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Synthetic Apomixis: A New Frontier in Fixing Hybrid Vigor

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In recent years, hybrid crops have transformed agriculture by exploiting heterosis, where offspring outperform their parents in yield, stability and adaptability. These high-yielding hybrids have significantly enhanced farmer incomes and productivity. However, their advantages are not maintained across generations. Farmers must purchase hybrid seeds each season, as saved seeds do not retain the same performance. This is due to meiosis during sexual reproduction, which reshuffles genetic material through segregation and recombination, disrupting favourable gene combinations. Consequently, the superior traits of hybrids are not preserved, increasing reliance on commercial seed systems.

Recognizing the limitations of hybrid seed systems, scientists have long aimed to fix heterosis to preserve superior traits across generations. In this search, nature offers a clue. Certain plant species reproduce through apomixis, a form of asexual seed formation where embryos develop without fertilization, producing genetically identical offspring. By bypassing meiosis and fertilization, apomixis ensures stable transmission of elite genotypes. However, it is restricted to a few taxa and controlled by complex genetics, limiting its direct use in major crops.

Building on these insights, recent advances in molecular genetics and genome engineering have enabled researchers to recreate key features of apomixis in crop plants. By replacing meiosis with mitosis and inducing embryo development without fertilization through targeted genetic modifications, scientists have developed synthetic apomixis. This engineered approach allows clonal propagation of elite genotypes through seeds, offering a practical strategy to fix hybrid vigor, improve breeding efficiency and strengthen future crop improvement efforts.

What is Apomixis?

Apomixis is a reproductive process in which plants produce seeds without meiosis and fertilization, resulting in progeny that are genetically identical to the maternal parent. Based on the origin of embryo development, apomixis is classified into:

1. Gametophytic apomixis – the embryo develops from an unreduced embryo sac.

- **Diplospory:** The embryo sac develops directly from the megaspore mother cell without meiosis.

Examples: *Taraxacum*, *Tripsacum*, *Ixeris*, *Antennaria*, *Parthenium*, *Datura*, *Allium* etc.

- **Apospory:** Somatic nucellar cells differentiate into an unreduced embryo sac bypassing meiosis.

Examples: *Hieracium*, *Pennisetum*, *Sorghum*, *Brachiaria*, etc.

2. Sporophytic apomixis (adventitious embryony) – embryos arise directly from somatic tissues such as the nucellus or integuments, often alongside sexually derived embryos.

Examples: *Citrus*, *Mangifera*, *Fortunella*, etc.

In addition to these pathways, two key developmental processes are associated with apomixis:

- **Parthenogenesis:** Development of an embryo from the egg cell without fertilization, a central component of most apomictic systems.
- **Apogamy:** Formation of embryos from non-egg cells of the embryo sac (e.g., synergids or antipodals), bypassing fertilization.

Despite its potential, natural apomixis is limited by its restricted occurrence and complex genetic regulation, which have hindered its direct use in major crops. These limitations have driven efforts to recreate this phenomenon through synthetic apomixis, where key components such as apomeiosis and parthenogenesis are engineered into sexually reproducing plants.

What is Synthetic Apomixis?

Synthetic apomixis refers to the deliberate engineering of apomictic reproduction in normally sexual plants, enabling the formation of seeds without meiosis and fertilization. It is achieved through targeted manipulation of key reproductive processes using modern molecular and genomic tools. Its primary objective is to enable clonal propagation through seeds in major crop species, ensuring genetic uniformity, maintaining heterosis and reducing the need for repeated hybrid seed production.

The central idea behind synthetic apomixis is to mimic the two essential components of natural apomixis: (i) apomeiosis, where meiosis is replaced by mitosis to produce unreduced (clonal) gametes and (ii) parthenogenesis, where the embryo develops without fertilization. By integrating these processes, it becomes possible to generate seeds that are genetically identical to the parent plant, thereby preserving elite genotypes and fixing hybrid vigor across generations.

Steps Involved and Molecular Mechanism of Synthetic Apomixis

The steps involved in Synthetic apomixis are.

