



Apomixis in Crop Improvement Opportunities and Challenges

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Article History

Received: 09.09.2026

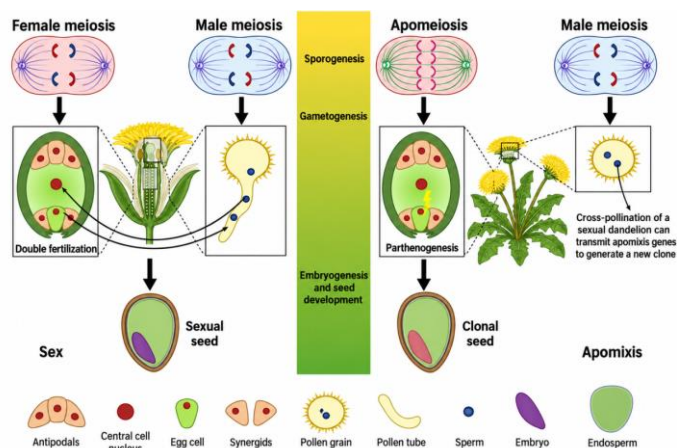
Revised: 14.09.2026

Accepted: 19.09.2026

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INTRODUCTION

Plant breeding relies heavily on sexual reproduction to shuffle parental genes and generate novel combinations. This variation allows breeders to select for improved cultivars, but it also splits up superior combinations in later generations. As a result, farmers growing hybrid crops typically cannot maintain the same yield by planting seed harvested from their crops, as the offspring will segregate and lose some of their hybrid vigour. Apomixis provides a striking biological alternative. Apomixis allows plants to produce seeds without undergoing meiosis and fertilization, resulting in offspring that are genetically similar or identical to the mother plant. The potential to incorporate this trait consistently into important crops could change hybrid breeding, seed production, and the release of improved varieties.



Understanding Apomixis

Apomixis is a type of asexual reproduction that occurs via seed. In contrast to typical sexual reproduction, which involves meiosis to produce reduced gametes and fertilization to combine maternal and paternal genomes, apomictic reproduction avoids one or both of these processes. Typically, the embryo formed through apomixis has the same genetic makeup as the mother plant.

Apomixis is not a single mechanism. There are several developmental pathways involved, and some apomictic plants still need pollination for normal endosperm development. This knowledge is important because successful crop improvement does not only require the embryo to be produced without fertilization, but also the coordinated production of a vigorous embryo, functional endosperm, viable seed, and fertile adult plant.

In gametophytic apomixis, an unreduced embryo sac is formed as a result of either diplospory or apospory. With diplospory, the megaspore mother cell produces an embryo sac without undergoing normal meiosis. In apospory, it is formed from a somatic cell of the ovule adjacent to the embryo sac. The unreduced egg then produces an embryo by parthenogenesis. In sporophytic apomixis (also known as adventive embryony), embryos are produced directly from nucellar or integumentary cells that surround the embryo sac. This phenomenon is commonly observed in crops such as citrus and mango, where both sexual and maternal embryos may be found in the same seed. Apomixis can thus lead to the formation of clonal seedlings, multiple embryos or a combination of sexual and asexual progeny.

Why Apomixis Attracts Plant Breeders

Apomixis is most commonly considered for its potential to fix a superior genotype and propagate it through seed. A breeder may work for years to bring together high yield, disease resistance, quality, stress tolerance and adaptation into one plant. With sexual reproduction, these traits may be segregated in the next generation due to recombination. Apomixis would allow preservation of the entire genetic combination without repeated cycles of crossing and selection. This would be especially useful for highly heterozygous crops and traits controlled by many genes. Rather than having to reassemble the ideal combination every time, breeders could simply multiply the elite genotype once it had been identified.

