



## Apomixis and Its Agricultural Potential

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### ABSTRACT

Apomixis is a form of reproduction without fertilization in plants. It has been observed in more than 400 plant species, although it is absent in major crop plants. Apomixis is considered to be a powerful biotechnology tool for maintaining hybrid vigor across generations by producing seeds that are genetically identical to maternal plant. However, the molecular mechanisms underlying apomixis remain poorly understood. Numerous studies have been conducted with the aim of introducing apomict phenotypes into crop species. This review provides a brief overview of apomixis, its mechanisms and current applications.

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### Introduction

Apomixis is a process of seed formation that occurs without fertilization. This trait is particularly important because it allows the production of clonal seeds of maternal plant. Although hybrid seed production through crossbreeding is very widely used and effective method, it is often time consuming and labor intensive. On the other hand, technologies such as CRISPR have reduced the time and effort required for such breeding processes [1]. A major challenge in conventional hybrid breeding is the difficulty in preserving hybrid vigor across generations due to segregation in the progeny. These limitations of sexual reproduction make apomixis a promising alternative for maintaining hybrid vigor by enabling the generation of cloned seed without fertilization. Several studies have demonstrated that the successful introduction of apomixis into crop plants could lead to significant economic benefits.

Apomixis involves complex genetic and developmental process, and its underlying mechanism are still not fully understood. Understanding how apomixis works and how it is regulated at the molecular level is essential for advancing agricultural biotechnology. Its genetic basis is still not fully understood. If apomixis can be introduced into breeding programs for agronomic crops, it would allow for fixation and propagation of desirable genetic traits. [2]

The phenomenon was first described in *Alchornea ilicifolia* [2] and has been observed in at least 400 different plant species including *Hieracium*, *Taraxacum*, and *Pennisetum*. However, it is rare among economically important crops, with notable exceptions such as apple and *Citrus*. It is believed that apomixis may be more widespread than currently recognized because identifying apomictic species through cytogenetic and molecular analyses is challenging. To understand the mechanism behind apomixis, it is necessary first to study the genes and regulatory pathways involved in sexual reproduction, since apomixis is thought to have evolved from these pathways [3].

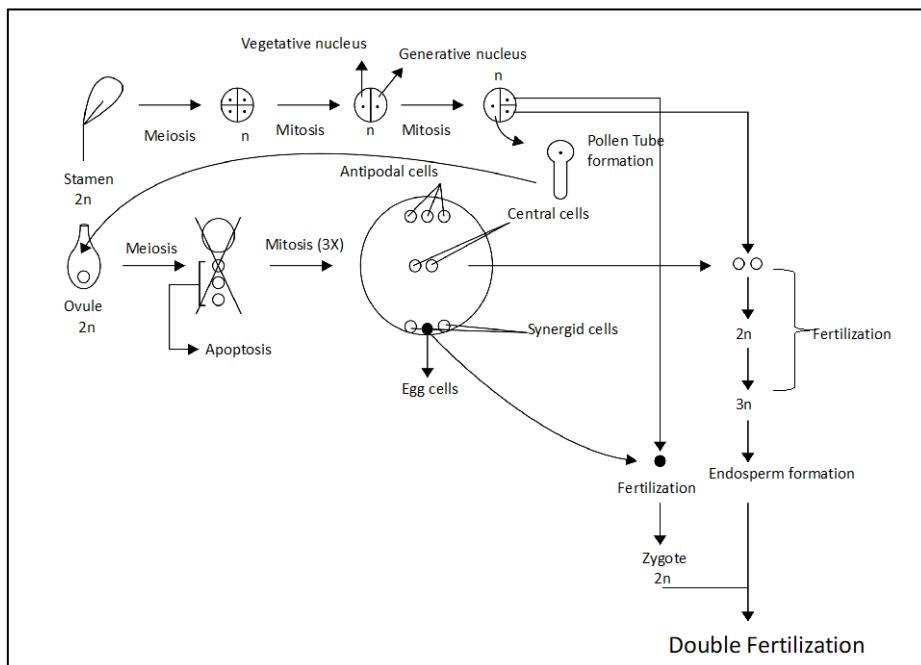
### Sexual reproduction in plants (amphimixis)

In sexual reproduction, the formation of male and female gametes through meiosis is essential, followed by the fusion of these gametes to form a zygote. Female gamete formation occurs within the ovule [4]. Inside the ovule, diploid megasporangium undergoes meiosis producing four haploid cells. Three of these cells undergo programmed cell death (apoptosis) while remaining cell undergoes three rounds of mitosis, ultimately forming an eight-nucleated embryo sac. Embryo sac consists of one egg cell, two central cells, two synergid cells, and three antipodal cells [5]. Male gamete formation, also known as microsporogenesis, takes place in pollen sac. Here, microspore mother cell undergoes meiosis to produce microspores which subsequently undergo two mitotic divisions to form mature male gametophytes with haploid (n) chromosome

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number. In most angiosperms, a single mitotic division leads to formation of bicellular pollen, which later undergoes a second mitotic division within pollen tube to produce two sperm cells [6]. During pollination, pollen grains germinate on the stigma and form pollen tube that grows down the style toward the ovule. The pollen tube carries sperm cells that fertilize two cells within female gametophyte. This process, known as double fertilization (Fig 1), involves one sperm cell fusing with the egg cell to form diploid zygote, while the other fuses with polar nuclei to produce the triploid endosperm.



**Fig 1** Double Fertilization: this process requires two essential steps: first step; microsporogenesis (microspore formation in pollen sac.) and megasporogenesis (formation of embryo sac), second step; fertilization of central cells for formation of endosperm and fertilization of egg cell to produce zygote.

### Biology of natural apomixis

Apomixis is a form of asexual reproduction in which seeds are produced without undergoing meiosis or fertilization. As a result, all offspring are genetic clones of maternal parent. Since apomictic plants produce clonal progeny, apomixis holds significant potential for use in agriculture, particularly in maintaining hybrid vigor and producing superior germplasm for plant breeders [7].

### Mechanisms of apomixis

Although various mechanisms of apomixis exist, the process typically involves three major developmental steps: (i) apomeiosis (the avoidance of meiosis during embryo sac development), (ii) parthenogenesis (embryo development without fertilization), and (iii) endosperm formation, which may occur with or without fertilization [8]. Apomeiosis refers to process by which meiosis is circumvented, leading to formation of unreduced (diploid) gametophytes. There are two primary types of apomeiosis are; diplospory and apospory. In diplospory, megasporangium (MMC) directly forms an unreduced embryo sac without undergoing meiosis [9]. In Apospory, somatic nucellar or integumental cells adjacent to MMC differentiate into unreduced embryo sacs [10]. Parthenogenesis is the development of an embryo from an unfertilized egg cell. Following apomeiosis, parthenogenesis ensures that the unreduced egg cell initiates embryogenesis without requiring male gametic fusion. For functional apomixis, apomeiosis and parthenogenesis must be tightly coordinated.

