

Viewpoints on apomictic and sexual reproduction in angiosperms

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Abstract

Gametophytic apomixis implies different changes of the reproductive cycle of sexual plants. Each of these "elements of apomixis" occurs in sexual plants, which may even display functional diploid parthenogenesis. Thus, apomixis, like vegetative reproduction, is part of the reproductive behaviour of sexual plants, becoming important when sexual reproduction is impaired. The elements of apomixis are probably to a large extent under polygenic control.

Apomixis has often been looked upon as an entity contrasted to sexual reproduction. However, established apomictic reproduction implies a series of changes of the reproductive behaviour of sexual plants. These changes have independent genetic regulation, and should preferably be studied separately.

Among these constituents, or elements of apomixis (Petrov, 1976) we first have the changes of meiosis necessary to bring out a functional diplospory: either, restitution takes place after the first meiotic division, or a substitution of mitotic for meiotic divisions occurs.

Unreduced gametes, especially egg cells, often function in sexual plants. They must usually be formed by some kind of diplospory. Unreduced egg cells often function when meiosis in the mother plant is impaired due to polyploidy and hybrid structure. In extreme cases, only the unreduced egg cells are able to function. Further, fertilization of unreduced egg cells often takes place in distant crosses. But also in diploids with regular meiosis, unreduced egg cells are formed to some extent, which is seen by the spontaneous occurrence of autotriploids in several diploid crops.

In apospory, somatic cells in the ovule enlarge, vacuolize, and give rise to unreduced embryo-sacs. Aposporous embryo-sacs are known to occur in certain sexual plants, especially within the *Compositae*. Hybridization greatly increases the frequency of aposporous, at the expense of reduced, embryo-sacs in *Sanguisorba* (Nordborg, 1967) and *Raphanobrassica* (Ellerström, Zagorcheva, 1977).

Haploid plants are usually formed by parthenogenetic development of reduced egg cells. Either they are "monoploids", derived from diploids

and usually weak and infertile, or polyhaploids, which are sometimes vigorous and fertile. This capacity for parthenogenetic development is realized at a low frequency only in normal cases. But especially after aberrant types of pollination, with pollen treated with X-rays, toluidine blue or colchicine, or when pollination is delayed, the frequency of haplo-parthenogenesis increases markedly.

Table 1

Modes of reproduction in sexual and apomictic plants

	Sexual plants	Apomictic plants
Embryo formation		
Reduced egg cells:		
— fertilization	Usual case	Facultative apomicts
— parthenogenesis	Sporadic (frequent for instance after foreign pollination)	Sporadic (in <i>Hieracium</i> and <i>Potentilla</i> following chromosome doubling)
Unreduced egg cells*:		
— fertilization	Sporadic (frequent in distant crosses and after meiotic disturbances)	Sporadic (giving rise to autotriploids and U-hybrids)
— parthenogenesis	Sporadic (i.e. matromorphy in <i>Brassica</i>)	Usual case in gametophytic apomixis (diplospory and apospory)
Somatic cells	Occasional	Usual case in nucellar embryony
Endosperm formation		
Central nucleus or polar nuclei:		
— fertilization	Usual case	Pseudogamy
— parthenogenesis	Occasional	Autonomous apomixis
Vegetative reproduction	Frequent	Frequent

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

Even unreduced egg cells may give rise to offspring parthenogenetically in sexual plants. In this way so-called matromorphic plants are formed, especially studied by Eenink (1974) in *Brassica*. This mode of reproduction has probably been overlooked. Matromorphic plants are not likely to be discovered in open-pollinated offspring, and in crosses, such plants may be judged to result from incomplete castration or pollen contamination. The occurrence of matromorphy can only be demonstrated by the use of suitable markers in controlled crosses.

In sexual plants, the egg cell usually divides after fertilization or — if the latter does not take place — only after a long delay. In apomicts,

division of the egg cell may take place very early. When the flowers open or when anthesis takes place, the ovules contain multicellular embryos instead of egg cells capable of fertilization. This is an adaptation enforcing stable apomictic reproduction, preventing fertilization of the unreduced egg cells especially in pseudogamous plants.

Adaptations which concern endosperm formation are also characteristic for apomicts. In autonomous apomicts, the central (polar) nuclei develop by parthenogenesis like the egg cell. Fertilization becomes unnecessary, and various disturbances of male meiosis and pollen formation are often observed. In a few cases, like in *Anemone nemorosa* (Trela, 1963) and in *Triticum aestivum* (Kandelaki, 1976), autonomous endosperm formation has been demonstrated in sexual plants.

In pseudogamous taxa, fertilization is necessary for normal endosperm and seed development. Within the *Ranunculus auricomus* group, the egg cell does not divide until the central nucleus has been fertilized (Rutishauser, 1976). In most other pseudogamous species, the egg cell divides independently of pollination. However, the embryos degenerate if no endosperm is formed.

Some aberrant types of endosperm formation are known from pseudogamous species. In *Ranunculus auricomus* (Nogler, 1978), fertilization of a central nucleus by two sperm nuclei, or of a polar nucleus by one sperm nucleus, has been observed. In the grass subfamily *Panicoideae*, aposporous embryo-sacs are monopolar. The single polar nucleus with the somatic chromosome number is fertilized by a reduced sperm nucleus. Such adaptations are thought to ensure a proper level of ploidy for the endosperm.

All people working in this field agree that apomixis is to some extent genetically regulated. This is true also of the frequency of elements of apomixis in sexual strains. It is well known that certain clones or strains of cultivated species form haploids at a much higher frequency than others. The genetic background seems, however, to be complicated in such cases (polygenic control).

Analyses of the gene background of apomixis have usually been performed by crosses between sexual and related apomictic plants, followed by studies of the mode of reproduction in F_1 and following generations. Several studies of this type have been performed, but for various reasons, their results are often difficult to interpret.

Based upon such analyses, however, various models for the genetic regulation of apomixis have been constructed. Some authors, first Powers (1945) in *Parthenium*, have proposed regulation by a few recessive genes with strong effects upon the mode of reproduction. In most cases, however, it has not been possible to prove the existence of such genes for apomixis. A probable exception is apospory, meaning the pre-

sence of aposporous embryo-sacs. A simple gene regulation is indicated from studies in the *Bothriochloa-Dichanthium*-group (Harlan et al., 1964), *Panicum* (Savidan, 1978), and *Ranunculus* (Nogler, 1978).

The connections between apomixis on one side, polyploidy and hybridization on another, are of a complex nature. Paradoxically enough, both hybridization and polyploidization may lead to the breakdown of apomixis. In hybrids between not very closely related apomicts, this implies that the gene systems causing apomixis are profoundly different in the parents. More difficult to explain is the partial or total breakdown of apomixis following chromosome doubling in *Hieracium* (Christoff, Christoff, 1948) and *Potentilla* (Müntzing, Müntzing, 1943; Müntzing, 1958; Asker, 1971). Polyploidization here seems to profoundly change the balance between reduced and unreduced embryo-sacs.

In conclusion, gametophytic apomixis seems to lie within the reproductive potential of sexual plants, the same way as vegetative reproduction does. It becomes an important resource for seed formation when sexual reproduction is impaired. The constituents of apomixis, for instance the frequency of parthenogenesis or of unreduced egg cells, must to a great extent be looked upon as quantitative characters under polygenic control.

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