous strain of *Gossypium barbadense*, about 40% haploids are formed in the $S_1$ progeny (Chaudhari 1978). When female plants of this strain are crossed with non-semigamous male parents, about 1% purely androgenetic haploids appear in the offspring. This technique allows the deliberate production of haploids of different strains of cotton.

Gerlach-Cruse (1970) induced semigamy in *Arabidopsis* by X-ray irradiation of floral parts, followed by pollination with untreated pollen. As the male nucleus uses the cytoplasm of the egg cell for its development into a sporophyte, the possibility of androgenetic or semigamous haploid formation allows the transfer of genomes to study their effects in different cytoplasms. Examples of androgenesis and semigamy are listed in Table 7.

| Occurrence                  | Reference                      |
|-----------------------------|--------------------------------|
| **ANDROGENESIS**            |                                |
| *Nicotiana*                 | Interspecific cross            |
| *Crepis*                    | X-ray treated plant + untreated pollen |
| *Antirrhinum*               | Irradiated × untreated plant   |
| *Zea*                       | ?                              |
| **SEMIGAMY**                |                                |
| *Rudbeckia*                 | Spontaneous                    |
| *Zephyranthes*              | Spontaneous                    |
| *Gossypium*                 | Special strain                 |
| *Arabidopsis*               | X-ray treated plant + untreated pollen |

Table 7. Examples of parthenogenetic development of male nuclei—androgenesis and semigamy (definitions in text)
4. Endosperm formation

Embryo growth and seed formation in most angiosperms depend on the development of the endosperm. In sexual plants, the polar nuclei of the embryo-sac usually fuse to form a central nucleus, which is fertilized by a sperm nucleus. In a diploid plant, the endosperm normally has the triploid chromosome number.

Autonomous endosperm development—with or without fertilization of the central nucleus or polar nuclei—has only occasionally been observed in sexual plants such as *Anemone nemorosa* (Trela 1963) and *Triticum aestivum* (Kandelaki 1976). In autonomous apomixis, depending on whether polar nuclei fuse or not, the endosperm will have double the somatic, or the somatic chromosome number.

It is doubtful if pseudogamy precedes autonomous apomixis in the evolution of apomictic taxa. Although in certain cases the genetic control of the parthenogenetic development of nuclei giving rise to endosperm seems to be independent of that of the egg cell, it is not excluded that parthenogenesis of both types of nuclei can be acquired in one single step. Pseudogamy and autonomous apomixis almost never occur in the same agamic complex, with the exceptions of *Malus* and *Poa* (Doll 1971). No transitions are known between pseudogamy and autonomous apomixis: they seem mutually exclusive.

The development and especially the cytology of the endosperm in pseudogamous species offer certain points of interest. Endosperm cytology in apomicts has been studied by Noack (1939) in *Hypericum; Gentscheff and Gustafsson* (1940) in *Potentilla; Åkerberg* (1943) and Nygren (1950) in *Poa; Böcher* (1951) in *Arabis; Rychlewski* (1961) in *Nardus; Malecka* (1971, 1973) in *Taraxacum;* and especially in *Ranunculus* by Rutishauser (1954 a.o.) and Nogler (1972 a.o.).

When pseudogamous plants are used as mothers in crosses, only the genetic constitution of the endosperm varies, whereas that of the embryo and the maternal tissue is constant. Like in sexual plants, some degree of seed incompatibility (Valentine 1960) exists in pseudogamous taxa. For instance, 4x × 2x crosses in *Ranunculus auricomus* using tetraploid pseudogamous plants give a very low seed set due to degeneration of the endosperm.

Nogler (1978) rightly points out that each fertilization of the central nucleus to form endosperm within a pseudogamous biotype is of the same type as that in a sexual 4x × 2x cross. A reduced male nucleus must fuse with a central nucleus with twice the somatic number.

Now the genetic constitution of the endosperm is thought to be the cause of seed incompatibility in crosses like 4x × 2x (von Wangenheim 1967). The relation genome: plasmon in the endosperm is normally 3:1 in sexual plants. In a 4x × 2x cross, this relation is instead 5:2, and this deviation from the normal ratio causes degeneration of the endosperm.—According to Rutishauser (1969), instead the relation between female and male genomes in the endosperm is decisive for its vigour. Skiebe (1973) states that endosperms with 3x or a multiple of that number function best.

Special mechanisms for the endosperm formation in pseudogamous plants have been developed to avoid the possible threat of seed incompatibility, according to Nogler. The most radical one is found in grasses of the subfamily Panicoideae. Here, four-nucleated sacs are formed with only one unreduced polar nucleus, which is fertilized by a reduced sperm nucleus to give an endosperm which is triploid in relation to the somatic number. In other cases there occurs fertilization of the central nucleus by two reduced or one unreduced sperm nucleus, or fertilization of polar nuclei (which have not fused) by reduced pollen.

To sum up, endosperm formation is variously modified in apomicts. Many of the changes probably occur after the transition to apomictic reproduction. So far, we know almost nothing of the genetic background of these events. Changes accompanying the transition from sexuality to (gametophytic) apomixis are listed in Table 8.

The genetic regulation of apomixis

1. Occasional apomixis in sexual plants

As emphasized in the preceding text, formation of unreduced female gametophytes, as well as haploid and diploid parthenogenesis, occurs even in sexual plants. Such phenomena depend on the plant's genetic constitution, but cannot generally be supposed to have a simple genetic background. The degree of apomixis is obviously influenced by environmental factors, the same way as the balance between apomictic and sexual reproduction in facultative apomicts.