Vegetative multiplication's limitations could be also bypassed in clonal propagation from seed. Potato, cassava, banana, sugarcane and a number of horticultural crops are raised through tubers, cuttings, suckers or grafted plants. These materials are heavy, expensive to ship and can harbor and carry pathogens across generations. True seed is usually easier to store, treat, distribute and sow. If elite vegetatively propagated genotypes could be faithfully reproduced through apomictic seed, farmers might have access to cleaner, more easily handled planting material. But the opportunity is contingent on obtaining viable seed production without altering the desirable traits of the cultivar.

Fixing Hybrid Vigour

Hybrid vigour (or heterosis) is one of the greatest accomplishments of modern crop breeding. Hybrids of maize, rice, sorghum, pearl millet and many other vegetables frequently surpass their parents in productivity, uniformity and sturdiness. Yet their superior gene combinations break up in the next generation. Commercial hybrid seed, therefore, needs to be generated once again through rigorously controlled parental crosses. This raises seed costs and it requires reliable parental lines, pollination control and seed-production infrastructure.

Apomixis might turn a triumphant hybrid into a quasi-permanent line that can be otherwise propagated. Rather than the progeny segregating into forms of variable natures, it would retain the parental genome and much of the original hybrid performance. This is what in the literature is frequently referred to as fixing heterosis. It could allow hybrid technology to be adapted for use in crops for which conventional hybrid-seed production is not feasible or not profitable. It could allow smallholder farmers to save seed without losing genetic uniformity. But these advantages will be fully realized only if apomictic seed continues to be viable, vigorous and genetically stable across multiple generations.

Broadening the Reach of Improved Varieties

Apomixis could shorten the pathway between breeding success and farmers fields. Clonal seed multiplication can ensure that a superior climate-resilient or disease-resistant genotype maintains its entire trait combination over a range of environments and generations once it has been bred. This can be particularly beneficial in crops that experience rapid temperature changes, erratic rainfall, new diseases and decreasing soil quality. Genotypes with multiple traits such as drought tolerance, heat tolerance, nutritional quality and pest resistance can be maintained without repeated genetic reshuffling.

The technique might also be applicable for locally adapted varieties. Breeders could pick exceptional individuals from heterogeneous populations and propagate them without lengthy inbreeding regimens. In the case of perennials with long juvenile phases, apomixis can reduce the period required to fix beneficial genotypes. However, apomixis should not be regarded as a replacement for genetic diversity. Planting a handful of extensively planted clones in a crop population might also leave that population open to new pests, diseases, or weather extremes. Its judicious use must be accompanied by ongoing breeding and germplasm conservation.

Learning from Natural Apomixis

Natural apomixis occurs in hundreds of flowering-plant species, including wild relatives of important crops. Researchers study genera such as *Hieracium*, *Taraxacum*, *Boechera*, *Paspalum* and *Brachiaria* to identify the genes and developmental signals controlling apomeiosis, parthenogenesis and endosperm formation. These studies show that apomixis is usually governed by coordinated processes rather than by one simple switch. Its genetic regions may contain suppressed recombination, repetitive DNA and several interacting regulatory genes, making them difficult to transfer through conventional crossing.

Natural apomicts are also often polyploid, in that they have more than two sets of chromosomes. Polyploidy may influence gene dosage and development of reproduction and endosperm. Furthermore, numerous natural apomicts continue to have some ability to sexually reproduce. This is a useful strategy in nature because it allows clonal persistence with infrequent variation, but it poses problems for agriculture. A commercial cultivar has to give a reliably high proportion of true clonal seed across a wide range of environments. Even a modest rate of sexual progeny could erode uniformity in the field and slowly transform the cultivar.

Synthetic Apomixis: A New Frontier

Modern gene editing techniques have enabled the transfer of apomixis from model plants to crops, or even the de novo design of apomixis in crops. Synthetic apomixis typically involves two main steps. First, meiosis is engineered to produce unreduced reproductive cells that maintain the maternal genome. MiMe or mitosis instead of meiosis, a commonly studied approach, involves mutating central genes in meiosis to make reproductive cell division resemble mitosis. Second, genes that activate embryo development without fertilization are used to induce parthenogenesis.

