



ECOLOGICAL AND EVOLUTIONARY IMPLICATIONS OF HYBRIDIZATION, POLYPLOIDY AND APOMIXIS IN ANGIOSPERMS

CINTHYA I. CERVANTES-DÍAZ^{1,2} KEN OYAMA³ AND EDUARDO CUEVAS^{2*}

¹ Laboratorio Nacional de Análisis y Síntesis Ecológica, Escuela Nacional de Estudios Superiores Unidad Morelia, Universidad Nacional Autónoma de México, Morelia, Michoacán, Mexico.

² Facultad de Biología, Universidad Michoacana de San Nicolás de Hidalgo, Morelia, Michoacán, Mexico.

³ Escuela Nacional de Estudios Superiores Unidad Morelia, Universidad Nacional Autónoma de México, Morelia, Michoacán, Mexico.

*Author for correspondence: eduardo.cuevas@umich.mx

Abstract

Hybridization, polyploidy, and apomixis are related to the diversification of angiosperms, generating complex taxonomic relationships between species. Despite the differences in the frequencies of these phenomena, apomixis, the asexual seed production, tends to be frequently associated with hybridization and polyploidy. Apomixis has received more attention due to its potential to preserve desirable phenotypes in agriculture. The joint study of these three phenomena has been little explored, so the main objective of this review was to describe hybridization, polyploidy and apomixis and then analyze how they can be related. A synthesis of the main results of the studies obtained from a specialized literature search, the main patterns that address these three phenomena together, and their evolutionary and ecological consequences are presented.

Keywords: agamospermy, apomeiosis, hybrids, parthenogenesis, polyploids.

Resumen:

La hibridación, la poliploidía y la apomixis están relacionadas con la diversificación de las angiospermas, generando relaciones taxonómicas complejas entre especies. A pesar de las diferencias en las frecuencias de estos fenómenos, la apomixis, la producción asexual de semillas, tiende a estar frecuentemente asociada con la hibridación y la poliploidía. La apomixis ha recibido más atención debido a su potencial para preservar fenotipos deseables en la agricultura. El estudio conjunto de estos tres fenómenos ha sido poco explorado, por lo que el objetivo principal de esta revisión fue describir la hibridación, la poliploidía y la apomixis y describir cómo se relacionan. Se presenta una síntesis de los principales resultados de los estudios obtenidos a partir de una búsqueda de literatura especializada, los principales patrones que abordan estos tres fenómenos en conjunto y sus consecuencias evolutivas y ecológicas.

Palabras clave: agamospermia, apomeiosis, híbridos, partenogénesis, poliploides.



Hybridization, polyploidy and apomixis are common processes in plants, which can cause enormous difficulties in delimiting one species from another and their relationships (Grusz *et al.* 2009). It has been estimated that 16-34 % of plant families and 6-16 % of genera have one or more hybrid reports (Rieseberg 1997). However, nearly 70 % of angiosperms have at least one polyploidization event in their history (Otto 2007, Soltis & Soltis 2009). In contrast, apomixis only occurs in 1 % of angiosperms and 75 % of apomictic taxa belong mainly to three families: Asteraceae, Poaceae and Rosaceae (Hörandl 2006). Despite the differences in the frequencies of these processes, apomixis is constantly associated with hybridization and polyploidy (Lovell *et al.* 2013).

Regarding angiosperms, attempts have been made to explain the relevance of these processes and to understand whether the occurrence of one phenomenon leads to the appearance of the other(s), and this has turned out to be a highly debated with multiple interpretations. Therefore, the main goal of this study is to investigate the relationships between these three processes and their relevance in ecological and evolutionary terms in angiosperm plant populations. First, the concepts of hybridization, polyploidy, and apomixis are defined. The results of a specialized literature search for studies to assess the three processes, are shown and the main results of the studies are described.