Data concerning gene regulation of parthenogenesis in sexual plants are meagre. In maize, genotypic influences of both female and male parents on the frequency of maternal haploidy have...
been confirmed (SARKAR and COE 1966). Lines with a high frequency of monoploid formation have been isolated in maize (CHASE 1969) and in barley (HAGBERG and HAGBERG 1980). The frequency of matromorphous plants in Brassica crosses is clearly dependent on the genetic constitution of both the female and male parent, according to EENINK (1974b). However, the gene background seems to be complicated. — Probably parthenogenetic development of reduced and unreduced egg cells is under similar genetic control, but the experimental evidence on this point is not clear.

The frequency of unreduced egg cells varies strongly among inbred lines of maize (ALEXANDER and BECKETT 1963). Also in other genera like Saccharum and Citrus, it is a well-known fact that some clones or stocks produce unreduced $\mathfrak{g}$ or $\mathfrak{d}$ gametes to a much greater extent than others (HARLAN and DE WET 1975).

BINGHAM and MC COY (1979) mention a case where formation of unreduced gametes at a high frequency seems to be under simple genetic control in Medicago. Meiotic mutants—including such that give rise to unreduced embryo-sacs—have been accounted for earlier (cf. Table 3). In Table 9, additional evidence on genetic regulation of gametophytic apomixis and its elements in sexual plants is summarized.

YUDIN (1970) conducted parallel crosses between diploid maize lines ($2x \times 2x$) and between their colchicine-induced tetraploid analogues ($4x \times 4x$). Using appropriate markers, a statistically significant increase in the frequency of reduced parthenogenesis was found in the tetraploids. If parthenogenesis would thus be enhanced by polyploidization, the connection between hybridization and formation of unreduced gametes is more obvious. Especially, interspecific hybridiza-

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**Table 8. Changes accompanying the transition from sexuality to permanent gametophytic apomixis**

| Type of apomixis   | Change                                                                 |
|--------------------|------------------------------------------------------------------------|
| Diplo- and apospory| Meiotic changes as listed in Table 4                                   |
| Apospory           | Sexual embryo-sacs sometimes suppressed by apomictic ones              |
| Autonomous apomixis| Parthenogenetic development of central nucleus (or polar nuclei)       |
| Pseudogamy         | Mechanisms to ensure a proper genomic constitution of the endosperm (see text) |
| Diplo- and apospory| Precocious parthenogenetic development of egg cells (before anthesis)  |

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**Table 9. Evidence of gene regulation of occasional gametophytic apomixis and its elements in sexual plants (cf. also Table 3)**

| Genus   | Property influenced                      | Evidence of genotypic influence                                      | References                      |
|---------|------------------------------------------|---------------------------------------------------------------------|---------------------------------|
| Zea     | Formation of unreduced egg cells         | Frequency strongly variable in inbred lines                         | ALEXANDER and BECKETT 1963      |
| Citrus. | ditto                                    | Great frequency difference between clones and stocks                | HARLAN and DE WET 1975          |
| Saccharum a.o. | ditto                                | Simple genetic regulation in one case                              | BINGHAM and MC COY 1979         |
| Medicago| ditto                                    | Frequency dependent on both female and male parents                | SARKAR and COE 1966             |
| Zea     | Haploid parthenogenesis (maternal)       | Frequency dependent on both female and male parents                |                                 |
| Hordeum | ditto                                    | Lines with high haploid frequencies isolated                      | HAGBERG and HAGBERG 1980         |
| Zea     | ditto                                    | Frequency dependent on both female and male parents                | CHASE 1969                      |
| Brassica| Diploid parthenogenesis (matromorph)     | Frequency dependent on both female and male parents                | EENINK 1974b                    |
tion often causes drastical disturbances of the meiosis. Only unreduced gametes will function in such cases.

2. Analyses in apomicts

To analyze the gene background of apomictic reproduction in established apomicts is a difficult task. The usual approach is to cross apomictic and related sexual strains and to study the mode of reproduction of the descendants. Several investigations of this type have been performed and extensive analyses of the results have been published, which cannot, however, be accounted for here. For various reasons, the results of such investigations are often difficult to evaluate.

Many authors deal only with the inheritance of apomictic reproduction as an entirety, contrasted to sexuality. In this sense, apomictic reproduction is usually recessive to sexuality, but an excess of "apomictic" genomes in a hybrid may shift the mode of reproduction towards apomixis. However, formation of unreduced gametes and parthenogenesis are certainly under independent genetic control. This is indicated by the occurrence, in offspring from crosses between apomicts and sexuals, of plants with haploid parthenogenesis or with fertilization of unreduced egg cells. The constituents of apomixis should preferably be analyzed separately.

Further, the sexual and apomictic types have not always been very closely related, which renders genetic analyses difficult. Where sexual diploids closely related to the apomicts are not known, a thorough search of natural populations may lead to their discovery (cf. Panicum maximum, Pernes et al. 1975).

A great part of the work in this field has been performed with the giant agamic complexes of Poa and Potentilla, where the conditions are likely to be more complicated than in several other apomictic groups.

3. Powers' model

Some models proposed for the genetic regulation of gametophytic apomixis deserve to be introduced here (Table 10). Important, although controversial, is the model given by Powers (1945) for pseudogamous diplospory in Parthenium. Powers

