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RESEARCH ARTICLE

APOMIXIS IN FLOWERING PLANTS – AN OVERVIEW

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Abstract

Apomixis is an asexual mode of reproduction through seeds in flowering plants. In contrast to sexual reproduction, apomictic processes can completely omit some of the events of megasporogenesis and megagametogenesis and still produce a fully formed, viable embryo within the ovule. It occurs in many widespread and ecologically diverse plant groups but curiously it appears to be absent among the gymnosperms. Of the plants known to use gametophytic apomixis, most of the cases belong to Asteraceae, Rosaceae, and Poaceae. Sporophytic apomixis is, however, taxonomically scattered, with representatives in Orchidaceae, Celastraceae and Rutaceae. Among crop species apomixis is very poorly represented. The phenomenon is heritable and under genetic control.

Introduction

Apomixis in flowering plants is defined as the formation of an asexual seed from the maternal tissues of the ovule, without the processes of meiosis and fertilization. This enigmatic process of asexual reproduction through seed occurs when the sexual life cycle is “short-circuited” (Vielle-Calzada et al, 1996). In angiosperms sexual reproduction follows a defined sequence of events leading to the formation of a fertile and genetically unique seed. The sequence comprises the following events:

1. Megaspore mother cell (MMC) differentiation from the nucellus,
2. Megaspore production by meiosis of MMC (megasporogenesis),
3. Megaspore selection,
4. Embryo sac development from selected megaspore by mitotic process (megagametogenesis),
5. Embryo sac maturation,
6. Double fertilization,
7. Embryo formation and
8. Endosperm development.

In contrast to sexual reproduction, apomictic processes can completely omit some of the events in this sequence and still produce a fully formed, viable embryo within the confines of the ovule (Bhat et al 2005). In sexual reproduction, the fusion of two unique haploid gametes, derived from the random assortment of the genetic material occurring during meiosis, results in the generation of diploid and genetically diverse progenies. Conversely, in apomictic reproduction, the embryo develops autonomously from an unreduced cell having the same set of maternal chromosomes and giving rise to plants that are clones of the mother plant.

The discovery of apomixis in higher plants is attributed to the observation that a solitary female plant of *Alchornea ilicifolia* from Australia continued to form seeds when planted at Kew Gardens in England (Smith, 1841). Winkler (1908) introduced the term apomixis to mean ‘‘substitution of sexual reproduction by an asexual multiplication process without the fusion of nucleus and cell.’’ Therefore, some authors have chosen to use apomixis to describe all forms of asexual reproduction in plants, but this wider interpretation is no longer generally accepted. Apomixis is often used loosely to mean agamospermy i.e. seed without sex (Nogler, 1984; Richards, 1997). Because seeds are found only among angiosperm and gymnosperm taxa, this definition of apomixis limits its use to those groups. In lower plants, phenomena similar to apomixis are known, but discussion remains about the use of this term in cases in which the reproductive structures involved are different yet are considered analogous (Asker and Jerling, 1992). The most comprehensive account on apomixis was given by Maheshwari (1950) in his classical book on embryology.

Types of apomixis

Apomixis can broadly be classified into two types – gametophytic and sporophytic (Fig. 1).

1. Gametophytic apomixis: It occurs in polyploids mostly and is characterized by circumvention of chromosome reduction (apomeiosis). Here meiosis is either altered or totally bypassed, and as a consequence, an unreduced female gametophyte, or embryo sac, is formed (Asker and Jerling, 1992; Nogler 1994; Koltunow, 1993; Vielle-Calzada et al 1996). There is no fusion of male and female gametes and the egg cell develops autonomously, by parthenogenesis, into an embryo that gives rise to a plant true to the maternal parent by keeping the same set of maternal chromosomes. Gametophytic apomixis may be either obligate (plants reproducing exclusively by apomixis) or facultative (plants reproducing both by apomictic and sexual means). This type of apomixis is further divided into two categories – diplospory and apospory.