Hybridization. Hybridization is a process that involves the joining of genomes of two species or taxa that differ in at least one heritable character; that is, it acts in opposition to evolutionary divergence (Rieseberg 1997, Rieseberg & Willis 2007). Hybridization can take place between species with the same or different chromosome number; however, its consequences on the evolution of lineages have been widely recognized because it can increase genetic diversity, originate or transfer adaptations, reinforce or break reproductive barriers, and ultimately give rise to new species or lineages (Rieseberg 1997, Goulet *et al.* 2016). It is worth mentioning that the probability of allopolyploid hybrid speciation (speciation between different species) is much more common compared to homoploid hybrid speciation (speciation between species with the same chromosome number). The higher probabilities of allopolyploid hybrid speciation are because a change in the chromosome number can generate immediate isolation of hybrids from their parents (Rieseberg 1997, Gross & Rieseberg 2005, Goulet *et al.* 2016, Rieseberg & Willis 2007, Soltis & Soltis 2009).

Polyploidy. Polyploidy is the inheritable condition of having more than two complete sets of chromosomes (Comai 2005). The main consequence of polyploidy is the production of unreduced gametes (with the same chromosome number as somatic cells). This situation is overlooked in many individuals but can arise from the duplication of chromosomes before meiosis, the complete loss of the first or second meiotic division, defects in the cell plate formation, or the cell spindle's orientation (Mason & Pires 2015). Polyploidy can be of the autopolyploid type, which results when an organism has more than two sets of chromosomes derived from the same individual, which generally occurs when an unreduced gamete joins a reduced one or two unreduced gametes belonging to the same species. On the contrary, allopolyploidy corresponds to organisms that contain more than two sets of non-homologous chromosomes due to hybridization between different species (Mason & Pires 2015, Otto 2007, Ramsey & Schemske 1998). Interspecific hybrids generally produce a higher frequency of unreduced gametes compared to their parents (27.5 vs. 0.6 %), probably because hybrids suffer severe meiotic irregularities that cause poor chromosome pairing and nondisjunction (Mason & Pires 2015, Ramsey & Schemske 1998). In some cases, the formation of unreduced gametes (2n) in interspecific hybrids is related to the genetic distance between the parents, *i.e.*, the greater the genetic distance, the greater the production of unreduced gametes (Chapman & Burke 2007).

Apomixis. Sexual reproduction in angiosperms has generated a great diversity of plants; however, plants have developed asexual mechanisms to produce seeds (Lovell *et al.* 2013), as in apomixis or agamospermy. For this to occur, three steps are necessary: first, elusion of meiosis (apomeiosis) to produce an unreduced embryo sac; second, developing the embryo independently of fertilization (parthenogenesis); and finally, forming a functional endosperm (Aliyu *et al.* 2010, Bicknell & Koltunow 2004, Grimanelli *et al.* 2001). If the unreduced embryo sac is fertilized by a sperm cell, ploidy increases; otherwise, an embryo sac after apomeiosis without fertilization maintains its ploidy

level (Hörandl 2006, Lovell *et al.* 2013). However, most apomictic plants are hermaphrodites and produce a functional pseudogamous endosperm; that is, they need a sperm cell (from the pollen grain) to fertilize the polar nuclei of the embryonic sac to generate a functional endosperm. It is known that some taxa of Asteraceae, among others, are capable of forming a functional endosperm in the absence of pollen (autogamous endosperm); however, they maintain the production of pollen, which can be exported to other flowers (Richards 2003, Hörandl 2006, Hörandl & Temsch 2009, Hojsgaard *et al.* 2014).

When the embryo develops directly from a somatic ovule cell, apomixis is called the sporophyte type, also called an adventitious embryo. In this case, the sexual reproductive route is still functional so that seeds can contain apomictic and sexual embryos. In addition, the apomictic embryo will depend entirely on the sexual endosperm because the production of seeds by sporophytic apomixis does not exclude sexual reproduction (Grimanelli *et al.* 2001, Tucker & Koltunow 2009). The second type of apomixis is gametophytic, which in turn is subdivided into diplosporic and aposporic apomixis. In diplosporic apomixis, the unreduced embryonic sac is formed from a mother cell of the megaspore in which meiosis was disrupted; in this case, the diplosporia replaces the process of sexual reproduction. In contrast, aposporic apomixis arises when the unreduced embryonic sac is formed from a somatic cell close to the mother cell of the megaspore that differentiates into an initial aposporic cell that will later elude meiosis and go directly to mitosis. In this case, the aposporia may allow the coexistence or degeneration of the sex cell (Carman 1997, Tucker & Koltunow 2009).

Literature search. A literature search was performed using Web of Science on August 1, 2024, using the following keyword combination: “hybrid* AND polyploidy* AND apomixis OR agamospermy”.