| Genus     | Type of apomixis | Proposed regulation                                                                 | Reference        |
|-----------|------------------|------------------------------------------------------------------------------------|------------------|
| Parthenium| D + P            | Different constituents of apomixis caused by homozygosity for a few recessive genes| POWERS 1945      |
| Sorbus    | A + P            | "Apomictic" genomes A with gene(s) for apomixis and "sexual" genomes B AAAA, AAB, AAB obligate apomicts ABB facultative apomicts ABB either sexual or apomictic BB totally sexual | LILJEFORS 1955   |
| Paspalum  | A + P            | Apomixis controlled by few recessive genes                                         | BURTON and FORBES 1960 |
| Pennisetum| A + P            | Apomixis controlled by a two-gene system where B causes sexuality. A apomixis Apomicts are usually Aabb, sexual aberrants Aabb | TALIAFERRO and BASHAW 1966 READ 1971 |
| Panicum   | A + P            | Apomixis controlled by a two gene system AaBb, AaBB, ABBB, AAbb, Aaab sexual aberrants AaBb | HANNA et al 1973  |
| Panicum   | A + P            | Apospory is controlled by one gene and is not recessive to sexuality (=absence of aposporous embryo-sacs) Parthenogenesis probably under more complex regulation | SAVIDAN 1978      |
| Ranunculus| A + P            |                                                                                     | NOGLER 1978      |
assumed that homozygosity for certain recessive genes is a prerequisite for apomictic reproduction. Three elements of apomixis were discriminated: (1) reduction as opposed to failure of reduction of chromosome number (controlled by the alleles \( AA \)), (2) fertilization vs. failure of fertilization of egg cells \( (Bb) \), and (3) non-development vs. development of the egg cell to an embryo without its being fertilized \( (Cc) \). Accordingly, apomicts should have the genotype \( aabbc \): apomixis is likely to arise on the diploid level.

Upon this, GUSTAFSSON (1947a) commented, that occurrence vs. failure of fertilization need not be under (simple) genetic control. It depends on the kind of pollen applied, on the time of pollination, and on the environmental conditions of the mother plant. Further, diploid apomicts are rare in nature, and it seems plausible that apomixis is usually acquired by polyploids. GERSTEL and MISHANEC \( (1950) \) and GERSTEL et al. \( (1953) \) only found sexual reproduction among \( F_2 \) plants from crosses between sexual and apomictic diploids of \( Parthenium argentatum \). It was concluded, that apomixis is based on at least four recessive genes here: a minimum of two being concerned with meiotic reduction and two more with the requirement of fertilization.

4. Other models for apomicts

In Scandinavian taxa of \( Sorbus \), the genome \( A \) from the apomictic autotetraploid \( S. aria \) carries gene(s) for apomixis, according to LIJEFORS \( (1955) \). The \( B \) genome from diploid \( S. aucuparia \) carries the corresponding gene(s) for sexuality. Among tetraploid and triploid derivatives, \( AAAA, AAAB \) and \( AAB \) are obligatorily apomictic, \( ABB \) are facultative apomicts, \( ABB \) either sexual or apomictic, whereas \( BB \) is totally sexual. Certain exceptions from this schedule could be due to interchanges between chromosomes from the \( A \)- and \( B \)-genomes. Thus if genes for apomixis or sexuality are predominant, they give rise to apomictic and sexual reproduction, respectively. Tetraploids where genes for apomixis and sexuality are numerically balanced have capacities both for apomictic and sexual reproduction.

Next, some studies in apomictic fodder grasses belonging to the Panicoideae will be reviewed. BURTON and FORBES \( (1960) \) studied offspring from crosses between sexual autotetraploid and apomictic tetraploid \( Paspalum notatum \). The sexual to apomictic ratios in \( F_2 \) indicated, in their opinion, that apomixis is controlled by a few recessive genes.

In buffelgrass and birdwoodgrass, \( Pennisetum ciliare \) (or \( Cenchrus ciliaris \)), the inheritance of apomixis has been studied by TALIAFERRO and BASHAW \( (1966) \) and READ \( (1971) \). Most cultivars are obligatorily apomictic, but occasional sexual aberrants are obtained. Crosses between such sexual and apomictic plants were performed. Data from offspring by selfing fit a ratio of 13:3 between sexual and apomictic plants. Hybrids between sexual aberrants and obligate apomicts give sexual apomictic ratios not significantly different from 5:3. The mode of reproduction is proposed to be controlled by a two-gene system where \( B \) conditions sexuality and is epistatic to gene \( A \), which controls apomixis. The genotypes of apomictic and sexual plants would then be \( Aabb \) and \( AaBb \), respectively.

Even in \( Panicum maximum \), HANNA et al. \( (1973) \) obtained sexual aberrants from tetraploid apomictic strains. In selfed progenies from sexuals, there was a predominance of sexual plants. The data agree rather well with an 11:5 ratio between sexual and apomictic plants. A two-locus control is presupposed where the genotypes \( aabb, Aabb \), and \( aaBb \) are apomictic. Offspring from sexual plants with the \( AaBb \) genotype contain both sexual and apomictic plants, whereas those with the genotypes \( AABB, AAAb, AAAb, ABB \), and \( aabb \) produce only sexual progeny. — Unfortunately, like the preceding authors HANNA et al. did not analyze the different components of apomictic reproduction separately.

Recent work indicates that apospory — meaning the presence of aposporous embryo-sacs — has a simple genetic control in \( Panicum \) \( (SAVIDAN 1978) \) and \( Ranunculus \) \( (NOGLER 1978) \). Earlier data from other genera — \( Hypericum \) \( (NOACK 1939) \), \( Hieracium \) \( (CHRISTOFF 1942) \), \( Sorbus \) \( (LIJEFORS 1955) \), \( Dichanthium \) \( (HARLAN et al. 1964) \), \( Poa \) \( (ALMGARD 1966) \), and \( Beta \) \( (CLEIJ et al. 1976) \) — seem to support this opinion. — However, the degree of apospory which is realized by the formation of maternal offspring is certainly also under complex genetic control and influenced by environmental factors.

Concerning diplospory, we have so far no conclusive data to prove a simple gene background for the necessary meiotic changes. They may partly depend on single gene mutations profoundly affecting the reproduction cycle, and partly be under polygenic control.

In the case of parthenogenesis, no case of sim-
ple genetic control seems to be known, with the possible exception for barley and maize strains with an excessive haploid formation. Most authors judge the gene background of parthenogenesis to be complicated.