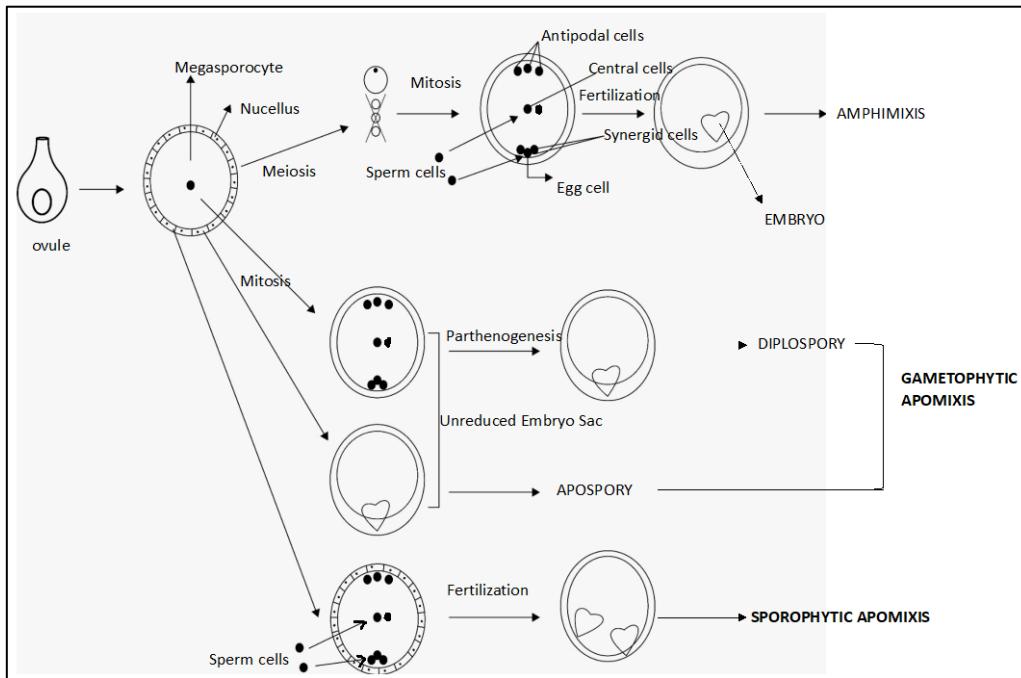
### Types of apomixis

Apomixis can generally be divided into two categories based on how the embryo develops: gametophytic and sporophytic (also called adventitious embryony) apomixis. If the embryo arises from a gametophyte, it is classified as gametophytic apomixis; if it originates from diploid somatic cells outside an embryo sac, it is considered sporophytic apomixis [3] (Fig 2).

In sporophytic apomixis, the embryo develops directly from sporophytic cells that have not undergone meiosis and located outside the embryo sac. These precursor cells typically differentiate from the nucellus or inner integument. After undergoing mitotic divisions, they form multiple globular embryos. Although sexual

pathway is still partially followed and embryo sac is formed, successful embryo development depends on endosperm formation, which generally requires fertilization of the sexual embryo sac.

Gametophytic apomixis can be further divided into diplosropy and apospory, depending on the origin of the initial cell forming the unreduced embryo sac [11]. In diplosropy, the megasporocyte undergoes mitosis-like division, resulting in the formation of two unreduced megasporocytes. One of these develops into diploid embryo sac via parthenogenesis without fertilization [12]. Diplosropy typically initiates early during megasporocyte differentiation. In contrast, apospory occurs later and involves the formation of embryo sac from somatic cells within the ovule that do not undergo meiosis [13]. In some cases, single ovule may contain multiple aposporous initial cells, leading to the formation of more than one embryo sac [4].



**Fig 2** Apomixis; inspired from [14]: Apomixis is classified into gametophytic and sporophytic types, depending on the origin of the embryo. In gametophytic apomixis, the embryo develops from an unreduced embryo sac. This can occur via diplosropy, where the megasporocyte skips meiosis, or via apospory, where somatic cells within the ovule give rise to the embryo sac. In both cases, the embryo forms without fertilization through parthenogenesis. In sporophytic apomixis, embryos arise directly from somatic cells outside the embryo sac, usually from the nucellus or inner integument, and develop through mitotic divisions.

Endosperm formation in apomictic species may occur autonomously, without the need for fertilization, or through pseudogamy, which involves the fusion of polar nuclei with sperm nucleus from pollen [8]. Facultative apomixis refers to plant species that are capable of both sexual and asexual reproduction. In such species, the formation of archesporial cells and aposporous cells may occur simultaneously during ovule development. Polyembryony, the phenomenon of multiple embryos forming within a single ovule, is commonly associated with apomixis. Apomictic species are predominantly polyploid and polyploidy is often associated with reproductive instability and the breakdown of mechanisms like self-incompatibility, leading to the evolution of novel reproductive strategies [15]. The emergence of apomictic trait is believed to be influenced by long term environmental conditions.

### How does an apomictic individual arise?

The emergence of apomixis is thought to be a consequence of genetic mutations and natural selection within the framework of double fertilization. While many mutations are deleterious, leading to infertility or poor environmental adaptation, some rare mutations give rise to apomictic development [16].

Plants can exhibit facultative apomixis, maintaining both sexual and asexual reproductive pathways. However, mutations that result in complete reliance on apomictic reproduction (obligate apomixis) are considered rare due to improbability of multiple concurrent gene mutations necessary to entirely replace sexual pathways [17].

Meiosis, being finely tuned and complex process, is highly susceptible to genetic mutations or environmental stressors, which can lead to reduced gamete viability or complete sterility. Such disturbances may initiate a shift from sexual reproduction to apomixis [18].

Frequent events like polyploidy and hybridization in apomictic plants have further disturb seed development, possibly facilitating the evolution of apomixis.

### Apomixis controlling loci and related genes

In several species, apomixis associated loci have diverged significantly from homologous regions in sexual plants, likely chromosomal arrangements and transposable element activity, leading to suppressed recombination [19, 20]. Each key component of apomixis; apomeiosis, parthenogenesis and endosperm development, is typically associated with specific locus [13, 21-23]. In *Erigaron annuus* and *Taraxacum officinale*, diplospory is inherited as dominant trait [24, 25]. In *Taraxacum*, diplospory and parthenogenesis are controlled by two distinct, unlinked loci (DIPLOSPOROUS, DIP, and PARTHENOGENESIS, PAR) [26]. Similarly, the apospory specific genomic regions (ASGR) in *Pennisetum squamulatum* and *Cenchrus ciliaris* are hemizygous, heterochromatic regions located [27-29] in single chromosomes. In *Paspalum simplex*, apomixis-controlling locus (ACL) is non-recombining hemizygous region [30].

In *Hieracium*, three loci have been mapped that control apospory (LOA), parthenogenesis (LOP), an autonomous endosperm development (AutE) [31]. The LOA locus, associated with the loss of apomeiosis, is situated on recombination-suppressed chromosome arm, embedded within complex repeats and transposons that are not essential for its function [32, 33]. Recent studies have identified long noncoding RNAs (lncRNAs) linked to apomixis regulation. For instance, lncRNA is associated with MAP3K gene named QUI-GON JINN (QGJ), was found to influence the aposporous embryo sac formation [34].

Evidence also suggests that non-coding RNAs regulate parthenogenesis and endosperm formation. In *Paspalum simplex*, antisense transcripts from three genes within the ACL region were identified, supporting the idea that epigenetic regulation underlies parthenogenesis [23, 30, 35, 36].

In *Hypericum perforatum*, the HAPPY locus cosegregates with apospory but not parthenogenesis. This region contains truncated version of the *Arabidopsis* ARIADNE7 (ARI7) gene, which encodes an E3 ligase involved in protein degradation [23]. Sequencing revealed 33 genes at the HAPPY locus, with 24 expressed during early ovule development [37]. In *Boechera*, the APOMixis Linked LOKus (APOLLO) gene is candidate for regulating female apomeiosis, being more highly expressed in apomictic ovules [38, 39]. Together, these findings suggest that subtle regulatory shifts rather than major mutations in coding sequences, underlie the acquisition of apomictic traits.