A. Diplospory: Here the MMC completely bypasses the meiotic process, but through mitosis forms an embryo sac with all unreduced cells, including the egg cell, distributed as in the meiotic embryo sac of the *Polygonum* type. The embryo develops parthenogenetically from the unreduced egg, whereas the endosperm develops either autonomously (without fertilization) from the unreduced polar nuclei or pseudogamously after fertilization of the unreduced polar nuclei with the reduced male gamete. It is further categorized into two types, meiotic and mitotic diplospory. In the former the MMC undergoes asyndetic meiotic prophase resulting in a restitution nucleus followed by a division similar to the second meiotic division except that it is not followed by cytokinesis while in the latter MMC does not enter into meiosis and functions as an unreduced megaspore that undergoes three mitoses to develop an eight nucleate embryo sac.

B. Apospory: Here some nucellar cells, called aposporous initials, enter the mitosis directly and unreduced embryo sacs are formed. Several cells of the nucellus may start aposporous development but usually only one of them gives rise to a mature embryo sac. Apospory is initiated after MMC differentiation and megaspore formation. The megaspore degenerates and the aposporous embryo sac occupies the position near the micropylar end of the ovule. The embryo develops parthenogenetically from the unreduced egg, but the pollination and fertilization are required for the development of endosperm. It is the most common mechanism of apomixis in higher plants particularly the grass family.

2. Sporophytic apomixis: In sporophytic apomixis or adventitious embryony, embryos are formed directly from unreduced cells of the nucellus, or the integument, while the developmental pathway of meiotic embryo sac is maintained (Lakshmanan and Ambegaokar 1984) resulting in polyembryony. It is initiated late in ovule development and usually occurs in mature ovules. In contrast to sexual, aposporous and diplosporous reproduction, apomictic embryos of sporophytic origin are initiated directly from the individual cells without being surrounded by embryo sac tissue.

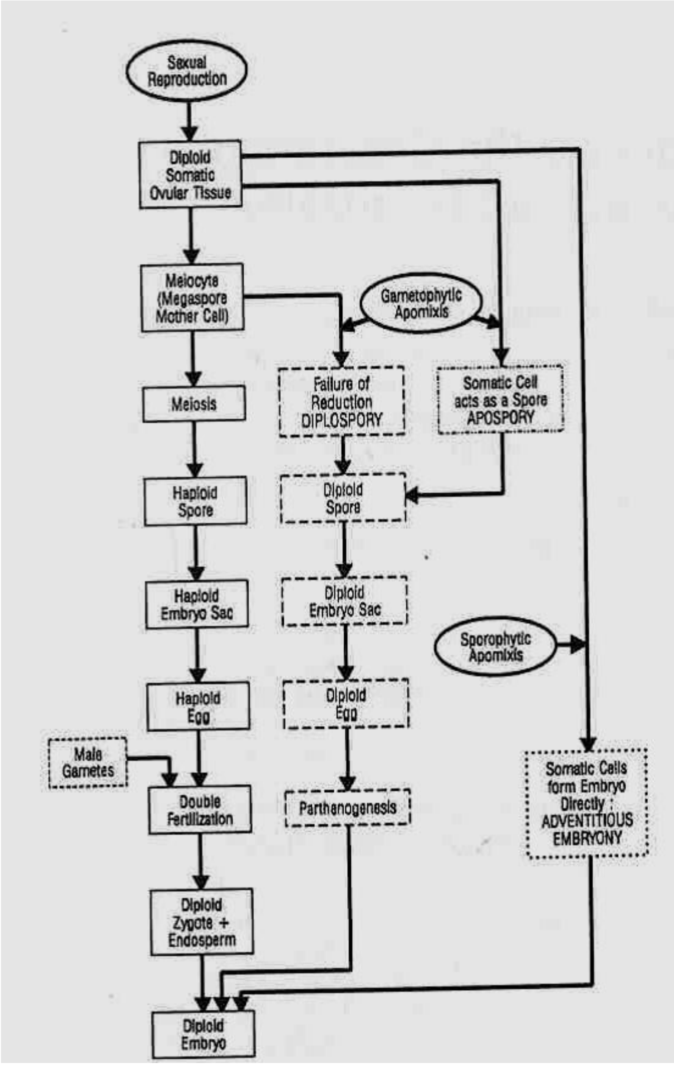

Figure 1. Comparison of sexual and apomictic pathways in angiospermic ovules (Koltunow et al 1995).