In cases where diplospory and apospory seem to occur together and the limit between them is difficult to draw—like in certain Rosaceae—it seems probable that the processes leading to the formation of unreduced gametophytes have a unitary genetic cause.

All species included in Table 10 are pseudogamous and all but one aposporous, which indicates our lack of knowledge concerning diplospory combined with autonomous apomixis.

5. Effects of polyploidy and hybridization

Sometimes, the apomictic reproduction seems to be stable only on a certain level of ploidy, as euploid or aneuploid changes of the chromosome number may affect the mode of reproduction. In triploid and diplosporous *Taraxacum* species with $2n=24$, eight morphologically different aberrants with $2n=23$ were produced by loss of individual chromosomes. Two of these types were partially sexual (SØRENSEN and GUDJONSSON 1946; SØRENSEN 1958). In aposporous and pseudogamous *Poa pratensis*, aberrants which are "triploid" or "haploid" as compared with the original strain have sometimes an increased degree of sexuality (MUNTZING 1940).

The connection between apomixis and polyploidy is often pointed out. In most agamic complexes, apomictic reproduction is restricted to polyploids. However, doubling of the chromosome number is known sometimes to change the mode of reproduction towards sexuality. In *Potentilla collina* (MUNTZING and MUNTZING 1943), *P. crantzii* (MUNTZING 1958), and *Hieracium hoppeanum* (CHRISTOFF and CHRISTOFF 1948), haploid parthenogenesis frequently occurs after chromosome doubling. Obviously, the inhibition of meiosis is no longer effective.

Diploid facultative apomicts of *Potentilla argentea* give rise to totally sexual autotetraploids (ASKER 1971). Aposporous initials occur, but probably no mature aposporous embryo-sacs are formed. However, further embryological studies are needed in this case. As stated earlier, polyploids have a shorter meiotic cycle than corresponding diploids (BENNETT 1977). In the present case, this may enhance the formation of meiotic at the expense of the aposporous embryo-sacs.

Many agamic complexes are largely of hybrid origin. However, hybridization between apomicts—if possible—sometimes leads to a breakdown of apomixis. This is the case in *Poa*, where, according to MUNTZING (1940), "apomixis is due to a rather delicate genetic balance. This balance may be upset in various ways, by crosses with other types or merely by a quantitative change in chromosome number either in a plus or minus direction".—In *Rubus*, crosses between different apomictic microspecies give rise to sexual plants. Only crosses between closely related individuals give rise to apomictic offspring (GUSTAFSSON 1943).

The breakdown of apomixis in such crosses is thought to depend on its different genetic regulation in the parents. If this is so, the degree of incompatibility between the genetic systems causing apomixis is not always correlated with the general taxonomic distance between the parents. Crosses between apomictic biotypes within *Potentilla argentea* may give rise to sexual hybrids (ASKER 1970b), whereas the interspecific hybrid *P. argentea* × *P. canescens* is obligatorily apomictic (ASKER 1970a). See Table 11.

Conclusions

1. Apomixis versus sexuality

It seems that the ideas concerning the inheritance of apomixis need some revaluation. To look upon apomixis as an antipode to sexuality is not correct, in my opinion. Sexual plants can form "matromorphous" offspring, usually by parthenogenetic development of egg cells in unreduced embryo-sacs, formed by some kind of diplospory. These capacities for apomictic reproduction are usually realized only to a limited extent. Under special circumstances—such as meiotic disturbances due to hybridization or polyploidy—only apomixis allows seed formation. This may be compared with cases where vegetative reproduction becomes the only way to form offspring, due to sterility or absence of male plants.

A simple genetic regulation, perhaps by a few recessive genes, has sometimes been proposed for diplospory and parthenogenesis. Even if such a regulation cannot be excluded in certain cases, the above-mentioned two processes are certainly to a great extent under polygenic control.

When fertility is impaired, the presence of a high dosage of polygenes promoting apomictic reproduction must be favourable. Such gene combi-
Table 11. Examples of breakdown of apomixis following changes of ploidy and hybridization

| Cause          | Effect                        | Genus       | References                        |
|----------------|-------------------------------|-------------|-----------------------------------|
| "Haploidy"     | Increased sexuality           | Poa         | MÜNTZING 1940                     |
| Aneuploidy     | Certain types with 3n - 1 sexual | Taraxacum  | SØRENSEN and GUDJÖNSSON 1946      |
|                |                               | Potentilla  | SØRENSEN 1958                     |
|                | All 2n + 1 types more or less totally sexual |           | ASKER 1971                        |
| "Triploidy"    | Increased sexuality           | Poa         | MÜNTZING 1940                     |
| "Tetraploidy"  | High frequencies of haploid parthenogenesis | Hieracium | CHISTOFF and CHISTOFF 1948       |
| Hybridization  | Increased sexuality           | Poa         | MÜNTZING 1940                     |
|                | Total sexuality               | Potentilla  | GUSTAFSSON 1943                   |
|                | Varying degrees of sexuality  | Potentilla  | ASKER 1970a, b                    |

nations can arise as transgressions and be one cause of the connection between apomixis and hybridization.

The presence of recessive genes with a strong effect upon the constituents of apomixis—and each taken separately strongly reducing fitness in homozygous state—is thus not a prerequisite in the population for the origin of apomictic reproduction. On the other hand, mutations enhancing apomixis will have a great selective value for instance in a sterile hybrid, which has a certain level of apomictic seed production but is mainly restricted to vegetative reproduction for its survival.

Concerning apospory, the occurrence and function of aposporous embryo-sacs seem to be independent of the sexual process. Apospory seems to have a simple genetic background, at least in certain cases, but superimposed are effects of several genes influencing the expression of the capacity for apomictic reproduction.