Both abiotic and biotic stress factors have been shown to influence apomixis in various plant species are other regulators on apomixis shown in various studies [40-44]. For example, oxidative stress conditions such as drought, heat, nutrient deprivation, and hydrogen peroxide ( $H_2O_2$ ) exposure have been associated with the transition from meiosis to apomeiosis [43]. Extended photoperiods have also been shown to affect apomeiosis and parthenogenesis in *Ranunculus auricomus*, where plants exhibited distinct variations in stress-related metabolite profiles [45]. Additional studies have demonstrated that light stress can modulate megasporogenesis and influence reproductive development [46].

Epigenetic mechanisms-such as DNA methylation, histone acetylation, and chromatin modifications- also play crucial roles in the transition from sexual to asexual reproduction. Small RNAs (sRNAs) and transposable elements (TEs) contribute to the plasticity of plant genomes response to environmental stress, and they are believed to influence the activity of apomixis-related genes. Although conclusive evidence is still lacking, many studies suggest that TEs are actively involved in regulating apomixis. These elements can alter the function and expression of nearby genes through insertional events and epigenetic modifications [47-49]. Retrotransposon activity is generally silenced in apomictic loci by suppression of recombination [50]. In *Pennisetum squamulatum* and *Cenchrus ciliaris*, six retrotransposons have been identified that are potentially involved in the apomixis process [51]. In another study, hypomethylation of the Gy163 retrotransposon led to overexpression in apomictic tissues compared to sexually reproducing tissues [28].

The Apomixis-specific genomic region (ASGR) found in both *Cenchrus ciliaris* and *P. squamulatum* contains a high density of transposons and repetitive DNA sequences [5,6]. These findings support the hypothesis that transposable elements play key role in genetic regulation of apomixis [52].

The centromeric or telomeric regions of plant genomes are typically highly methylated and tightly packed (heterochromatic). In maize, for instance, certain TEs are known to be specially targeted for methylation within heterochromatin. Several retrotransposons have also been proposed as candidates for involvement in apomictic development. Epigenetic changes affecting sexual reproduction pathways may be associated with

apomixis. For instance, the *AGO104* protein in maize, a homolog of the small RNA-silencing protein *AGO9*, has been linked to apomictic-like phenotypes when silenced [53].

### Limitations of natural apomixis and need for synthetic apomixis

Although apomixis known to be heritable, identifying the gene loci or genomic elements associated with it remain challenging. This is due to the presence of recombination-suppressed regions and repetitive flanked regions near apomixis-related genes. As a result, researchers have employed sequencing technologies and map-based cloning techniques to identify these regions [13, 22, 54-57]. Studies have shown that apomixis-related loci are often located in chromosomal regions that are significantly divergent from sexual counterparts. These regions are believed to have arisen through chromosomal rearrangements and the activity of transposable elements, both of which can lead to reduced or absent recombinations [19, 20].

Introducing apomixis to crop plants is considered essential for preserving superior genetic traits and maintaining hybrid vigor across generations.

### Mimicking apomeiosis, composite methods for engineering apomixis

In affords to implement apomixis in crops such as rice and *Arabidopsis*, researchers have employed combined strategies involving apomeiosis with parthenogenesis or genome elimination. Composite approaches have successfully enabled the introduction of apomixis into sexual plants by combining MiMe mutants with other pathways promoting uniparental embryo development. For instance, in rice combining MiMe triple mutant with ectopic expression of OsBBM1 in egg cells enabled asexual reproduction with 11-29% efficiency and transgenerational heritability of clonal offspring.

### Synthetic apomixis: details on MiMe (Mitosis Instead of Meiosis) and related technologies

Apomixis enables the production of clonal seeds that preserve hybrid vigor, making it a major goal in plant breeding [19, 20]. Despite progress, fertility problems limit synthetic apomixis in grain crops like rice, where high clonal seed rates often reduce seed yield [19, 20]. In contrast, fruit and vegetable crops tolerate lower fertility, and apomixis components have been shown in tomato, opening new possibilities [19, 20]. Apomixis could also help fix hybrid genotypes in complex crops like potato [19, 20]. Synthetic apomixis involves bypassing sexual reproduction to clonally fix hybrid genotypes. Recent advances have shown that key mechanisms from haploid induction (HI)- single fertilization, chromosome elimination, and parthenogenesis- can be leveraged to achieve this goal. In single fertilization, only the central cell fertilized, while the egg cell remains unfertilized but can still develop into an embryo, producing a maternal haploid [19, 20]. In chromosome elimination, fertilization occurs normally, but paternal chromosomes are later lost, often due to disruptions in centromere components like CENH3 or genes such as *ZmPLA1* and *ZmDMP* [19, 20]. Parthenogenesis, the development of an embryo from an unfertilized egg, is induced by genes like *PsASGR-BBM1* and *PAR*, and plays a central role in enabling fertilization-independent seed formation [19, 20]. These mechanisms can be combined with the MiMe system-which converts meiosis into mitosis-to generate diploid progeny [19, 20]. Altogether, this integrated strategy represents a promising synthetic route to stable, clonal seed production in hybrid crops.

In *Arabidopsis*, a set of mutations that resulted in apomict-like phenotypes have been reported, such as *ago9* [58] and *swi1* [59], *spo11-1/2* [59], *mtopVIB* 78, *dfo* [60], *prd1* [59], and *rad50* [61, 62], *dmc1* [63] *msh4* [64], *asy1* [65] *rec8* [66], *scc3* [67], and *ahp2* [68], *osd1* [69], *tam* [70], *tdm1* [71], *msi1* [72], *cenh3* [73], *fie* [74], and *fis* [75]. Collectively, these mutations are known as "Mime" (Mitosis instead of Meiosis) mutations [76], a strategy in which meiosis is replaced by mitosis to create clonal seeds. However, Mime alone is not sufficient to produce clonal progeny, as it does not include the parthenogenetic component required for embryogenesis. Parthenogenesis refers to formation embryos without fertilization, leading to haploid or diploid offspring [77, 78]. Transgenic rice and maize lines expressing the *PsASGRBBM1* constructed by a *P. squamulatum* promoter or a DD45 promoter resulted in egg cell-specific expression in haploid embryos [79]. Previous studies demonstrated that expression of the *OsBBM1* gene of rice induced somatic embryos prior to fertilization [61]. According to that, the *BBM1* gene is shown as a candidate as an inducer of embryogenesis. Most recently, it was shown in the CRISPR-Cas9 screening of candidate genes analysis that the *PAR* locus is responsible for the single dominant gene of dandelion parthenogenesis [80].

It was challenging to clone genes related to apomixis because of limited genomic resources, polyploidy, and low recombination rates. There have been many ventures for identifying genes related to apomeiosis. In *Poa pratensis*, *APOSTART* genes have been identified [34]. It was demonstrated in the study that a long non-coding RNA regulates the gene QUI-GON JINN, affecting aposporous embryo sac formation in *Paspalum notatum* [81]. The DIPLOSPOROUS (DIP) locus is associated with unreduced female gamete formation in

*Taraxacum* [82]. The LOSS OF APOMEIOSIS (LOA) locus regulates apospory in *Pilosella piloselloides* [83]. APOLLO alleles show strong correlation with apomicts in *Boechera* accessions, with the 5' UTR of the APOLLO apomictic allele being crucial for expression in reproductive tissues in *Arabidopsis* [84]. *TRIMETHYLGUANOSINE SYNTHASE1* (TGS1) in *Arabidopsis* has shown promising evidence as a candidate gene for apomeiosis [85]. Apomeiosis and parthenogenesis associated candidate genes are demonstrated in Table 1.