1. Apomeiosis (MiMe system)

This step produces unreduced ($2n$) clonal gametes by converting meiosis into mitosis.

- **SPO11-1:** Prevents meiotic recombination by blocking double-strand breaks.
- **REC8:** Alters chromosome segregation to mimic mitosis.
- **OSD1:** Skips the second meiotic division.

Together, mutations in these genes form the MiMe system, effectively converting meiosis into mitosis and producing clonal gametes.

2. Autonomous Embryo Development

A. Chromosome Elimination (Genome Elimination Approach)

This approach enables haploid or clonal embryo formation by selectively eliminating one parental genome after fertilization.

- **CENH3**

A centromere-specific histone essential for chromosome segregation. Altered CENH3 leads to genome elimination, producing haploid embryos by removing one parental set.

- **MTL/PLA1/NLD**

A pollen-specific phospholipase. Mutation triggers genome elimination during fertilization, resulting in haploid induction.

- **DMP (DOMAIN OF UNKNOWN FUNCTION 679 MEMBRANE PROTEIN)**
Involved in gamete fusion and fertilization processes. Mutation enhances haploid induction efficiency by disrupting normal fertilization dynamics.

B. Parthenogenesis (Embryo Formation Without Fertilization)

This step is critical for true apomixis, where the embryo develops directly from the egg cell without fertilization.

- **ASGR-BBML (BABY BOOM-like gene)**

A transcription factor that triggers embryogenesis from the egg cell. It initiates cell division and embryo formation in the absence of fertilization.

- **PAR (Parthenogenesis gene)**

Regulates egg cell activation and promotes embryo development without fertilization.

These genes are essential to induce autonomous embryo formation, a core feature of apomixis.

C. Sporophytic Apomixis (Adventitious Embryony)

• **RWP (RWP-RK domain protein)**

Involved in somatic embryogenesis pathways, enabling embryo formation from nucellar or somatic tissues rather than the egg cell.

This represents an alternative route where embryos arise directly from somatic cells.

3. Autonomous Endosperm Development

For viable seed formation, proper endosperm development is necessary.

• **FIS (Fertilization-Independent Seed genes)**

A group of Polycomb group proteins that regulate endosperm development. Mutations in FIS genes allow endosperm formation without fertilization, supporting complete seed development in apomictic systems.

4. Integration of Components

The successful implementation of synthetic apomixis requires coordination of all three modules:

- Apomeiosis - production of clonal gametes
- Parthenogenesis - embryo formation without fertilization
- Endosperm development - seed viability

When combined, these processes enable clonal seed production, effectively fixing hybrid vigor. This integrated genetic framework represents the foundation of synthetic apomixis and demonstrates how targeted manipulation of reproductive pathways can transform plant breeding.

Table 1. Key Genes and Molecular Mechanisms Involved in Synthetic Apomixis

Approach	Mechanism	Genes	Crop	Reference
Apomeiosis	MiMe	<i>AtSPO11-1, AtREC8 and AtOSD1</i>	Arabidopsis (<i>Arabidopsis thaliana</i>)	D'Erfurth et al. (2009)
		<i>Ospair1, Osrec8 and Ososd1</i>	Rice (<i>Oryza sativa</i>)	Mieulet et al. (2016)
		<i>SISPO11-1, SIREC8 and TARDY ASYNCHRONOUS MEIOSIS (SITAM)</i>	Tomato (<i>Solanum lycopersicum</i>)	Wang et al. (2024)
Autonomous Embryo Development	Chromosome elimination	CENH3	Arabidopsis (<i>Arabidopsis thaliana</i>)	Marimuthu et al. (2011)
		MTL/PLA1/NLD	Maize (<i>Zea mays</i>)	Kelliher et al. (2017), Liu et al. (2017) and Gilles et al. (2017)
	Parthenogenesis	DMP	Maize (<i>Zea mays</i>)	Zhong et al. (2020)
		<i>PsASGR-BBML</i>	<i>Pennisetum squamulatum</i>	Conner et al. (2015)
		<i>ToPAR</i>	Dandelion (<i>Taraxacum officinale</i>)	Underwood et al. (2022)
Sporophytic apomixis	RWP	Citrus	Nakano et al., 2012	
Autonomous endosperm development		FIS (FERTILIZATION-INDEPENDENT SEED)	Arabidopsis (<i>Arabidopsis thaliana</i>)	Hands et al., 2016