In studies on the balance between apomictic and sexual reproduction, the dependence on a level of ploidy is a factor to be taken into consideration. For reasons still not clearly understood, apomictic reproduction is often impaired after changes of chromosomes number. Further, hybridization between facultative apomicts may give sexual offspring. This could support the theory of recessive genes for apomixis—different gene backgrounds in the parents would combine to create heterozygosity for the dominant genes for "sexuality".

However, alternative explanations are possible. We need more experimental evidence in this area, like in the case of the genetic background for anomalous endosperm formation in apomicts.

2. Models for the origin of gametophytic apomixis

Short-time and long-time advantages of apomictic reproduction were discussed in the beginning of this paper. Here were also discussed the pre-requisites of certain plant populations for the development of apomixis. It is possible to construct simple models for its origin. POWERS (1945), based on his conception of a few recessive genes for apomixis, presented a hypothesis for the origin of apomixis in sexual populations. Even later authors have treated this question.

It must be kept in mind that different kinds of gametophytic apomixis have a different origin and genetic regulation. The background may differ, for instance, (1) in dioecious and hermaphroditic plant populations and (2) in the case of diplospory (often with autonomous endosperm development, more or less obligate and combined with the occurrence of triploid apomicts) as contrasted to apospory (often with pseudogamy, facultative apomixis, and rareness of triploids). Theories concerning the origin of apomixis will be the subject of a future paper.

Mathematical models of the evolution of mating systems, including gametophytic apomixis, have
been proposed by Maynard Smith (1977) and Lloyd (1977). Models for genetic variability in parthenogenetic animal populations have been constructed by Asher (1970), Nace et al. (1970), and Templeton and Rothman (1973). Concerning plant populations, a model for estimating the level of apomixis was presented by Marshall and Brown (1974), and a single-locus model for the maintenance of genetic variation, by Marshall and Weir (1979).

3. Introduction of apomixis in sexual crops

Finally, the possibility of inducing permanent apomixis in sexual crops to fix heterosis will be regarded. Apomixis may be induced in any of the following ways:

(1) by selection of and crossing between lines with high frequencies of haploid formation and with high frequencies of formation of unreduced embryo-sacs;

(2) by combination of suitable induced or spontaneous mutations with strong effects upon the reproductive system to give an "artificial" apomix (of course, (1) and (2) may be combined in various ways);

(3) crosses between distantly related sexual forms followed by selection for apomixis in the hybrid offspring;

(4) crosses with related apomictic species (for references, see Ask, 1979).

Work along these lines is under way, but difficulties have to be overcome, for instance the reduced fertility occurring in (4), and lack of good screening techniques for reproductive mutants in (2). So far, only preliminary results have been obtained. With improved basic knowledge of the regulation of apomixis, future progress in this field will be achieved.

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Literature cited

Åkerberg, E. 1943. Further studies of the embryo and endosperm development in Poa pratensis. — Hereditas 29: 199-201

Åkerberg, E. and Bingefors, S. 1953. Progeny studies in the hybrid Poa pratensis × Poa alpina. — Hereditas 39: 125-136

Alexander, D. E. and Beckett, J. B. 1963. Spontaneous triploidy and tetraploidy in maize. — J. Hered. 54: 103-106

Almgård, G. 1966. Experiments with Poa. III. Further studies of Poa longifolia Trin. with special reference to its cross with Poa pratensis L. — K. Lantbrukshögsk. Ann. 32: 3-64

Arendt, N. K. and Kazas, A. N. 1977. Use of induced apomixis in the breeding of figs. — Cytol. Genet. 11: 172-175

Marker, J., JR. 1970. Parthenogenesis and genetic variability. I. One-locus models for various diploid populations. — Genetics 66: 369-391

Ask, S. 1970a. Apomixis and sexuality in the Potentilla argentea complex. I. Crosses with other species. — Hereditas 66: 127-144

Ask, S. 1970b. Apomixis and sexuality in the Potentilla argentea complex. II. Crosses within the complex. — Hereditas 66: 189-204

Ask, S. 1971. Apomixis and sexuality in the Potentilla argentea complex. III. Euploid and aneuploid derivatives (including trisomics) of some apomitic biotypes. — Hereditas 67: 114-121

Ask, S. 1979. Progress in apomixis research. — Hereditas 91: 231-240

Battaglia, E. 1945. Fenomeni citologici nuovi nella embriogenesi ("semigamia") e nella microsporogenesi ("doppio nucleo di restituzione") die Rudbeckia laciniata L. — Nuovo G. Bot. Ital. 52: 34-38

Beadle, G. W. 1930. Genetic and cytological studies of Mendelian asynapsis in Zea mays. — Cornell Univ. Agr. Exp. Sta. Mem. 129

Beadle, G. W. 1932. A gene in Zea mays for failure of cytokinesis during meiosis. — Cytologia 3: 142-155

Beadle, G. W. 1933. Further studies of asynaptic maize. — Cytologia 4: 269-287

Bennett, M. D. 1977. The time and duration of meiosis. — Phil. Trans. Roy. Soc. Lond. Ser. B 277: 201-226

Bingham, E. T and McCoy, T. J. 1979. Cultivated alfalfa at the diploid level: Origin, reproductive stability, and yield of seed and forage. — Crop Sci. 19: 97-100

Bocher, T. W. 1951. Cytological and embryological studies in the amphi-apomictic Arabis holboellii complex. — K. Danske Videnskab. Selskab. Biol. Medd. 6: 1-59

Breukeleen, E. W. M., Van, Ramanna, M. S. and Hermsen, J. G. H. 1975. Monohaploids (n=x=12) from autotetraploid Solanum tuberosum (2n=4x=48) through two successive cycles of female parthenogenesis. — Euphytica 24: 569-574

