

Apomixis: A Boon to Plant Breeding

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ABSTRACT

Apomixis is a method of asexual reproduction in plants i.e., seed formation without fertilization with three main variants, viz., apospory, diplospory, and adventitious embryony. Genetic understanding of apomixis has been handicapped for a long time due to lack of techniques viz., for isolation of embryo sacs, use of flow cytometry, and availability of molecular markers for a rapid and accurate identification of apomictic genotypes (Crane and Carman, 1987; Peel, 1993). Apomixis is a consequence of deregulation of the genes involved in sexual reproduction. Harnessing apomixis is a major goal in applied plant genetic engineering. In this regard, efforts are focused on genetic and breeding strategies in various plant species, combined with molecular methods to analyze apomictic and sexual modes of reproduction and to identify key regulatory genes and mechanisms underlying these processes. These can open new avenues for the transfer of the apomixis trait to important crop species and will have far-reaching potentials in crop improvement regarding agricultural production and the quality of the products. This review paper contains an idea about apomixes, types, genes involved in genetic and molecular basis of apomixis and role in crop improvement. Therefore, it seems that apomixis is about to change the face of plant breeding forever.

Keywords

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Introduction

Apomixis (apo = detached/separate; mixis = union/combination) term introduced in 1908 by Winkler, seeds are formed but the embryos develop without fertilization (Nogler, 1984). When sexual reproduction does occur, the apomixis is termed as 'Facultative', ex- Blue grass, Pearl millet and Sorghum.

When sexual reproduction is absent, it is referred to as 'Obligate', ex- *Panicum maximum*. Apomixis is usually found at a higher ploidy level. Apomixis is a complex and coordinately regulated cascades of events controlled by one or a few genes (Savidan

2000). Apomixes is controlled by large sectors of DNA in which recombination is suppressed (Bicknell *et al.*, 2000).

Apomixis deviates from sexual reproduction in following aspects (Ramulu *et al.*, 1998)

Modification or complete omission of meiosis.

Formation of unreduced megaspore.

Parthenogenetic development of embryo.

Autonomous or pseudogamous endosperm development.

Three developmental components of apomixes (Naumova, 1993)

Apomeiosis

Imperfect or suppressed meiosis, a characteristic of the life cycle of many higher polyploids.

Parthenogenesis

A type of asexual reproduction in which a female gamete or egg cell develops into an individual without fertilization.

Pseudo apomixis or autonomous apomixes

Apomixis requires fertilization to produce the endosperm of the seed.

Conversion of apomictic plant

Three ways to convert sexual crops into apomictic plant

Wide crosses with apomictic wild relatives

Mutation

Genetic transformation.

Types of apomixis

Two types of apomixis (Stebbins, 1950)

Sporophytic

A sporophyte is the diploid multicellular stage in the life cycle of a plant. It develops from the zygote produced when a haploid egg cell is fertilized by a haploid sperm and each sporophyte cell therefore has a double set of chromosomes, one set from each parent.

Types of sporophytic (Bashaw, 1980)

Adventive embryony

Also called sporophytic apomixis, sporophytic budding, or nucellar embryony, megagametophyte in the ovule, but the embryos do not arise from the cells of the gametophyte; they arise from cells of nucellus or the integument. *e.g.*, citrus, mango, jamun etc.

Parthenogenesis

Asexual reproduction in which growth and development of embryos occur without fertilization.

Haploid parthenogenesis

The haploid eggs are not fertilised by the male gamete and develop into the haploid individuals.

e.g., *Solanum nigrum*, *Nicotiana* and Maize

Diploid parthenogenesis

In the diploid parthenogenesis, the embryo develop from the unfertilized diploid eggs

e.g., Grasses like *Taraxacum*

Apogamy

The asexual development of a sporophyte from a cell or cells of the gametophyte other than the egg.

e.g., *Allium* sps.

Gametophytic

Apomixis where the maternal seed embryo develops from the egg cell of a well-developed embryo sac, without fertilization.