Applications in crop plants

Synthetic apomixis has been most successfully demonstrated in rice (*Oryza sativa*), where the integration of the MiMe system with parthenogenesis-inducing genes such as BBM-like genes, ToPAR and OsWUS has enabled the production of clonal seeds. Studies have reported up to 95% clonal progeny, highlighting its feasibility in major cereals. Beyond cereals, key components of synthetic apomixis have also been developed in tomato (*Solanum lycopersicum*), where both MiMe and parthenogenesis pathways are functional, indicating strong potential for future application

Table 2. Recent Developments in Synthetic Apomixis Systems in Rice.

Crop	Synthetic Apomixis Strategy	Year	Remarks
Rice (<i>Oryza sativa</i>)	Rice clonal seeds (<i>MiMe + mtl</i>)	2019	low penetrance clonal seed formation
Rice (<i>Oryza sativa</i>)	Rice clonal seeds (<i>MiMe + ToPAR</i>)	2024	67% clonal rate and no significant seed set differences
Rice (<i>Oryza sativa</i>)	Rice clonal seeds (<i>MiMe + OsWUS</i>)	2024	22% clonal rate and 80% seed set
Rice (<i>Oryza sativa</i>)	High-efficiency clonal rice seeds with normal seed set (<i>MiMe + OsECA1-AZP2::OsBBM1</i>)	2024	95% clonal seed formation and 80 to 87% seed set

Applications

Synthetic apomixis is considered a “holy grail” in plant breeding as it enables clonal seed production and fixation of hybrid vigor across generations. It allows:

- Stable transmission of elite genotypes without segregation
- Reduced need for repeated hybrid seed production
- Lower seed costs and better farmer accessibility
- Rapid multiplication of superior varieties

Even without fully engineered systems, individual elements of apomixis can be highly valuable in crop breeding. For example, bypassing meiosis (apomeiosis) produces non-recombinant gametes, which helps preserve desirable gene combinations and is useful in developing polyploid crops. Likewise, parthenogenesis can be applied in double haploid production to quickly fix genetic variation, thereby speeding up breeding programs. In addition, autonomous endosperm development can support proper seed formation under stressful conditions, contributing to more stable yields.

Challenges and Limitations

Despite significant progress, several challenges limit the practical application of synthetic apomixis:

- **Reduced fertility and seed set:** High rates of clonal seed formation are often associated with decreased fertility, particularly in grain crops, directly affecting yield.
- **Endosperm development constraints:** Proper seed formation still often depends on fertilization, complicating fully autonomous systems.
- **Genetic and regulatory complexity:** Coordinated expression of multiple genes controlling meiosis, embryogenesis and seed development remains difficult.
- **Crop-specific limitations:** While cereals require high seed set for yield, this constraint is less critical in fruit and vegetable crops, where synthetic apomixis remains underexplored.
- **Field-level stability:** Achieving consistent performance across environments and generations is still a challenge.

Conclusion

Synthetic apomixis represents one of the most exciting frontiers in plant breeding. A concept that brings us closer to fixing hybrid vigor and truly harnessing the full potential of elite genotypes. The idea of producing clonal seeds, where superior traits can be preserved generation after generation, has long been a dream and today it is gradually becoming a reality through advances in molecular genetics. While significant progress has been made, especially in crops like rice, challenges such as reduced fertility and complex genetic regulation still need to be addressed. Yet, the possibilities it offers, greater breeding efficiency, reduced seed dependency and improved accessibility for farmers are immense. With continued research and refinement, synthetic apomixis will be playing a defining role in shaping the future of sustainable and resilient agriculture in the future.

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