The central goal of engineering apomixis is the preserve favorable traits carried by a single parental genotype. One strategy involves post-fertilization genome elimination in diploid zygotes, where removing either maternal or paternal chromosome set can lead to haploid induction.

**Table 1** Genes involved in apomeiosis and parthenogenesis

Gene Name	Organism	Function	Reference
AGO9	<i>Arabidopsis thaliana</i>	Apomeiosis	[58]
SWI1	<i>Arabidopsis thaliana</i>	Apomeiosis	[59]
SPO11-1/2	<i>Arabidopsis thaliana</i>	Apomeiosis	[86, 87]
MTOPVIB	<i>Arabidopsis thaliana</i>	Apomeiosis	[88]
DFO	<i>Arabidopsis thaliana</i>	Apomeiosis	[60]
PRD1	<i>Arabidopsis thaliana</i>	Apomeiosis	[89]
RAD50	<i>Arabidopsis thaliana</i>	Apomeiosis	[61, 62]
DMC1	<i>Arabidopsis thaliana</i>	Apomeiosis	[63]
MSH4	<i>Arabidopsis thaliana</i>	Apomeiosis	[64]
ASY1	<i>Arabidopsis thaliana</i>	Apomeiosis	[65]
REC8	<i>Arabidopsis thaliana</i>	Apomeiosis	[66]
SCC3	<i>Arabidopsis thaliana</i>	Apomeiosis	[67]
AHP2	<i>Arabidopsis thaliana</i>	Apomeiosis	[68]
OSD1	<i>Arabidopsis thaliana</i>	Apomeiosis	[69]
TAM	<i>Arabidopsis thaliana</i>	Apomeiosis	[70]
TDM1	<i>Arabidopsis thaliana</i>	Apomeiosis	[71]
MSI1	<i>Arabidopsis thaliana</i>	Apomeiosis	[72]
CENH3	<i>Arabidopsis thaliana</i>	Apomeiosis	[73]
FIE	<i>Arabidopsis thaliana</i>	Apomeiosis	[74]
FIS	<i>Arabidopsis thaliana</i>	Apomeiosis	[75]
TGS1	<i>Arabidopsis thaliana</i>	Apomeiosis	[85]
QUI-GON JINN	<i>Paspalum notatum</i>	Apomeiosis	[81]
DIP	<i>Taraxacum</i>	Apomeiosis	[77]
LOA	<i>Pilosella piloselloides</i>	Apomeiosis	[78]
APOLLO	<i>Boechera</i>	Apomeiosis	[84]
APOSTART	<i>Poa pratensis</i>	Apomeiosis	[34]
PsASGR-BBML	<i>Panicum squamulatum</i>	Parthenogenesis	[79]
OsBBM1	<i>Oryza sativa</i>	Parthenogenesis	[6]
BBM1	<i>Oryza sativa</i>	Parthenogenesis	[80]
PAR	<i>Taraxacum</i>	Parthenogenesis	[80]

In plants this can be achieved using modifications to centromere specific histone H3 protein, known as CENH3, which plays key role in chromosome segregation [90]. In *Arabidopsis*, a null mutation in cenh3-1 causes embryo lethality but can be rescued by expressing GFP-tagged versions of CENH3. While the GFP-CENH3 fusion rescues fertility with low haploid induction, the GFP- tailswap- variant where the N-terminal tail is replaced with that conventional H3- induces haploids efficiently but causes male sterility [73].

### Genetic and evolutionary implications of apomixis

The evolutionary implications of facultative apomixis in plants remain underexplored. Mendelian genetic research has shown that regions controlling apomixis in angiosperm typically exist in heterozygous state [19]. For instance, in *Ranunculus auricomus*, the expression of apomixis is quantitatively depend on the apospory factor (A), dominant Mendelian gene with variable penetrance. However it exhibits lethal effects in haploid or homozygous form implying that apomixis-controlling gene (A) is typically heterozygous when paired with wild type allele (a) [91]. This suggest that apomixis can't be entirely fixed in population, as the dominant allele doesn't fully express in all configurations [91].

Research in facultative sexuality's long term effect is still lacking. However, a study [92] suggest that apomictic polyploid lineages experience a dual process: they accumulate natural mutations similar to the Meselson effect in diverging gene copies, while also masking partially dominant deleterious alleles in clones. These harmful mutations could eventually be purged via facultative sexual reproduction.

Sexual reproduction offers evolutionary advantages by facilitating the removal of harmful mutations through recombination, which enables natural selection to eliminate disadvantageous genotypes [93, 94]. In contrast, apomict reproduction bypasses recombination, resulting in offspring that are genetic clones of maternal parents, thus perpetuating any mutations arise [94, 95]. This leads to irreversible accumulations of mutations, known as Muller's ratchet, which increases genetic load and may drive clonal lineages toward extinction [96]. The Hill Robertson effect further exacerbates this issue by limiting selection efficacy across linked loci [93, 97], leading to reduced adaptive capacity and fitness in several populations [98, 99].

Apomixis is often associated with polyploidy and hybrid origins [100-102], where polyploidy can buffer deleterious mutations through gene redundancy. However, it also increases mutational target size, and recessive mutations may remain masked unless they exhibit partial dominance [18, 103]. Long term asexuality under polyploidy could increase the mutational load due to reduced haploid selection and sustained masking of harmful alleles [104].

## Conclusion and Perspective

The molecular mechanism and regulatory pathways underlying apomixis remain one of the most intriguing challenges in plant biology. Although apomixis is thought to arise from shift between sexual and asexual reproductive models [7], it is not controlled by single mechanism. Instead, it appears to be governed by a complex network of overlapping pathways that influence its developmental process. These pathways include epigenetic regulation as well as the accumulation of mutations in genes associated with sexual reproduction [7]. Research into apomixis has become increasingly important for developing innovative plant breeding strategies, particularly in the context of a growing global population and limited natural resources. Apomixis technology holds the potential to be applied to wide range of agronomic crops. By enabling clonal seed production, apomixis could substantially increase yields in economically important cereals, industrial crops, fruits, vegetables, and even forest species.

Furthermore, the widespread use of apomixis could significantly reduce the costs associated with hybrid seed production. This would revolutionize agricultural systems at multiple levels- from individual farmers to large-scale seed producers- ultimately paving the way for powerful new strategies in both marketing and agricultural biotechnology [11]. Integration of genetic tools such as CRISPR/Cas9 offers a promising avenue to accelerate the commercial use of apomictic plants by simplifying their creation.

## Abbreviations

ACL: Apomixis-controlling locus, AGO9: Argonaute 9, APOLLO: APOmixin Linked LOKus, APOSTART: apomixis-associated gene family in *Poa pratensis*, ARI7: ARIADNE7 E3 ubiquitin ligase, ASGR: apospory-specific genomic region, AutE: autonomous endosperm development, BBM: BABY BOOM transcription factor, CENH3: centromere-specific histone H3, CRISPR: clustered regularly interspaced short palindromic repeats, DFO: defective in female meiosis, DIP: diplospory locus, HI: haploid induction, H<sub>2</sub>O<sub>2</sub>: hydrogen peroxide, lncRNA: long non-coding RNA, LOA: loss of apomeiosis, MiMe: mitosis instead of meiosis, MMC: megasporangium mother cell, PAR: parthenogenesis locus, PCR: polymerase chain reaction, sRNA: small RNA, TE: transposable element.

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The author confirms that the data supporting this study are cited in the article.

## Compliance with ethical standards

### Conflict of interest

The author declares no conflict of interest.

### Ethical standards

The study is proper with ethical standards.

### Authors' contributions

The author conducted and wrote the study without any external support.