Prevalence

Although it is sometimes referred to as a botanical curiosity, apomixis is relatively prevalent among angiosperms comprising about 440 genera belonging to more than 40 families (Carman, 1997). According to another estimate (Khokhlov 1976) about 80 families and over 300 genera reproduce through apomixis. The phenomenon is well represented among both monocots and dicots. At the species level, it occurs in less than 1% of the species (Mogie 1992). It occurs in many widespread and ecologically diverse plant groups (e.g., dandelions, hawkweeds, hawthorns, blackberries, Kentucky bluegrass, *Citrus* spp.). Curiously, it appears to be absent among the gymnosperms. These estimates are almost certainly very conservative. It seems likely that as our understanding of this phenomenon grows and methods to determine its presence improve, many more angiosperm taxa will be found to exhibit this phenomenon and some suspected cases will be revised. A recent study by Plitman (2002) supports this prediction. Several authors have noted that the distribution of apomixis among angiosperms is highly biased (Asker and Jerling, 1992; Mogie, 1992; Carman, 1997; Richards, 1997). Of the plants known to use gametophytic apomixis, 75% of confirmed examples belong to three families, the Asteraceae, Rosaceae, and Poaceae, which collectively constitute only 10% of flowering plant species. Adventitious embryony or sporophytic apomixis is taxonomically scattered, with representatives in Orchidaceae, the largest flowering plant family, Celastraceae and Rutaceae or to be simple, it is mainly found in tropical and subtropical woody plants with multiseeded fruits. Some authors have postulated that the current patterns of distribution may reflect the predisposition of certain plant groups to the unique developmental and genetic changes that characterize apomixes (Grimanelli et al., 2001b). Despite its broad distribution within the angiosperms, apomixis is not very common in the major crops. Most plants with gametophytic apomixis are polyploids while those with adventive embryony are generally diploids (Asker and Jerling, 1992).

Apomictic species also are almost invariably perennials, and they often use a vegetative mechanism of asexual reproduction, such as stolon or rhizome growth. Thus, in the field, through a combination of apomixis and vegetative division, apomicts can form large clonal stands, and these may persist through long periods of time. Apomixis also frequently leads to the formation and maintenance of numerous morphologically distinct, yet inter-fertile, varieties growing true to type from seed. The taxonomy of such agamic complexes can be a difficult and contentious task (Dickinson, 1998; Horandl, 1998). Examples of genera in which the apomictic mode of reproduction is strongly combined with morphological polymorphism include *Alchemilla*, *Hieracium*, *Poa*, *Potentilla*, *Ranunculus*, *Rubus*, and *Taraxacum* (Czapik, 1994). Apomicts are found more commonly in habitats that are frequently disturbed and/or either where the growing season is short (such as arctic and alpine sites), or where other barriers operate to inhibit the successful crossing of compatible individuals, such as among widely dispersed individuals within a tropical rain forest (Asker and Jerling, 1992). Gametophytic apomixis is known among herbaceous and tree species, but it is considerably more common among the former. This may simply be a reflection of the predominance of the phenomenon in the Poaceae and the Asteraceae, both of which are composed largely of herbaceous species. Similarly, gametophytic apomixis is common among plants that have dehiscent fruits, as seen in the Poaceae, Asteraceae, and Ranunculaceae, but again, this may be more coincidence than causally linked. Association between apomixis, polyploidy and polyembriony is recorded for many species. Apomicts are generally polyploids, tetraploidy being the commonest level and very few diploid apomicts existing in nature (Asker and Jerling 1992; Carman 1997). The reason for this association is still not understood (Bicknell and Koltunow 2004).

Apomixis is very poorly represented among crop species. The main exception to this appear to be tropical and subtropical fruits such as mango and citrus, and tropical forage grasses such as *Panicum*, *Brachiaria*, *Dicahnthium* and *Pennisetum*. Efforts aimed at introducing apomixis in maize (Sokolov et al 1998, Savidan 2000,) from wild relative *Tripsacum dactyloides* have failed to a larger extent in terms of generating apomictic plants with agronomically acceptable levels of seed set.