Burton, G. W. and Forbes, I., JR. 1960. The genetics and manipulation of obligate apomixis in common bahiagrass (Paspalum notatum Flugge). — Int. Grassl. Congr. Proc. 8: 66-71

Catchside, D. G. 1977. The genetics of recombination. — Genetics — principles and perspectives. 2. Edward Arnold, London

 Chase, S. 1969. Monoploids and monoploid-derivatives of maize (Zea mays L.). — Bot. Rev. 35: 117-167

Chaudhuri, H. K. 1978. Use of semigamy in the production of cotton haploids. — Bull. Torrey Bot. Club 105: 98-103

Christoff, M. 1942. Die genetische Grundlage der apomiktischen Fortpflanzung bei Hieracium aurantiacum. — Z. Indukt. Abstamm.-Vererbungsl. 80: 103-125

Christoff, M. and Christoff, M. A. 1948. Meiosis in the somatic tissues responsible for the reduction of chromosome number in the progeny of Hieracium hoppeanum. — Genetics 33: 36-42

Clau sen, J. 1954. Partial apomixis as an equilibrium system in evolution. — Caryologia, Vol. suppl. 1954: 469-479

Clau sen, R. E. and Lam merts, W. E. 1979. Interspecific hybridization in Nicotiana. X. Haploid and diploid merogony. — Am. Naturl. 63: 279-282

Clayberg, C. 1960. Cytogenetic studies of precocious meiotic centromere division in Lycopersicum esculentum L. — Genetics 44 (1959): 1335-1346

Cleij, G., Bock, T. S. M. De and Lemkerkerker, B. 1976.
Crossethes between Beta vulgaris L. and Beta lomatogona F. et M. — Euphytica 25: 539-547

DARLINGTON, C. D. 1939. The evolution of genetic systems. — Cambridge University Press

DAVIS, G. 1965. Apomixis in the Compositae. — Phytomorphology 17: 270-277

DEANON, J. R., JR. 1957. Treatment of sweet corn silks with maleic hydrazide and colchicine as a means of increasing the frequency of monoploids. — Philipp. Agric. 41: 344-347

DOLL, R. 1971. Probleme der Apomixis bei höheren Pflanzen. — Biol. Rundschau 9: 215-239

EENINK, A. H. 1974a. Matromorphy in Brassica oleracea L. I. Terminology, parthenogenesis in Cruciferae and the formation and usability of matromorphic plants. — Euphytica 23: 429-433

EENINK, A. H. 1974b. Matromorphy in Brassica oleracea L. II. Differences in parthenogenetic ability and parthenogenesis inducing ability. — Euphytica 23: 435-445

EENINK, A. H. 1974c. Matromorphy in Brassica oleracea L. III. The influence of temperature, delayed prickle pollination and growth regulators on the number of matromorphic seeds formed. — Euphytica 23: 711-718

EENINK, A. H. 1974d. Matromorphy in Brassica oleracea L. IV. Formation of homozygous and heterozygous diploid products of gametogenesis and qualitative genetic research on matromorphic plants. — Euphytica 23: 719-724

EENINK, A. H. 1974e. Matromorphy in Brassica oleracea L. V. Studies on quantitative characters of matromorphic plants and their progeny. — Euphytica 23: 725-736

EENINK, A. H. 1975a. Matromorphy in Brassica oleracea L. VI. Research on ovules, embryos and endosperms after prickle pollination. — Euphytica 24: 33-43

EENINK, A. H. 1975b. Matromorphy in Brassica oleracea L. VII. Research on products of microsporogenesis and gametogenesis from prickle pollinated plants. — Euphytica 24: 45-52

EHRENBERGER, R. 1948. Versuche zur Auslösung von Ha- ploidie bei Blütenpflanzen. — Biol. Zentralbl. 67: 537-546

ELLERSTROM, S. and ZAGORCHEVA, L. 1977. Sterility and apomorphic embryo-sac formation in Raphanobrassica. — Hereditas 87: 107-120

ERNST, A. 1951. "Maternal hybrids" by interspezifischen Bestäubungen in der Gattung Primula. 2. Sektion Farinosae. — Arch. Julius Klaus-Stift. Vererbungsforsch. 26: 187-322

FRANKES, R. 1975. Uber Stimulation von unreduzierten Gameten bei Angiospermen. — Arch. Züchtungsforsch. 5: 200-208

GENTCHEFF, G. and GUSTAFSSON, A. 1940. Parthenogenesis and pseudogamy in Potentilla. — Bot. Notiser 93: 109-132

GERASSIMOVA, H. 1936. Experimental erhaltene haploide Pflanzen von Crepis tectorum. — Planta 25: 696-702

GERLACH-KRUSE, D. 1970. Experimentelle Auslösung von Semigamie bei Arabidopsis thaliana (L.) Heynh. — Biol. Zentralbl. 98: 435-456

GERSTEL, D. U., HAMMOND, B. L. and KIDD, C. 1953. An additional note on the inheritance of apomixis in guayule. — Bot. Gaz. 112: 89-93

GERSTEL, D. U. and MISHANEK, W. M. 1950. On the inheritance of apomixis in Parthenium argentatum. — Bot. Gaz. 112: 96-106

GUSTAFSSON, A. 1943. The genesis of the European blackberry flora. — Lunds. Univ. Årsskr., N. F. Avd. 2, 39: 1-200

GUSTAFSSON, A. 1946. Apomixis in higher plants. Part I. The mechanisms of apomixis. — Lunds. Univ. Årsskr., N. F. Avd. 2, 42: 1-66

GUSTAFSSON, A. 1947a. Apomixis in higher plants. Part II. The causal aspect of apomixis. — Lunds. Univ. Årsskr., N. F. Avd. 2, 43: 71-178