According to the specialized literature search, 50 studies assessed hybridization, polyploidy, and apomixis in angiosperms (Table 1). Many articles were discarded because they only focused on two phenomena, mainly apomixis, and polyploidy, although in some cases, they mentioned possible past hybridizations. Table 1 only covers 9 families and 16 different genera, emphasizing Asteraceae (15) and Rosaceae (11).

Many studies cited in Table 1 aimed to investigate the inheritance of apomixis by performing artificial crosses between individuals with different ploidy levels and reproductive modes. Therefore, it is relevant to note that although apomixis is the least common phenomenon, it is of great interest, especially in agriculture. For this reason, a summary of the origin of natural and synthetic apomixis is given.

Table 1. Studies about hybridization, polyploidy and apomixis in angiosperms.

Family	Genus	Species	Main objective	Author
Asteraceae	<i>Hieracium</i>	<i>H. aurantiacum</i> y <i>H. pilosella</i>	To understand the heredity patterns of apomixis in outcrossing plant species with different ploidy levels and reproductive modes.	Bicknell <i>et al.</i> 2000
Asteraceae	<i>Hieracium</i>	<i>H. pilosella</i> , <i>H. bauhini</i>	To compare the capacity to generate offspring with different ploidy levels and reproductive modes between apomictic and sexual plants.	Krahulcová <i>et al.</i> 2009
Asteraceae	<i>Hieracium</i> subgenus <i>Pilosella</i>		To build the phylogeny for the subgenus <i>Pilosella</i> .	Fehrer <i>et al.</i> 2007

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Family	Genus	Species	Main objective	Author
Asteraceae	<i>Taraxacum</i>	<i>T. scanicum</i>	Evaluate the genotypic diversity among seven apomictic microspecies coexisting in Central Europe.	Majeský <i>et al.</i> 2015
Asteraceae	<i>Taraxacum</i>		Study the inheritance of apomixis in intraspecific crosses between different ploidy levels.	Tas & Van Dijk 1999
Asteraceae	<i>Taraxacum</i>	<i>T. officinale</i>	To evaluate meiosis in sexual diploid and apomictic triploid plants to find mechanisms that explain the high levels of genetic variation.	Van Baarlen <i>et al.</i> 2000
Asteraceae	<i>Taraxacum</i>	<i>T. officinale</i>	Describe how the apomictic development of seeds is carried out in sexual and apomictic individuals with different ploidy levels.	Van Baarlen <i>et al.</i> 2002
Asteraceae	<i>Taraxacum</i>		To evaluate the inheritance of apomixis by backcrossing F1 hybrids.	Van Dijk <i>et al.</i> 1999
Asteraceae	<i>Taraxacum</i>		Describe the evolutionary patterns of the genus regarding processes such as hybridization, polyploidy and apomixis.	Kirschmer & Stepanek 1996
Asteraceae	<i>Crepis</i>	<i>Crepis atribarba</i> subsp. <i>originalis</i> , <i>C. barbiger</i>	To determine whether interspecific pollen flow from apomicts can exert reproductive interference on the sexual species in the <i>Crepis</i> agamic complex.	Hersh <i>et al.</i> 2016
Asteraceae	<i>Pilosella</i>	<i>Pilosella bauhini</i> , <i>P. hoppeana</i> subsp. <i>testimonialis</i> , <i>P. officinarum</i> , <i>P. onegensis</i> , <i>P. pavichii</i> , <i>P. pseudopilosella</i>	Describe the processes that affect the population structure of the agamic complex of <i>Pilosella</i> in Bulgaria.	Krahulcová <i>et al.</i> 2018
Asteraceae	<i>Taraxacum</i> sect. <i>Ruderalia</i>		Analyze the progeny of hybrids resulting from crosses between 2× and 3×.	Mártonfiová <i>et al.</i> 2007
Asteraceae	<i>Pilosella</i>		To compare male function among sexual, facultatively apomictic and seed-(semi) sterile field plants.	Rotreklová <i>et al.</i> 2016
Asteraceae	<i>Erigeron</i>	<i>E. annus</i> , <i>E. strigosus</i>	Explore the genetic basis of agamospermy in the flowering plant genus <i>Erigeron</i> .	Noyes <i>et al.</i> 2000