## References

1. Barman, H.N., et al., Generation of a new thermo-sensitive genic male sterile rice line by targeted mutagenesis of TMS5 gene through CRISPR/Cas9 system. *BMC Plant Biology*, 2019. 19(1). <https://doi.org/10.1186/s12870-019-1715-0>
2. Smith, J., XXXII. Notice of a Plant which produces perfect Seeds without any apparent Action of Pollen. *Transactions of the Linnean Society of London*, 1841. 18(4): p. 509-512. <https://doi.org/10.1111/j.1095-8339.1838.tb00200.x>
3. Barcaccia, G., et al., A Reappraisal of the Evolutionary and Developmental Pathway of Apomixis and Its Genetic Control in Angiosperms. *Genes*, 2020. 11(8). <https://doi.org/10.3390/genes11080859>
4. Drews, G.N., D. Lee, and C.A. Christensen, Genetic Analysis of Female Gametophyte Development and Function. *The Plant Cell*, 1998. 10(1): p. 5-17. DOI:10.1105/tpc.10.1.5
5. Tucker, M.R. and A.M.G. Koltunow, Sexual and asexual (apomictic) seed development in flowering plants: molecular, morphological and evolutionary relationships. *Functional Plant Biology*, 2009. 36(6). <https://doi.org/10.1071/FP09078>
6. Brewbaker, J.L., The Distribution and Phylogenetic Significance of Binucleate and Trinucleate Pollen Grains in the Angiosperms. *American Journal of Botany*, 1967. 54(9): p. 1069-1083. <https://doi.org/10.1002/j.1537-2197.1967.tb10735.x>
7. Spillane, C., M.D. Curtis, and U. Grossniklaus, Apomixis technology development—virgin births in farmers' fields? *Nature Biotechnology*, 2004. 22(6): p. 687-691. <https://doi.org/10.1038/nbt976>
8. Koltunow, A.M. and U. Grossniklaus, Apomixis: A Developmental Perspective. *Annual Review of Plant Biology*, 2003. 54(1): p. 547-574. <https://doi.org/10.1146/annurev.arplant.54.110901.160842>
9. Bicknell, R.A., Understanding Apomixis: Recent Advances and Remaining Conundrums. *The Plant Cell Online*, 2004. 16(suppl\_1): p. S228-S245. <https://doi.org/10.1105/tpc.017921>
10. Koltunow, A.M., Apomixis: Embryo Sacs and Embryos Formed without Meiosis or Fertilization in Ovules. *The Plant Cell*, 1993: p. 1425-1437. <https://doi.org/10.1105/tpc.5.10.1425>
11. Fei, X., et al., The steps from sexual reproduction to apomixis. *Planta*, 2019. 249(6): p. 1715-1730. <https://doi.org/10.1007/s00425-019-03113-6>
12. Koltunow, A.M., et al., Anther, ovule, seed, and nucellar embryo development in *Citrus sinensis* cv. Valencia. *Canadian Journal of Botany*, 1995. 73(10): p. 1567-1582. <https://doi.org/10.1139/b95-170>
13. Schmidt, A., Controlling Apomixis: Shared Features and Distinct Characteristics of Gene Regulation. *Genes*, 2020. 11(3). <https://doi.org/10.3390/genes11030329>
14. Grimanelli, D., et al., Developmental genetics of gametophytic apomixis. *Trends in Genetics*, 2001. 17(10): p. 597-604. DOI: 10.1016/s0168-9525(01)02454-4
15. Barrett, S.C.H., The Evolution, Maintenance, and Loss of Self-Incompatibility Systems, in *Plant Reproductive Ecology*. 1990. p. 98-124. <https://doi.org/10.1093/oso/9780195063943.003.0005>
16. Boldrini, K.R., M.S. Pagliarini, and C.B. do Valle, Cell fusion and cytomixis during microsporogenesis in *Brachiaria humidicola* (Poaceae). *South African Journal of Botany*, 2006. 72(3): p. 478-481. <https://doi.org/10.1016/j.sajb.2005.11.004>
17. Sharbel, T.F., et al., Molecular signatures of apomictic and sexual ovules in the *Boechera holboellii* complex. *The Plant Journal*, 2009. 58(5): p. 870-882. DOI: 10.1111/j.1365-313X.2009.03826.x
18. Hörndl, E. and F. Hadacek, The oxidative damage initiation hypothesis for meiosis. *Plant Reproduction*, 2013. 26(4): p. 351-367. doi: 10.1007/s00497-013-0234-7
19. Ozias-Akins, P. and P.J. van Dijk, Mendelian Genetics of Apomixis in Plants. *Annual Review of Genetics*, 2007. 41(1): p. 509-537. DOI: 10.1146/annurev.genet.40.110405.090511
20. Pupilli, F. and G. Barcaccia, Cloning plants by seeds: Inheritance models and candidate genes to increase fundamental knowledge for engineering apomixis in sexual crops. *Journal of Biotechnology*, 2012. 159(4): p. 291-311. DOI: 10.1016/j.jbiotec.2011.08.028
21. Barcaccia, G. and E. Albertini, Apomixis in plant reproduction: a novel perspective on an old dilemma. *Plant Reproduction*, 2013. 26(3): p. 159-179. doi: 10.1007/s00497-013-0222-y
22. Hand, M.L. and A.M.G. Koltunow, The Genetic Control of Apomixis: Asexual Seed Formation. *Genetics*, 2014. 197(2): p. 441-450. DOI: 10.1534/genetics.114.163105
23. Schallau, A., et al., Identification and genetic analysis of the APOSPORY locus in *Hypericum perforatum* L. *The Plant Journal*, 2010. 62(5): p. 773-784. DOI: 10.1111/j.1365-313X.2010.04188.x
24. Noyes, R.D. and L.H. Rieseberg, Two Independent Loci Control Agamospermy (Apomixis) in the Triploid Flowering Plant *Erigeron annuus*. *Genetics*, 2000. 155(1): p. 379-390. DOI: 10.1093/genetics/155.1.379
25. van Dijk, P.J. and J.M.T. Bakx-Schotman, Formation of Unreduced Megaspores (Diplospory) in Apomictic *Dandelions* (*Taraxacum officinale*, s.l.) Is Controlled by a Sex-Specific Dominant Locus. *Genetics*, 2004. 166(1): p. 483-492. DOI: 10.1534/genetics.166.1.483
26. Vašut, R.J., et al., Fluorescent in situ hybridization shows DIPLOSPOROUS located on one of the NOR chromosomes in apomictic dandelions (*Taraxacum*) in the absence of a large hemizygous chromosomal region. *Genome*, 2014. 57(11/12): p. 609-620. DOI: 10.1139/gen-2014-0143
27. Akiyama, Y., W.W. Hanna, and P. Ozias-Akins, High-resolution physical mapping reveals that the apospory-specific genomic region (ASGR) in *Cenchrus ciliaris* is located on a heterochromatic and hemizygous region of a single chromosome. *Theoretical and Applied Genetics*, 2005. 111(6): p. 1042-1051. DOI: 10.1007/s00122-005-0020-5
28. Conner, J.A., et al., Sequence Analysis of Bacterial Artificial Chromosome Clones from the Apospory-Specific Genomic Region of *Pennisetum* and *Cenchrus*. *Plant Physiology*, 2008. 147(3): p. 1396-1411. DOI: 10.1104/pp.108.119081
29. Goel, S., et al., Comparative Physical Mapping of the Apospory-Specific Genomic Region in Two Apomictic Grasses: *Pennisetum squamulatum* and *Cenchrus ciliaris*. *Genetics*, 2006. 173(1): p. 389-400. DOI: 10.1534/genetics.105.054429
30. Galla, G., et al., A Portion of the Apomixis Locus of *Paspalum Simplex* is Microsyntenic with an Unstable Chromosome Segment Highly Conserved Among Poaceae. *Scientific Reports*, 2019. 9(1). <https://doi.org/10.1038/s41598-019-39649-6>