Genetics of apomixis

The genetics of apomixis is appearing to be more complex than was understood earlier (Bhat et al 2005). The phenomenon is heritable and under genetic control, but hardly ever obligatory. Research on the developmental features and control mechanisms has shown that gametophytic apomixis is rather a deregulation of the normal sexual pathway than an independent trait. A temporal and/or spatial deregulation of gene expression may cause apomeiotic formation of the embryo sac and the parthenogenetic development of the embryo (Koltunow and Grossniklaus 2003; Curtis and Grossniklaus 2007). Polyploidy and hybridization may trigger the shifts in control mechanisms resulting in gametophytic apomixis via repatterning of gene expression (e.g., Grimanelli et al. 2001; Carman

1997, 2001, 2007). Studies on grasses viz., *Panicum* (Savidan 1981), *Pennisetum* (Sherwood et al 1994), *Brachiaria* (Valle et al 1994) and *Paspalum* (Martinez et al 2001) indicate that apomixis is controlled by a single dominant Mendelian factor or by a complex of a few, closely linked genes (Ozians-Akins and Van Dijk 2007). Mapping studies of the apomixis locus suggest a clustering of apomixis-specific molecular markers in large non-recombinant regions (Vijverberg and Van Dijk 2007; Ozias-Akins and Van Dijk 2007). Segregation studies on *Citrus* suggest a single-locus dominant control of apomixis (Garcia et al. 1999).

The inheritance of gametophytic apomixis has long been reported to be associated with the transfer of either single locus or a small number of loci in most of the systems studied so far. In aposporous grasses such as *Pennisetum*, *Panicum*, and *Brachiaria*, apomixis is known to be simply inherited by the transfer of a single dominant factor (Sherwood et al 1994; Savidan, 1981; Valle et al 1994). Such a type of inheritance has also been reported in dicotyledonous genera like *Ranunculus* and *Hieracium* (Nogler, 1984; Bicknell et al 2000).

In the majority of apomictic plants (ca. 90%; Mogie 1992), production of viable seed depends on the presence of pollen, i.e., fertilization of the polar nuclei is still required for normal endosperm development (pseudogamy). Only a few apomictic taxa, mainly occurring in Asteraceae, can develop the endosperm autonomously. In many angiosperms, a 2:1 maternal/paternal ratio in the endosperm is optimal for seed development because of genomic imprinting (Vinkenoog et al. 2003). Paternal genes promote growth of the endosperm, whereas maternal genes reduce growth, presumably to allocate resources evenly to the progeny. A lower ratio of the paternal genome results in underdevelopment of seeds, while a higher paternal contribution will result in over-proliferation of seeds (Vinkenoog et al. 2003). In the case of gametophytic apomixis, this ratio is disturbed, because an unreduced embryo sac has proportionally a much larger maternal contribution in the endosperm than the paternal one (e.g., a tetraploid apomict with a Polygonum type embryo sac has an octoploid endosperm nucleus, 4x + 4x, which is fertilized by a 2x pollen nucleus). Plants with gametophytic apomixis have developed various modifications of developmental pathways to maintain the optimal 2 m:1p ratio in the endosperm (Koltunow and Grossniklaus 2003; Savidan 2007). For instance, in polyploid apomictic *Ranunculus auricomus*, and in many Rosaceous taxa, the majority of seeds are formed by fertilization of polar nuclei with both sperm nuclei, thus preserving the 2 m:1p ratio in the endosperm (Spielmann et al. 2003; Savidan 2007, Talent and Dickinson 2007). Some taxa tolerate deviations from the endosperm balance (e.g., in Rosaceae subtribe Pyrinae, Talent and Dickinson 2007). In mutants of *Arabidopsis*, double fertilization events can be uncoupled, and both embryo and endosperm can develop autonomously (Koltunow and Grossniklaus 2003).

Apomixis evolves almost exclusively in perennials, including both herbaceous and woody plants. Apomictic annuals are extremely rare (e.g., some species of *Erigeron*, *Aphanes*). Apomixis not only provides reproductive assurance, but also avoids a loss of heterozygosity in the offspring because the egg cell maintains the parental genotype. Apomixis therefore avoids effects of inbreeding depression and may additionally confer some advantages because of heterosis effects. Isoenzyme studies on various genera show that levels of observed heterozygosity of apomicts markedly exceed the values of their sexual relatives in all genera studied so far (Hörandl et al. 2001; Hörandl and Paun 2007). Apomixis maintains heterozygosity of hybrid genotypes by the avoidance of meiotic segregation and therefore harbors intra-individual allelic variation.