Family	Genus	Species	Main objective	Author
Bachiaria	<i>Urochloa</i>		To characterize the nature of their genomes, the repetitive DNA and the genome composition of polyploids, including many apomictic species.	Tomaszewska <i>et al.</i> 2023
Brassicaceae	<i>Boechera</i>		To identify whether the apomictic diploids of <i>Boechera</i> are of hybrid origin.	Beck <i>et al.</i> 2012
Brassicaceae	<i>Arabis</i>	<i>Arabis drummondii</i> , <i>A. holboellii</i> , <i>A. × divaricarpa</i>	Identify the phylogeographic pattern of the <i>Arabis holboellii</i> complex to understand its evolution.	Dobes <i>et al.</i> 2004
Brassicaceae	<i>Boechera</i>		Summarize the knowledge of the genus <i>Boechera</i> about apomixis, polyploidy and hybridization.	Dobes <i>et al.</i> 2007
Brassicaceae	<i>Arabis</i>	<i>A. drummondii</i> , <i>A. holboellii</i> y <i>A. divaricarpa</i>	Identify the inheritance of ITS regions between parental species and hybrids in <i>Arabis</i> complex.	Koch <i>et al.</i> 2003
Brassicaceae	<i>Boechera</i>		Analyze the origin and evolution of apomixis in the genus <i>Boechera</i> .	Lovell <i>et al.</i> 2013
Brassicaceae	<i>Boechera</i>		Investigate phylogenetic relationships, ability to hybridize, mating system, and ploidy levels between 19 <i>Boechera</i> species.	Schranz <i>et al.</i> 2005
Brassicaceae	<i>Boechera</i>	<i>B. holboellii</i> , <i>B. divaricarpa</i> y <i>B. stricta</i>	Identify transcriptomic differences between sexual and apomictic ovules in the <i>B. holboellii</i> complex.	Sharbel <i>et al.</i> 2009
Brassicaceae	<i>Boechera</i>		Test the potential of haploid vs. diploid pollen from apomicts to transmit apomixis factors to obligate sexual recipient lines and initiate viable apomictic progeny.	Mau <i>et al.</i> 2021
Lactuceae, Asteraceae	<i>Hieracium</i> subgen. <i>Hieracium</i>		For the first time, molecular markers have been used to disentangle relationships and species origins of the taxonomically highly complex <i>Hieracium</i> s.str.	Fehrer <i>et al.</i> 2009

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Family	Genus	Species	Main objective	Author
Orchidaceae	<i>Zygopetalum</i>	<i>Zygopetalum mackayi</i>	Describe patterns of genetic diversity of pure and mixed-cytotype populations to evaluate the expected occurrence of a higher frequency of apomictic (clonal) individuals in the contact zone compared to pure cytotype populations.	Moura <i>et al.</i> 2020
Plumbaginaceae	<i>Limonium</i>	<i>L. dufourii</i>	Evaluate the genetic contribution of each putative paternal taxon in an asexual hybrid using microsatellites (SSRs).	Palop-Esteban <i>et al.</i> 2007
Poaceae	<i>Paspalum</i>	<i>P. procurrens</i> , <i>P. simplex</i> , <i>P. usterii</i> y <i>P. malacophyllum</i>	Evaluate the reproductive mode the ploidy level and perform interspecific crosses between four species of <i>Paspalum</i> to determine how similar their genomes are.	Hojsgaard <i>et al.</i> 2008
Poaceae	<i>Paspalum</i>	<i>Paspalum compressifolium</i> , <i>P. lenticulare</i> , <i>P. nicorae</i> , <i>P. rojasii</i>	To conduct cytogenetic analyses of inter- and intraspecific hybridizations involving a sexual, colchicine-induced autotetraploid plant and five Indigenous apomictic tetraploid (2n = 40) species.	Novo <i>et al.</i> 2019
Ranunculaceae	<i>Ranunculus</i>	<i>R. auricomus</i>	Determine the effect of hybridization and ploidy level on the male and female sporogenesis process.	Barke <i>et al.</i> 2020
Ranunculaceae	<i>Ranunculus</i>	<i>Ranunculus auricomus</i>	Identify the changes in the reproductive mode in homoploid and heteroploidy hybrid plants of the <i>Ranunculus auricomus</i> complex.	Hojsgaard <i>et al.</i> 2014
Ranunculaceae	<i>Ranunculus</i>	<i>R. auricomus</i> , <i>R. cassubicifolius</i> y <i>R. carpaticola</i>	Crosses between different species with different ploidy levels are performed to evaluate whether it is possible to introgress apomixis.	Hörandl & Temsch 2009
Ranunculaceae	<i>Ranunculus</i>	<i>R. auricomus</i>	To know the genetic variation between sexual diploids and apomictic polyploids.	Paun <i>et al.</i> 2006
Ranunculaceae	<i>Ranunculus</i>	<i>R. notabilis</i> , <i>R. carpaticola</i> y <i>R. cassubicifolius</i>	Compare the accumulated mutations and genetic divergence between apomictic and sexual species of the <i>Ranunculus auricomus</i> complex.	Pellino <i>et al.</i> 2013