31. Catanach, A.S., et al., Deletion mapping of genetic regions associated with apomixis in *Hieracium*. Proceedings of the National Academy of Sciences, 2006. 103(49): p. 18650-18655. DOI: 10.1073/pnas.0605588103

32. Kotani, Y., et al., The LOSS OF APOMEIOSIS (LOA) locus in *Hieracium paealtum* can function independently of the associated large-scale repetitive chromosomal structure. New Phytologist, 2013. 201(3): p. 973-981. DOI: 10.1111/nph.12574

33. Okada, T., et al., Chromosomes Carrying Meiotic Avoidance Loci in Three Apomictic Eudicot *Hieracium* Subgenus *Pilosella* Species Share Structural Features with Two Monocot Apomicts Plant Physiology, 2011. 157(3): p. 1327-1341. <https://doi.org/10.1104/pp.111.181164>

34. Mancini, M., et al., The MAP3K-Coding QUI-GON JINN (QGJ) Gene Is Essential to the Formation of Unreduced Embryo Sacs in *Paspalum*. Frontiers in Plant Science, 2018. 9. doi: 10.3389/fpls.2018.01547

35. Podio, M., et al., A methylation status analysis of the apomixis-specific region in *Paspalum spp.* suggests an epigenetic control of parthenogenesis. Journal of Experimental Botany, 2014. 65(22): p. 6411-6424. DOI: 10.1093/jxb/eru354

36. Siena, L.A., et al., An apomixis-linked ORC3-like pseudogene is associated with silencing of its functional homolog in apomictic *Paspalum simplex*. Journal of Experimental Botany, 2016. 67(6): p. 1965-1978. <https://doi.org/10.1093/jxb/erw018>

37. Galla, G., et al., Ovule Gene Expression Analysis in Sexual and Aposporous Apomictic *Hypericum perforatum L.* (*Hypericaceae*) Accessions. Frontiers in Plant Science, 2019. 10. DOI: 10.3389/fpls.2019.00654

38. Corral, J.M., et al., A Conserved Apomixis-Specific Polymorphism Is Correlated with Exclusive Exonuclease Expression in Premeiotic Ovules of Apomictic *Boechera* Species. Plant Physiology, 2013. 163(4): p. 1660-1672. DOI: 10.1104/pp.113.222430

39. Mau, M., et al., Hybrid apomicts trapped in the ecological niches of their sexual ancestors. Proceedings of the National Academy of Sciences, 2015. 112(18). <https://doi.org/10.1073/pnas.1423447112>

40. Mateo de Arias, M., et al., Whether Gametophytes Are Reduced or Unreduced in Angiosperms Might Be Determined Metabolically. Genes, 2020. 11(12). DOI: 10.3390/genes11121449

41. Selva, J.P., et al., Genes Modulating the Increase in Sexuality in the Facultative Diplosporous Grass *Eragrostis curvula* under Water Stress Conditions. Genes, 2020. 11(9). DOI: 10.3390/genes11090969

42. Wyder, S., et al., Differential gene expression profiling of one- and two-dimensional apogamous gametophytes of the fern *Dryopteris affinis* ssp. *affinis*. Plant Physiology and Biochemistry, 2020. 148: p. 302-311. DOI: 10.1016/j.plaphy.2020.01.021

43. Fei, X., et al., Small RNA sequencing provides candidate miRNA-target pairs for revealing the mechanism of apomixis in *Zanthoxylum bungeanum*. BMC Plant Biology, 2021. 21(1). <https://doi.org/10.1186/s12870-021-02935-5>

44. Klatt, S., et al., Photoperiod Extension Enhances Sexual Megaspore Formation and Triggers Metabolic Reprogramming in Facultative Apomictic *Ranunculus auricomus*. Frontiers in Plant Science, 2016. 7. DOI: 10.3389/fpls.2016.00278

45. Ulum, F.B., C. Costa Castro, and E. Hörndl, Ploidy-Dependent Effects of Light Stress on the Mode of Reproduction in the *Ranunculus auricomus* Complex (*Ranunculaceae*). Frontiers in Plant Science, 2020. 11. DOI: 10.3389/fpls.2020.00104

46. Chuong, E.B., N.C. Elde, and C. Feschotte, Regulatory activities of transposable elements: from conflicts to benefits. Nature Reviews Genetics, 2016. 18(2): p. 71-86. <https://doi.org/10.1038/nrg.2016.139>

47. Martin, A., et al., A transposon-induced epigenetic change leads to sex determination in melon. Nature, 2009. 461(7267): p. 1135-1138. DOI: 10.1038/nature08498

48. Ong-Abdullah, M., et al., Loss of Karma transposon methylation underlies the mantled somaclonal variant of oil palm. Nature, 2015. 525(7570): p. 533-537. DOI: 10.1038/nature15365

49. Hojsgaard, D., Apomixis Technology: Separating the Wheat from the Chaff. Genes, 2020. 11(4). <https://doi.org/10.3390/genes11040411>

50. Fiaz, S., et al., Apomixis and strategies to induce apomixis to preserve hybrid vigor for multiple generations. GM Crops & Food, 2020. 12(1): p. 57-70. DOI: 10.1080/21645698.2020.1808423

51. Rathore, P., et al., Retro-Element Gypsy-163 Is Differentially Methylated in Reproductive Tissues of Apomictic and Sexual Plants of *Cenchrus ciliaris*. Frontiers in Genetics, 2020. 11. <https://doi.org/10.3389/fgene.2020.00795>

52. Nonomura, K.-I., et al., The MSP1 Gene Is Necessary to Restrict the Number of Cells Entering into Male and Female Sporogenesis and to Initiate Anther Wall Formation in Rice. The Plant Cell, 2003. 15(8): p. 1728-1739. DOI: 10.1105/tpc.012401

53. Brukhin, V., Molecular and genetic regulation of apomixis. Russian Journal of Genetics, 2017. 53(9): p. 943-964. DOI: 10.1134/S1022795417090046

54. Ozias-Akins, P., D. Roche, and W.W. Hanna, Tight clustering and hemizygosity of apomixis-linked molecular markers in *Pennisetum squamulatum* implies genetic control of apospory by a divergent locus that may have no allelic form in sexual genotypes. Proceedings of the National Academy of Sciences, 1998. 95(9): p. 5127-5132. DOI: 10.1073/pnas.95.9.5127

55. Grimanelli, D., et al., Mapping diplosporous apomixis in tetraploid *Tripsacum*: one gene or several genes? Heredity, 1998. 80(1): p. 33-39. DOI: 10.1046/j.1365-2540.1998.00263.x

56. Ozias-Akins, P., Y. Akiyama, and W.W. Hanna, Molecular characterization of the genomic region linked with apomixis in *Pennisetum/Cenchrus*. Functional & Integrative Genomics, 2003. 3(3): p. 94-104. DOI: 10.1007/s10142-003-0084-8

57. Zappacosta, D., et al., A High-Density Linkage Map of the Forage Grass *Eragrostis curvula* and Localization of the Diplospory Locus. Frontiers in Plant Science, 2019. 10. <https://doi.org/10.3389/fpls.2019.00918>

58. Olmedo-Monfil, V., et al., Control of female gamete formation by a small RNA pathway in *Arabidopsis*. Nature, 2010. 464(7288): p. 628-632. doi: 10.1038/nature08828.