Types of gametophytic (Bashaw, 1980)

Apospory

Apospory is the development of 2 n gametophytes, without meiosis and spores, from vegetative, or nonreproductive, cells of the sporophyte.

e.g., Malus, Crepis, Paspalum, Pennisetum, Poaceae, Ranunculus, Sorghum

Diplospory

Diplospory is an apomeiotic pathway where a diploid embryo sac develops from an unreduced megaspore mother cell. *e.g., Ixeris, Antennaria Tripsacum, Eragrostis, and Taraxacum*

Embryo sac development in apomictic plant

There are seven types of diplosporic embryosac development

Taraxacum type: Genera of Compositae and in *Arabis* and *Paspalum* species.

Ixeris type

Antennaria type

Allium type: *Allium* species

Blumea type

Elymus type: *Elymus rectisetus*

Eragrostis type

There are two types of aposporic embryosac development

Hieracium type

Panicum type

Genetic basis of apomixis are involved in shaping the apomictic phenotype (Ortiz *et al.*, 2013)

Termination of meiosis.

Formation of aposporous embryo sacs and their parthenogenetic development

Sporophytic and Gametophytic factors

Modify gene expression

Segregation distortion

Suppressed recombination and environmental effects

Presence of asymmetric genome regions

Techniques for isolation of apomictic plant (Spillane *et al.*, 2004)

There are five types of techniques for isolation of apomictic plant:

Morphological

Uniformity of progeny from heterozygous or cross-pollinated parents. Occurrence of maternal phenotypes in crosses

Cytological

Cytological analysis of developing embryo sac is made at different stages from initiation of MMC to the formation of mature embryo sac.

Histological

Female florets at different stages of maturity are collected. Fixed in FAA for 24 h and are then transferred to 70% ethanol. Pistils are dissected and dehydrated using the ovule clearing method.

Fig.1 Normal double fertilization

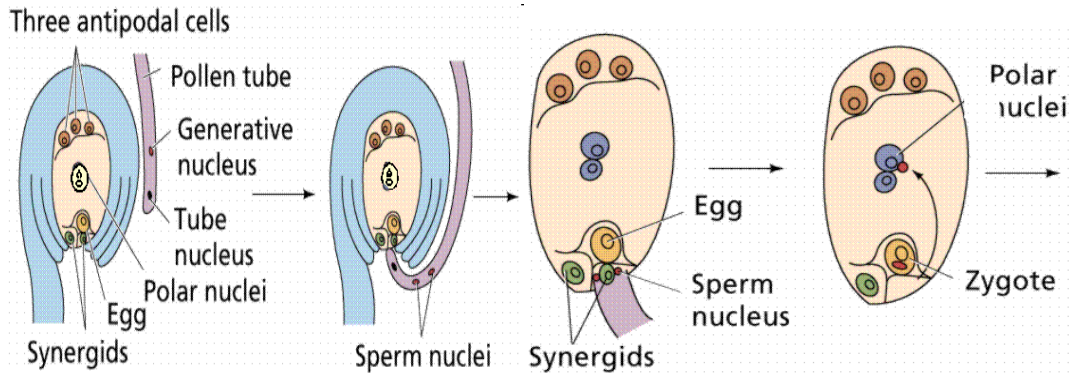


Fig.2 Initiation and progression of apomictic mechanisms relative to events in the sexual life cycle of angiosperms