Family	Genus	Species	Main objective	Author
Ranunculaceae	<i>Ranunculus</i>	<i>R. kuepferi</i>	Explore the relationship between polyploidy and apomixis in an altitudinal gradient.	Schinkel <i>et al.</i> 2016
Ranunculaceae	<i>Ranunculus</i>	<i>Ranunculus auricomus</i>	Investigate F2 hybrid plants generated by manual crossing, where both or one parent had apospory before.	Barke <i>et al.</i> 2018
Ranunculaceae	<i>Ranunculus</i>	<i>R. carpaticola</i> , <i>R. cassubicifolius</i> , <i>R. notabilis</i> , <i>R. variabilis</i>	To shed light on intraspecific ITS nrDNA variability in closely related but morphologically diversified taxa of the <i>Ranunculus auricomus</i> complex in Central Europe.	Hodac <i>et al.</i> 2014
Rosaceae	<i>Amelanchier</i>	<i>A. erecta</i> , <i>A. laevis</i>	Establish the relevance of apomixis and hybridization in the genus.	Campbell & Wright 1996
Rosaceae			Describe the distribution of apomixis and ploidy across the Rosaceae family.	Dickinson <i>et al.</i> 2007
Rosaceae	<i>Rosa section Caninae</i>	<i>R. caesia</i> , <i>R. rubiginosa</i> , <i>R. sherardii</i> , <i>R. villosa</i>	Perform interspecific crosses between different ploidy levels to evaluate the reproductive mode, ploidy, and genomic composition of hybrids.	Nybom <i>et al.</i> 2006
Rosaceae	<i>Rubus</i>		Investigate the origin of stable apomictic species and their genetic diversity.	Sarhanová <i>et al.</i> 2017
Rosaceae	<i>Rubus subgenus Rubus</i>		Evaluate the usefulness of ITS in reconstructing evolutionary pathways in apomictic genera.	Sochor <i>et al.</i> 2015
Rosaceae	<i>Amelanchier</i>		Understand the role of diploids in polyploid diversification and study the species delimitation problem in the genus.	Burgess <i>et al.</i> 2015
Rosaceae	<i>Sorbus subgen. Tormaria</i>	<i>S. x decipiens</i>	Investigate hybrids derived from crosses between <i>Sorbus aria</i> agg. and <i>Sorbus torminalis</i> .	Feulner <i>et al.</i> 2023
Rosaceae	<i>Sorbus</i>		Investigate the evolutionary relationships among <i>Sorbus</i> taxa.	Robertson <i>et al.</i> 2010
Rosaceae	<i>Sorbus</i>		Elucidate evolutionary relationships among the study taxa and determine the breeding systems within the <i>Sorbus</i> complex.	Hamston <i>et al.</i> 2018

Family	Genus	Species	Main objective	Author
Rosaceae (subf. Maloidea)			Study the reproductive mode of <i>Amelanchier</i> .	Campbell <i>et al.</i> 1991
			Describes the theory of gen effect: genomic collision and apomixis.	Carman 2001
			Review the causes that lead to geographical parthenogenesis in plants.	Hörandl 2006
			Review the origin of apomixis in natural plant populations.	Hojsgaard & Hörandl 2019
			Review the actual hypotheses of geographic parthenogenesis.	Hörandl 2009