GUSTAFSSON, A. 1947b. Apomixis in higher plants. Part III. Biotype and species formation. — Lunds. Univ. Årsskr., N. F. Avd. 2, 43: 183-370

HAGBERG, A. and HAGBERG, G. 1980. High frequency of spontaneous haploids in the progeny of an induced mutation in barley. — Hereditas 93: 341-343

HANNA, W., POWELL, J., MILLOT, J. and BURTON, G. 1973. Cytology of obligate sexual plants in Panicum maximum Jacq. and their use in controlled hybrids. — Crop Sci. 12: 695-697

HARLAN, J. R., BROOKS, M. H., BORGANOAKAR, D. S. and WET, J. M. J. DE. 1964. Nature and inheritance of apomixis in Bothriochloa and Dichanthium. — Bot. Gaz. 125: 41-46

HARLAN, J. R. and WET, J. M. J. DE. 1975. On O. Winge and a prayer: The origins of polyploidy. — Bot. Rev. 41: 361-390

JØRGENSEN, C. A. 1928. The experimental formation of heteroploid plants in the genus Solanum. — J. Genet. 19: 132-211

KANDELAKI, G. V. 1976. Remote hybridization and the phenomenon of pseudoogy. — In Apomixis and Breeding (Ed. S. S. KHOKHLOV), Amerind., New Delhi, p. 179-189

KATAYAMA, Y. 1934. Ha- ploid formation by X-rays in Triticum monococcum. — Cytologia 5: 235-237

KATAYAMA, Y and ADACHI, T. 1969. Studies on the haploidy in relation to plant breeding. — Seiken Zihō 21: 31-35

KHOKHLOV, S. S. 1976. Evolutionary-genetic problems of apomixis in angiosperms. — In Apomixis and Breeding, Amerind., New Delhi, p. 3-17

KIELLANDER, C. L. 1942. A subhaploid Poa pratensis L. and its progeny. — Sven. Bot. Tidskr. 36: 200-220

KIMBER, G. and RILEY, R. 1963. Haploid angiosperms. — Bot. Rev. 29: 480-531

LANGLEY, O. F. 1927. Beiträge zur Zytologie der Ranuncula- zen. — Sven. Bot. Tidskr. 21: 1-17

LILJEFORS, A. 1955. Cytological studies in Sorbus. — Acta Hort. Bergiani 17: 47-113

LODD, D. G. 1977. Genetic and phenotypic models of natural selection. — J. Theor. Biol. 69: 543-560

MALECKA, J. 1971. Cyto-taxonomical and embryological in- vestigations on a natural hybrid between Taraxacum kok-sag- hyz Rodin and T. officinale Web. and their putative parent species. — Acta Biol. Crac., Ser. Bot. 14: 179-197

MALECKA, J. 1973. Problems of the mode of reproduction in microspecies of Taraxacum section Palustria Dahlstedt. — Acta Biol. Crac., Ser. Bot. 16: 37-84

MARSHALL, D. R. and BROWN, A. H. D. 1974. Estimation of the level of apomixis in plant populations. — Heredity 32: 321-333

MARSHALL, D. R. and WEIR, B. S. 1979. Maintenance of genet- ic variation in apomitic plant populations. 1. Single locus models. — Heredity 42: 159-172

MATHER, K. 1943. Polygenic inheritance and natural selection. — Biol. Rev. 18: 32-64

MAYNARD SMITH, J. 1977. The sex habit in plants and animals. — Lecture Notes in Biomatics (Eds. F. B. CHRISTIANSSEN and T. M. FENCHEL), Springer-Verlag, New York p. 315-331

MILLARDET, M. A. 1894. Note sur l’hybridation sans croisement ou fausse hybridation. — Mem. Soc. Sci. Phys. Inst. Bordeaux 4: 347-372

MÜNtzING, A. 1940. Further studies on apomixis and sexuality in Poa. — Hereditas 26: 115-190

MÜNtzING, A. 1958. Heteroploidy and polymorphism in some apomictic species of Potentilla. — Hereditas 44: 280-329

MÜNtzING, A. and MÜNtzING, G. 1943. Spontaneous changes in chromosome number in apomictic Potentilla collina. — Hereditas 29: 451-460

NACE, G. W., RICHARDS, C. M., and ASHER, J. H. 1970. Parthenogenesis and genetic variability. I. Linkage and in- breeding estimations in the frog, Rana pipiens. — Genetics 65: 349-368

Hereditas 93 (1980)
NOACK, K. L. 1939. Über Hypericum-Kreuzungen. VI. Fortpflanzungsverhältnisse und Bastarden von Hypericum performatum. — Z. Indukt. Abstam.-Vererbung. 76: 569-601

NÖGLER, G. A. 1972. Genetik der Aposporie bei Ranunculus auricomus. II. Endospermmyzologt. — Ber. Schweiz. Bot. Ges. 82: 54-63

NÖGLER, G. A. 1978. Zur Zytogenetik der Aposmie bei Ranunculus auricomus. — Habilitationsschrift ETH Zürich, 916 704: 218 H

NORDBOG, G. 1967. Embryologische Studien in the Sanguisorba minor complex (Rosacaeae). — Bot. Not. 129: 109-120

NYGREN, A. 1930. Cytologische und embryologische studies in arctic Poae. — Symb. Bot. Ups. 10: 1-64

PALMER, R. G. 1971. Cytologische studies of aneiotic and normal maize with references to premeiotic pairing. — Chromosoma 35: 233-246

PERNES, J., COMBES, D., RENÉ-CHAUME, R. and SAVIDAN, Y. 1975. Biologie et populations naturelles du Panicum maximum Jacq. — Cah. ORSTOM, Sér. Biol. 10: 77-89