59. Underwood, C.J., et al., A PARTHENOGENESIS allele from apomictic dandelion can induce egg cell division without fertilization in lettuce. Nature Genetics, 2022. 54(1): p. 84-93. DOI: 10.1038/s41588-021-00984-y

60. Dan, J., Xia, Y., Wang, Y., Zhan, Y., Tian, J., Tang, N., et al., One-line hybrid rice with high-efficiency synthetic apomixis and near-normal fertility. Plant Cell Reports, 2024. 43: p. 79. <https://doi.org/10.1007/s00299-024-03154-6>

61. Vernet, A., Meynard, D., Lian, Q., Mieulet, D., Gibert, O., Bissah, M., et al., High-frequency synthetic apomixis in hybrid rice. Nature Communications, 2022. 13(1): p. 7963. <https://doi.org/10.1038/s41467-022-35679-3>

62. Chen, B., Maas, L., Figueiredo, D., Zhong, Y., Reis, R., Li, M., et al., BABY BOOM regulates early embryo and endosperm development. *Proceedings of the National Academy of Sciences*, 2022. 119: p. e2201761119. <https://doi.org/10.1073/pnas.2201761119>

63. Wang, Y., Fuentes, R.R., Van Rengs, W.M.J., Effgen, S., Zaidan, M.W.A.M., Franzen, R., et al., Harnessing clonal gametes in hybrid crops to engineer polyploid genomes. *Nature Genetics*, 2024. 56: p. 1075-1079. <https://doi.org/10.1038/s41588-024-01750-6>

64. Zhang, C., Yang, Z., Tang, D., Zhu, Y., Wang, P., Li, D., et al., Genome design of hybrid potato. *Cell*, 2021. 184: p. 3873-3883.e12. DOI: 10.1016/j.cell.2021.06.006

65. Mao, Y., Nakel, T., Erbasol Serbes, I., Joshi, S., Tekleyohans, D.G., Baum, T., and Gross-Hardt, R., ECS1 and ECS2 suppress polyspermy and the formation of haploid plants by promoting double fertilization. *Elife*, 2023. 12: p. e85832. DOI: 10.7554/elife.85832

66. Ravi, M., and Chan, S.W.L., Haploid plants produced by centromere-mediated genome elimination. *Nature*, 2010. 464: p. 615-618. DOI: 10.1038/nature08842

67. Gilles, L.M., Khaled, A., Laffaire, J.B., Chaignon, S., Gendrot, G., Laplaige, J., Bergès, H., Beydon, G., Bayle, V., Barret, P., et al., Loss of pollen-specific phospholipase NOT LIKE DAD triggers gynogenesis in maize. *EMBO Journal*, 2017. 36: p. 707-717. DOI: 10.1525/embj.201796603

68. Zhong, Y., Liu, C., Qi, X., Jiao, Y., Wang, D., Wang, Y., Liu, Z., Chen, C., Chen, B., Tian, X., et al., Mutation of ZmDMP enhances haploid induction in maize. *Nature Plants*, 2019. 5: p. 575-580. DOI: 10.1038/s41477-019-0443-7

69. Conner, J.A., Podio, M., and Ozias-Akins, P., Haploid embryo production in rice and maize induced by PsASGR-BBML transgenes. *Plant Reproduction*, 2017. 30: p. 41-52. DOI: 10.1007/s00497-017-0298-x

70. Huang, Y., Liang, Y., Xie, Y., Rao, Y., Xiong, J., Liu, C., Wang, C., Wang, X., Qian, Q., and Wang, K., Efficient haploid induction via egg cell expression of dandelion PARTHENOGENESIS in foxtail millet (*Setaria italica*). *Plant Biotechnology Journal*, 2024. DOI: 10.1111/pbi.14302

71. d'Erfurth, I., Jolivet, S., Froger, N., Catrice, O., Novatchkova, M., and Mercier, R., Turning meiosis into mitosis. *PLoS Biology*, 2009. 7: p. e1000124. DOI: 10.1371/journal.pbio.1000124

72. Wang, C., Liu, Q., Shen, Y., Hua, Y., Wang, J., Lin, J., et al., Clonal seeds from hybrid rice by simultaneous genome engineering of meiosis and fertilization genes. *Nature Biotechnology*, 2019. 37: p. 283-286. DOI: 10.1038/s41587-018-0003-0

74. Liu, C., He, Z., Zhang, Y., Hu, F., Li, M., Liu, Q., et al., Synthetic apomixis enables stable transgenerational transmission of heterotic phenotypes in hybrid rice. *Plant Communications*, 2023. 4: p. 100470. <https://doi.org/10.1016/j.xplc.2022.100470>

75. Boateng, K.A., et al., SWI1 is required for meiotic chromosome remodeling events. *Mol Plant*, 2008. 1(4): p. 620-33. DOI: 10.1093/mp/ssp030

76. Hartung, F., et al., The catalytically active tyrosine residues of both SPO11-1 and SPO11-2 are required for meiotic double-strand break induction in *Arabidopsis*. *Plant Cell*, 2007. 19(10): p. 3090-9. doi: 10.1105/tpc.107.054817

77. Grelon, M., et al., AtSPO11-1 is necessary for efficient meiotic recombination in plants. *EMBO J*, 2001. 20(3): p. 589-600. DOI: 10.1093/emboj/20.3.589

78. Vrielynck, N., et al., A DNA topoisomerase VI-like complex initiates meiotic recombination. *Science*, 2016. 351(6276): p. 939-43. DOI: 10.1126/science.aad5196

79. Zhang, C., et al., The *Arabidopsis thaliana* DSB formation (AtDFO) gene is required for meiotic double-strand break formation. *Plant J*, 2012. 72(2): p. 271-81. DOI: 10.1111/j.1365-313X.2012.05075.x

80. De Muyt, A., et al., AtPRD1 is required for meiotic double strand break formation in *Arabidopsis thaliana*. *EMBO J*, 2007. 26(18): p. 4126-37. DOI: 10.1038/sj.emboj.7601815

81. Gherbi, H., et al., Homologous recombination in planta is stimulated in the absence of Rad50. *EMBO Rep*, 2001. 2(4): p. 287-91. DOI: 10.1093/embo-reports/kve069

82. Vannier, J.B., et al., Two roles for Rad50 in telomere maintenance. *EMBO J*, 2006. 25(19): p. 4577-85. DOI: 10.1038/sj.emboj.7601345

83. Couteau, F., et al., Random chromosome segregation without meiotic arrest in both male and female meiocytes of a dmc1 mutant of *Arabidopsis*. *Plant Cell*, 1999. 11(9): p. 1623-34. DOI: 10.1105/tpc.11.9.1623

84. Higgins, J.D., et al., The *Arabidopsis* MutS homolog AtMSH4 functions at an early step in recombination: evidence for two classes of recombination in *Arabidopsis*. *Genes Dev*, 2004. 18(20): p. 2557-70. doi: 10.1101/gad.317504

85. Caryl, A.P., et al., A homologue of the yeast HOP1 gene is inactivated in the *Arabidopsis* meiotic mutant asy1. *Chromosoma*, 2000. 109(1-2): p. 62-71. DOI: 10.1007/s004120050413

86. Watanabe, Y. and P. Nurse, Cohesin Rec8 is required for reductional chromosome segregation at meiosis. *Nature*, 1999. 400(6743): p. 461-4. DOI: 10.1038/22774

87. Chelysheva, L., et al., AtREC8 and AtSCC3 are essential to the monopolar orientation of the kinetochores during meiosis. *J Cell Sci*, 2005. 118(Pt 20): p. 4621-32. DOI: 10.1242/jcs.02583