Experiments in rice have shown that combining altered meiosis with embryo-inducing factors such as *BABY BOOM* or *WUSCHEL*-related activity can generate clonal seed from hybrid plants. More recent work in cereals, including sorghum, indicates that engineered apomictic reproduction can preserve hybrid genotypes across seed generations. These achievements represent major progress because they demonstrate that apomixis can be assembled from defined developmental components. However, clonal-seed frequency, fertility and seed yield still vary among genetic backgrounds, and experimental performance does not automatically guarantee field-ready technology.

Biological and Technical Challenges

The biggest challenge lies in the synchronisation of embryo and endosperm development. The embryo may at times start development without fertilization, and the endosperm, which is the nutritive tissue that supports the embryo, may still require pollen. An improper balance between the maternal and paternal genomes can result in seed abortion, poor germination or weak seedlings. Thus, parthenogenesis alone is not enough. Scientists have to regulate embryo initiation, endosperm formation, ovule development, seed filling and maturation as a unified reproductive process.

Another hurdle is genetic background. A gene combination that works well in one rice variety, for example, may show different effects in another species or even in another genotype of the same species. Unintentional changes in chromosome number, fertility or plant growth can also be caused by altering genes controlling meiosis. Gene-editing systems also have the potential to create chimeric edits or plants with multiple cell lineages. Stringent molecular analysis, progeny test and multi-generation evaluation are thus necessary to prove that the progeny are true maternal clones and that their performance is stable.

Agronomic, Ecological and Regulatory Concerns

Apomictic cultivars, like conventional varieties, are subject to practical requirements. They require high seed set, vigorous germination, uniform emergence, competitive yield and stability across heat, drought and other field stresses. The ratio of sexual to apomictic reproduction might be environmentally regulated especially in facultative apomicts. A system that tends to produce mostly clonal seed in controlled environment conditions might have more sexual leakage in the hands of farmers. Efficient detection methods will thus

be needed for seed certification and quality control.

The ecological consequences also require careful evaluation. Apomixis might facilitate the persistence and spread of a genotype because reproduction is less reliant on compatible pollen. An engineered apomictic trait that introgresses into related wild populations could have differing effects among species and environments. High maternal persistence and low dependence on fertilization may also restrict certain types of gene flow and promote maternal persistence. Assessment of risk, then, needs to be made on the basis of the crop, its mode of reproduction, the surrounding flora, and the region of cultivation rather than on generic assumptions.

The Way Forward

Potential advances will require considering apomixis as a full seed- development programme, not as a single-gene trait. The clonal-seed frequency, reproductive fertility and endosperm robustness need to be enhanced, and the system needs to be validated in a wide range of genetic backgrounds. High-throughput sequencing, single-cell analysis, gene editing, molecular imaging, and automated seed screening can be used to explore the changing identities of reproductive cells and the initiation of clonal embryos. Field evaluations over environments will be critical to test whether engineered systems can hold in real production environments.

Apomixis should initially be directed to crops and production systems where it has a strong potential for benefits, including maintaining complex hybrids, simplifying propagation, or providing better seed to developing regions. Maintenance of diverse breeding populations, as well as apomictic cultivars, will ensure future adaptability. The public and clear regulation should evolve with the technology and not following commercialisation.

CONCLUSION

Apomixis can combine the ease of seed propagation with the genetic stability of clonal reproduction. It can maintain hybrid vigour, reduce breeding time, facilitate multiplication and increase access to improved varieties. Recent breakthroughs in gene editing and synthetic apomixis are bringing this ancient breeding goal within reach. However, embryo formation is only part of the story. The

effective use of apomixis also requires stable endosperm development, high fertility, field performance, biosafety, genetic diversity and equitable seed systems. Apomixis is thus not a panacea, nor is it a far-off novelty. It is a powerful new tool that can contribute significantly to crop improvement, provided it is developed and introduced thoughtfully, scientifically and with a focus on farmers needs.