PETROV, D. F. 1976. Genetically regulated apomixis as a method of fixing heterosis and its significance in breeding. — In Apomixis and Breeding (Ed. S. S. KHOKHLOV), Anerind., New Delhi, p. 18-28

PODDUBNAYA-ARNOLDI, W. A. 1939. Embryogenesis in remote hybridization in the genus Taraxacum. — C. R. Acad. Sci. U.R.S.S. 24: 374-377

POWERS, L. 1945. Fertilization without reduction in guayule (Parthenium argentatum Gray) and a hypothesis as to the evolution of apomixis and polyploidy. — Genetics 30: 323-346

RANDOLPH, L. F. 1932. Some effects of high temperatures on polyploidy and other variations in maize. — Proc. Nat. Acad. Sci. 18: 222-229

READ, J. C. 1971. Cytotaxonomic relationships in the genera Pennisetum and Cenchrus and the manipulation of apomixis. — Doctor’s thesis, Texas A&M University (abstract)

RHOADES, M. M. 1948. Androgenesis. — Maize Genet. Coop. News Lett. 22: 10

RHOADES, M. M. 1956. Genetic control of chromosome behaviour. — Maize Genet. Coop. News Lett. 30: 38-42

RILEY, R. and CHAPMAN, V. 1958. Genetic control of the cytological diploid behaviour of hexaploid wheat. — Nature 182: 713-715

RUTSHAUSER, A. 1954. Die Entwicklungsregierung des Endosperms bei pseudogamen Ranunculus-arten. — Mitt. Naturf. Ges. Schaffhausen 25: 1-45

RUTSHAUSER, A. 1967. Fortpflanzungsmodus und Meiose apomiktischer Blütenpflanzen. — Protoplasmatologia VII/F I, Springer-Verlag, New York

RUTSHAUSER, A. 1969. Die embryologischen und cytogenetischen Grundlagen der Sameninkompatabilität. — Ber. Schweiz. Bot. Ges. 79: 5-48

RYCHELEWSKI, J. 1961. Cyto-embryological studies in the apomorphic species Nardus stricta L. — Acta Biol. Crac., Ser. Bot. 4: 1-21

SARKAR, K. R. and COE, E. H., Jr. 1966. A genetic analysis of the origin of maternal haploids in maize. — Genetics 54: 453-464

Satin, S. and Blakeslee, A. F. 1935. Cytological effects of a gene in Datura which causes dyad formation in sporogenesis. — Bot. Gaz. 96: 521-532

Savidan, Y. 1978. Genetic control of facultative apomixis and application in breeding Panicum maximum. — Communicaton to the XIVth International Congress of Genetics, Moscow 21-3018 1978. Office de la Recherche Scientifique et Technique Outre-Mer, Abidjan, Ivory Coast

Skieke, K. 1973. Genetische Voraussetzungen für die Samenbildung nach intergenomatisch verschieden Kreuzungen. — Arch. Züchtungsf. 3: 183-202

Solntseva, M. P. 1978. Apomixis and hemigamy as one of its forms. — Proc. Ind. Acad. Sci., Sect. B 44: 78-90

Sørensen, Th. 1958. Sexual chromosome-aberrants in triploid apomictic Taraxacum. — Bot. Tidskr. 54: 1-22

Sørensen, Th. and Gudjonsson, G. 1946. Spontaneous chromosome-aberrants in apomictic Taraxacum. — K. Danske Videnskab. Selskab Biol. Medd. 4: 3-48

Stebbins, G. L. 1958. Longevity, habitat, and release of genetic variability in the higher plants. — Cold Spring Harbor Symp. Quant. Biol. 23: 365-378

Taliaferro, C. M. and Bashaw, E. C. 1966. Inheritance and control of obligate apomixis in breeding buffelgrass, Pennisetum ciliare. — Crop Sci. 6: 473-476

Templeton, A. R. and Rothman, E. D. 1973. The population genetics of parthenogenetic strains of Drosophila melanogaster. I. One locus model and statistics. — Theoret. Appl. Genet. 43: 204-212

Thomas, P. T. 1940. Reproductive versatility in Rubus. II. The chromosomes and development. — J. Genet. 40: 119-128

Todua, V. A., Terovskii, M. F and Sarychev, M. K. 1931. Induced diploid apomixis in tobacco. — Dokl. Akad. Nauk SSSR 21: 216-217

Trela, Z. 1963. Embryological studies in Anemone nemorosa L. — Acta Biol. Crac., Ser. Bot. 6: 1-14

Tschermak-SEYSENIGG, E. 1951. Reifzuchtung (Samenbildung ohne Befruchtung). — Biol. Gen. 19: 3-30

Valentine, D. H. 1960. Seed-incompatibility in Primula. — Nature 185: 778-779

Vermeil, E. M. and Solovova, K. P. 1973a. Artificial parthenogenesis in flowering plants and some aspects of breeding. — Ontogeny 4: 240-248

Vermeil, E. M. and Solovova, K. P. 1973b. Artificial diploid parthenogenesis in flowering plants. — Dokl. Akad. Nauk SSSR 210: 457-460

Wangenheim, K. H. Von. 1967. Entwicklungphysiologische Untersuchungen über die Beteiligung nukleärer und extranukleärer Erbträger an der Phänotogenese. — Ber. Deut. Bot. Ges. 80: 228-236

Weet, J. M. J. De. 1968. Diploid-tetraploid-haploid cycles and the origin of variability in Dichanthium agamosspecies. — Evolution 22: 394-397

Yudin, B. F. 1970. Capacity for parthenogenesis and effectiveness of selection on the basis of this character in diploid and autotetraploid maize. — Genetika 6: 13-22

Zabinska, D. 1977. Embryology of the dioecious species Cirsium arvense (L.) Scop. — Acta Biol. Crac., Ser. Bot. 20: 133-146