88. Schommer, C., et al., AHP2 is required for bivalent formation and for segregation of homologous chromosomes in *Arabidopsis* meiosis. *Plant J*, 2003. 36(1): p. 1-11. DOI: 10.1046/j.1365-313X.2003.01850.x

89. Cromer, L., et al., OSD1 promotes meiotic progression via APC/C inhibition and forms a regulatory network with TDM and CYCA1;2/TAM. *PLoS Genet*, 2012. 8(7): p. e1002865. DOI: 10.1371/journal.pgen.1002865

90. Wang, Y., et al., Progression through meiosis I and meiosis II in *Arabidopsis* anthers is regulated by an A-type cyclin predominately expressed in prophase I. *Plant Physiol*, 2004. 136(4): p. 4127-35. DOI: 10.1104/pp.104.051201

91. Cifuentes, M., et al., TDM1 Regulation Determines the Number of Meiotic Divisions. *PLoS Genet*, 2016. 12(2): p. e1005856. DOI: 10.1371/journal.pgen.1005856

92. Guitton, A.E. and F. Berger, Loss of function of MULTICOPY SUPPRESSOR OF IRA 1 produces nonviable parthenogenetic embryos in *Arabidopsis*. *Curr Biol*, 2005. 15(8): p. 750-4. <https://doi.org/10.1016/j.cub.2005.02.066>

93. Ravi, M. and S.W. Chan, Haploid plants produced by centromere-mediated genome elimination. *Nature*, 2010. 464(7288): p. 615-8. DOI: 10.1038/nature08842

94. Ohad, N., et al., Mutations in FIE, a WD polycomb group gene, allow endosperm development without fertilization. *Plant Cell*, 1999. 11(3): p. 407-16. DOI: 10.1105/tpc.11.3.407

95. Chaudhury, A.M., et al., Fertilization-independent seed development in *Arabidopsis thaliana*. *Proc Natl Acad Sci U S A*, 1997. 94(8): p. 4223-8. <https://doi.org/10.1073/pnas.94.8.4223>

96. Bierzychudek, P., Patterns in plant parthenogenesis. *Experientia*, 1985. 41(10): p. 1255-1264. DOI: 10.1007/978-3-0348-6273-8\_9

97. Nygren, A., Apomixis in the angiosperms. II. The Botanical Review, 1954. 20(10): p. 577-649. DOI: 10.1007/978-3-642-95000-1\_21

98. Conner, J.A., et al., A parthenogenesis gene of apomict origin elicits embryo formation from unfertilized eggs in a sexual plant. *Proc Natl Acad Sci U S A*, 2015. 112(36): p. 11205-10. <https://doi.org/10.1073/pnas.1505856112>

99. Khanday, I., et al., A male-expressed rice embryogenic trigger redirected for asexual propagation through seeds. *Nature*, 2018. 565(7737): p. 91-95. DOI: 10.1038/s41586-018-0785-8

100. Vijverberg, K., et al., Genetic fine-mapping of DIPLOSPOROUS in *Taraxacum* (dandelion; *Asteraceae*) indicates a duplicated DIP-gene. *BMC Plant Biology*, 2010. 10(1). doi: 10.1186/1471-2229-10-154

101. Bicknell, R., et al., Genetic mapping of the LOSS OF PARTHENOGENESIS locus in *Pilosella piloselloides* and the evolution of apomixis in the Lactuceae. *Frontiers in Plant Science*, 2023. 14. DOI: 10.3389/fpls.2023.1239191

102. Brukhin, V., et al., The *Boechera* Genus as a Resource for Apomixis Research. *Frontiers in Plant Science*, 2019. 10. doi: 10.3389/fpls.2019.00392

103. Gao, J., et al., Trimethylguanosine Synthase1 (TGS1) Is Essential for Chilling Tolerance. *Plant Physiology*, 2017. 174(3): p. 1713-1727. DOI: 10.1104/pp.17.00340

104. Ortiz, J.P.A., et al., Small RNA-seq reveals novel regulatory components for apomixis in *Paspalum notatum*. *BMC Genomics*, 2019. 20(1). <https://doi.org/10.1186/s12864-019-5881-0>

105. Henikoff, S. and Y. Dalal, Centromeric chromatin: what makes it unique? *Current Opinion in Genetics & Development*, 2005. 15(2): p. 177-184. DOI: 10.1016/j.gde.2005.01.004

106. Nogler, G.A., Gametophytic Apomixis, in *Embryology of Angiosperms*. 1984. p. 475-518. doi:10.1007/978-3-642-69302-1\_10

107. Pellino, M., et al., Asexual genome evolution in the apomictic *Ranunculus auricomus* complex: examining the effects of hybridization and mutation accumulation. *Molecular Ecology*, 2013. 22(23): p. 5908-5921. DOI: 10.1111/mec.12533

108. Kondrashov, A.S., Deleterious mutations and the evolution of sexual reproduction. *Nature*, 1988. 336(6198): p. 435-440. <https://doi.org/10.1038/336435a0>

109. Muller, H.J., The relation of recombination to mutational advance. *Mutation Research/Fundamental and Molecular Mechanisms of Mutagenesis*, 1964. 1(1): p. 2-9. [https://doi.org/10.1016/0027-5107\(64\)90047-8](https://doi.org/10.1016/0027-5107(64)90047-8)

110. Kimura, M., T. Maruyama, and J.F. Crow, The Mutation Load in Small Populations. *Genetics*, 1963. 48(10): p. 1303-1312. doi: 10.1093/genetics/48.10.1303

111. Felsenstein, J., The Evolutionary Advantage of Recombination. *Genetics*, 1974. 78(2): p. 737-756. DOI: 10.1093/genetics/78.2.737

112. Hill, W.G. and A. Robertson, The effect of linkage on limits to artificial selection. *Genetical Research*, 2009. 8(3): p. 269-294. DOI: <https://doi.org/10.1017/S0016672300010156>

113. Maynard Smith, J., *The evolution of sex*. 1978, Cambridge Eng. ; New York: Cambridge University Press. x, 222 p. ISBN: 9780521293020

114. Bell, G., *The masterpiece of nature : the evolution and genetics of sexuality*. 1982, Berkeley: University of California Press. 635 p. <https://doi.org/10.4324/9780429322884>

115. Trivers, R., *The Evolution of Sex* The Masterpiece of Nature: The Evolution and Genetics of Sexuality. Graham Bell. *The Quarterly Review of Biology*, 1983. 58(1): p. 62-67. DOI:10.1086/413059

116. Paun, O., et al., Patterns, sources and ecological implications of clonal diversity in apomictic *Ranunculus carpaticola* (*Ranunculus auricomus* complex, *Ranunculaceae*). *Molecular Ecology*, 2006. 15(4): p. 897-910. DOI: 10.1111/j.1365-294X.2006.02800.x

117. Koch, M.A., Multiple Hybrid Formation in Natural Populations: Concerted Evolution of the Internal Transcribed Spacer of Nuclear Ribosomal DNA (ITS) in North American *Arabis divaricarpa* (*Brassicaceae*). *Molecular Biology and Evolution*, 2003. 20(3): p. 338-350. DOI: 10.1093/molbev/msg046

118. Otto, S.P. and J. Whitton, Polyploid Incidence and Evolution. *Annual Review of Genetics*, 2000. 34(1): p. 401-437. DOI: 10.1146/annurev.genet.34.1.401

119. Hojsgaard, D. and E. HÅrandl, A little bit of sex matters for genome evolution in asexual plants. *Frontiers in Plant Science*, 2015. 6. DOI: 10.3389/fpls.2015.00082