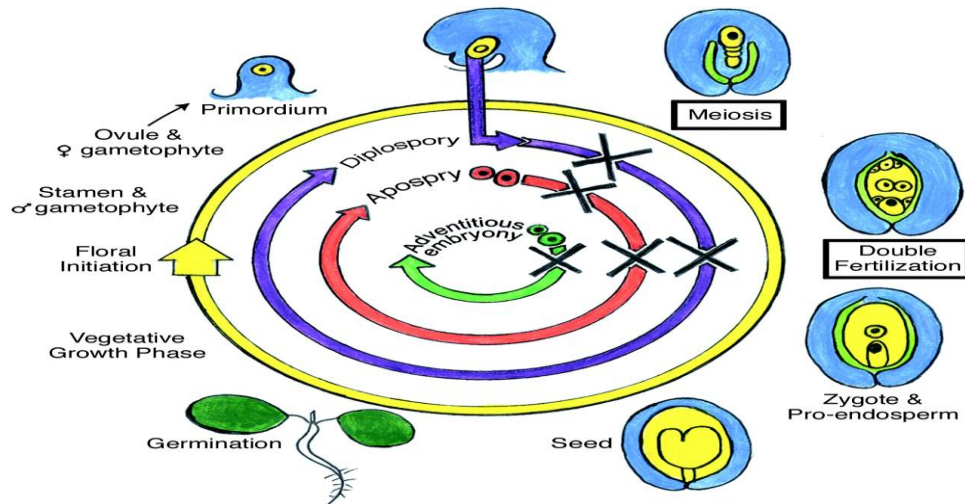


Table.1 A brief overview of the genetic basis of different types of apomixes

Species	Type of apomixis	No. of loci	Genome
<i>Brachiaria</i>	Apospory, Parthenogenesis	1	Aaaa
<i>Cenchrus</i>	Apospory, Parthenogenesis	1	Aaaa;+
<i>Erigeron</i>	Diplospory	2	D/dd;+Fff
<i>Hieracium</i>	Apospory, Parthenogenesis	2	Aaaa, Pppp;+
<i>Panicum</i>	Apospory	1	Aaaa;+
<i>Paspalum</i>	Apospory, Parthenogenesis	1	Aaaa;+
<i>Paspalum</i>	Apospory, Parthenogenesis	1	Aaaa;+
<i>Pennisetum</i>	Apospory, Parthenogenesis	1	Aaaa;+
<i>Poa</i>	Apospory	2	Aaaa, Pppp
<i>Ranunculus</i>	Apospory, Parthenogenesis	1	Aaaa
<i>Taraxacum</i>	Diplospory	3	Ddd, Ppp;+
<i>Tripsacum</i>	Diplospory	1	Dddd;+

Table.2 A brief overview of the molecular basis of different types of apomixes

Species	Endosperm development	Candidate genes	Reference
<i>Brachiaria</i>	Pseudogamous	RPS8-RPS1a-RPL41	Lacerda <i>et al.</i> , 2013
<i>C. Ciliaris</i>	Pseudogamous	BMM-like	Conner <i>et al.</i> , 2008
<i>Heiracium spp.</i>	Autonomous	HFIE	Rodrigues <i>et al.</i> , 2008
<i>Heiracium performatum</i>	Pseudogamous	HAPPY locus	Galla <i>et al.</i> , 2010
<i>Pennisetum notatum</i>	Pseudogamous	LORELE1	Felitti <i>et al.</i> , 2011
<i>Boechera</i>	Pseudogamous	APOLLO	Corral <i>et al.</i> , 2013

Table.3 Current research on apomixes

APOMICTIC SPECIES	ORGANIZATION	LOCATION
WHEAT	Institute of Plant Genetics	Germany
<i>Hieracium</i>	C&FR	New Zealand
Evolution of apomicts	Utah State University	Logan, USA
Histology of apomixis	Jagellonian University	Poland
<i>Taraxacum</i>	NIOO	Netherlands
<i>Pennisetum</i>	USDA -ARS	Tifton, USA
Molecular tools for apomixis	CAMBIA	Australia
<i>Allium</i>	Kyusu National Agricultural experimental staion	Japan
Rice	Academia Sinica	China
<i>Hieracium</i>	CSIRO	Adelaid, Australia
<i>Pennisetum</i>	University of Georgia	Tifton, USA
<i>Paspalum</i>	IBONE	Argentina
<i>Tripsacum dactyloides</i>	CIMMYT	Mexico
<i>Brachiaria</i>	CIAT	Coloumbia
Somatic Embryogenesis	Wageningen Agricultural University	Netherlands
Cassava	University of Brasilia	USA
<i>Arabidopsis Mutagensis</i>	CSIRO	Australia

The pistils are embedded in parafilm, sectioned at 10 mm and stained with safranin O-fast green.