The lethal effect theory by Nogler (1984b) based on experimental work on *Ranunculus auricomus* suggests that the allele controlling aposporous embryo sac development (A−) is dominant for apomixis but has lethal recessive effects in the gametes. Apomixis can therefore be inherited only by diploid gametes heterozygous for A+ A−, while haploid gametes carrying A−would not be viable. Recessive lethal effects in the pollen or in the egg cell have indeed been observed in a couple of other apomictic taxa, mainly in Asteraceae and Poaceae (Ozias-Akins and Van Dijk 2007). Thus, mutations leading to apomixis are more likely established in lineages that had previously become polyploid (Whitton et al. 2008).

Nogler (1982) showed that diploid offspring that developed parthenogenetically from reduced diploid eggs of tetraploid apomictics or diploids produced through anther culture were able to reproduce apomictically, putting aside the earlier reports (Bicknell, 1997; Kojima & Nagato, 1997) that apomixis and diploidy are not compatible. However, what matters is the origin of the diploid offspring, because in *Ranunculus* zygotic diploids derived from the fusion of haploid egg cells and haploid sperm never produced apomictically.

Apomixis and polyploidy

Polyploidy and apomixis are also closely linked. Plants with gametophytic apomixis are almost exclusively polyploid; the only well-documented cases of apomixis on the diploid level are *Boechera* *holboellii*, which is probably a paleopolyploid (Koltunow and Grossniklaus 2003), and some species of *Paspalum* (Siena et al. 2008). In both cases, sexuality is also present on the diploid level. Most taxa with gametophytic apomixis have a genetically controlled and heritable formation of unreduced embryo sacs, but maintain the meiotic reduction of pollen. It is still under intense dispute whether polyploidy is a prerequisite or a supporting factor of apomixis.

It has long been known that sexual relatives of apomictic plants are usually self-incompatible and obligate outcrossers (Gustafsson 1953; Asker and Jerling 1992). Gustafsson's (1953) detailed survey of sexual taxa from ca. 48 genera containing apomicts shows that eleven of them are dioecious or monoecious, 25 are self-sterile and 10 more are probably self-sterile as inferred from floral structure, but no genus is entirely self-fertile on the diploid sexual level.

Apomixis and self-fertility

Self-fertilization (selfing) and apomixis are the two major pathways of reproduction in angiosperms besides the normal sexual outcrossing system (Hörandl 2010). Both modes of reproduction are derived features, and both of them have multiple origins in various lineages of angiosperms (Charlesworth et al. 2005; Van Dijk and Vijverberg 2005). Both breeding systems allow for the reproduction via a single parental individual and potentially the founding of a population from a single seed. Both breeding systems potentially provide reproductive assurance independently from pollinators or pollen vectors. Therefore, both apomixis and selfing have been thought to be major advantages for colonization scenarios (Baker's Law; Baker 1955, 1967; Baker and Stebbins 1965) and genetic bottlenecks. Selfing is often found in pioneer plants, in weeds and in island endemics (e.g., Barrett 1996; Bernardello et al. 2001), while apomixis is a frequent mode of reproduction of species colonizing previously glaciated areas and high altitudes (Bierzychudek 1985; Hörandl 2006). Both modes of reproduction result in a reduction of genotypic diversity within populations.

Conclusions

Apomixis is a novel and puzzling phenomenon to overcome genetic bottlenecks (including meiotic division) and dependence on pollinators. However, reduction in genetic diversity through this phenomenon and the potential of apomicts to become colonizers are a matter of great concern. In agricultural crop improvement apomixis has a tremendous potential as it leads to the formation of genetically uniform populations and helps in perpetuating hybrid vigour through successive seed generations. Studying the genetics of apomixis has become the thrust area of research. Incorporating genes for apomixis can contribute to developing new cultivars from varieties that are locally adapted.

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