Biochemical

Isozyme markers can be used to study genetic variation and to detect the presence of apomixis. The apomictic breeding behaviour was detected in *Arabis holboelli* and *Allium tuberosum* through enzyme electrophoresis.

Molecular

If the genes for apomixis can be tagged with molecular markers such as RAPD, RFLP or AFLPs, breeding material can be screened for apomixis.

Two molecular markers (UGT 197 and OPC-04) were identified while making crosses between two wild species of *Pennisetum* and sexual Pearl millet.

Effect of apomixis

Biodiversity

Transfer or introduction of apomixis promotes uniformity. *Pennisetum olystachion* and *Pennisetum subangustum* (Schmelzer and Renno, 1997).

Mutation

“Conditional apomixis” approach in which apomictic reproduction is temporarily switched to sexual reproduction (or vice versa) has gained importance. Conditional apomixis can be achieved using special promoters whose expression level is changed by certain chemical mutagens (Spillane *et al.*, 2004).

Polyploidy

Apomixis arose from asynchronous expression of duplicate sexual reproductive gene sets in hybrid or polyploid genomes. Alleles responsible for apomixis may act as or linked to recessive lethal factors, thus they can only be transferred by a diploid or polyploid gamete (Nogler, 1993; Naumova, 1987 and Vielle-Calzada, 1996).

Application of apomixis

Fixation of heterosis.
Production of homozygous line
Production of vybrids.

Advantages of apomixis

Higher multiplication rate of superior genotypes, including hybrids, as clones in form of seed.

Multiply apomictic hybrid seeds forever since they are clones. This will cause enormous reductions in the price for industry and

breeding companies and seed costs for farmers’ apomictic hybrid seeds. Apomictic hybrids will not need cytoplasmic male sterility and fertility restorer systems, which means much shorter and easier hybrid development procedures

Easy in storage and planting
Suitability for machine planting
Usage of less seed material

Less bearing of diseases with those of propagation by clone (maintaining genetic structure and fixing superior genotypes after crossing).

“Boutique Breeding” approach to develop specific hybrids for microproduction areas (Jefferson, 1994).

Yield increases of 20%–50% can be expected from hybrids in self-pollinating major crops such as rice and wheat (Tester and Langridge, 2010) as a result of apomixis technology.

In self-pollinating crops no need for six or seven selfing generations to make segregating loci homozygous allow the development of new varieties with one cross.

Apomixis for plant breeding will increase the survival of interspecific crosses.

Apomixis is known to facilitate the survival of hybrids from wide species, at least under natural conditions (Bashaw and Hanna, 1990).

Apomixis will allow multiplication of clonal propagation material in the form of seeds in crops such as potato (Spillane *et al.*, 2004) and cassava (Freitas and Nassar, 2013).

Disadvantages

Apomixis genes could escape into wild relatives and cause genetic erosion

Gene transfers from apomictic crops to sexual wild relatives, both of which might have the same ploidy level.

Epigenetics and genomic imprinting problems

The unsuccessful attempts to transfer apomixis to an experimental or crop species through conventional breeding procedures results in phenomenon called genomic imprinting.

Ecological risks

A dominant apomixis transgene spread through pollen across populations to a related outcrossing species resulting in rapid fixation of genotypes, displacement of sexual siblings and lead to a reduction in the genetic diversity both within a crop and among its close relatives. Apomixis technology is that it may entrench the trend of monocultures in agriculture thus reducing biodiversity.

Future prospects of apomixis

Ease of multiplying and maintaining elite hybrid genotypes.

Ease of producing high-quality pure seed without isolation.

Possibilities for selection of more closely adapted diverse genotypes are expected for fixation of hybrid vigor and lower the cost of hybrid seed production.

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