Some general patterns derived from the study reviewed are: 1) all apomictic lineages tend to have a diploid sexual counterpart, either recent or ancestral 2) gene flow between apomictic and sexual populations commonly occurs in the genera *Pilosella*, *Taraxacum*, *Rubus*, *Boechera* and *Ranunculus*, suggesting the relevance in these genera of purging asexual genomes with accumulated deleterious mutations to provide new genetic variation to apomictic populations and ultimately produce new apomictic lineages. Consequently, when trying to determine the origin of an apomictic lineage, it is found that it comes from the hybridization of some sexual taxon with another apomictic. This situation is a significant impediment to discern from where the initial apomictic lineages have arisen, whether diploid or polyploid (Koch *et al.* 2003, Grusz *et al.* 2009, Sochor *et al.* 2015, Sarhanová *et al.* 2017).

Under natural conditions, hybridization in combination with polyploidy appears to be a natural route to asexuality, which in turn is considered an escape route for sterile hybrids, allowing their maintenance within natural populations (Bicknell *et al.* 2000, Paun *et al.* 2006, Hörandl 2010, Hojsgaard *et al.* 2014). A common topic related to polyploidy and apomixis is geographic parthenogenesis, which suggests that organisms with these characteristics are more tolerant and adapted to climatic regions with higher elevations and latitudes, as well as having broader distributions than their sexual relatives (Kearney 2005, Hörandl 2006, 2009, Thompson & Whitton 2006, Hörandl *et al.* 2008, Schinkel *et al.* 2016).

It is worth mentioning that there is a bias in the study of apomixis and polyploidy due to their great potential to satisfy the future nutritional demands of humanity (Toenniessen 2001). Many crops are polyploid due to intentional crosses, and such hybridization often increases the vigor or yield of these crops (Renny-Byfield & Wendel 2014).

How is apomixis inherited? Usually, intraspecific and interspecific hybridizations have been carried out between individuals with different ploidy levels and reproductive modes (*i.e.*, sexual reproduction vs. apomixis) to evaluate and compare their effects as well as to determine the mode of inheritance of apomixis (Table 1, Tas & Van Dijk 1999, Van Dijk *et al.* 1999, Bicknell *et al.* 2000, Schranz *et al.* 2005, Hojsgaard *et al.* 2008, 2014, Hörandl & Tensch 2009, Barke *et al.* 2018, Feulner *et al.* 2023, Mártonfióvá *et al.* 2007, Nybom *et al.* 2006). To evaluate the causes of apomixis, it is necessary to distinguish the effects of ploidy and interspecific hybridization, which is possible in taxa that show apomixis in a diploid state, as occurs in the *Boechera holboellii* complex, *Potentilla argentea* and *Hierochloa australis* (Beck *et al.* 2012, Lovell *et al.* 2013). *Boechera divaricarpa* is an apomictic diploid species, and when it is crossed with a sexual diploid, it generates fertile triploid progeny that is potentially apomictic, highlighting that apomixis in *Boechera* is not given by a single locus or factor causing “apomixis” (Schranz *et al.* 2005). The diploid apomictic condition is transmitted through haploid pollen (infectious asexuality) within a single generation, and polyploids can form through multiple pathways (Mau *et al.* 2021).

In the *Ranunculus auricomus* complex, apospory emerged spontaneously in the first hybrid generation of two sexually obligate diploid species, and this increased in the F2 where functional apomictic seeds had already developed (Barke *et al.* 2018, Hojsgaard *et al.* 2014).

Regarding artificial crosses between species with different ploidy and apomictic capacity, in the genus *Boechera*, one-third of the crosses showed evidence of apomixis and/or increased ploidy (Schranz *et al.* 2005). Similarly, in *Taraxacum*, it has been proposed that several loci are involved in the genetic control of apomixis, (by performing crosses between 2× sexual and 3× apomictics they produced 2×, 3×, and 4× individuals). After that, those individuals can cross again with 2× sexual individuals, resulting in fewer apomictic progeny and more no apomictic progeny with reduced, irregular chromosome numbers (Tas & Van Dijk 1999, Mártonfiová *et al.* 2007). Therefore, the apomictic of *Taraxacum* can generate pollen that transfers apomixis to diploid individuals (Baarlen *et al.* 2000).

Apomixis, in some cases, is controlled by few alleles, so it is suggested that individuals with genome duplications provide the necessary number of these alleles for apomeiosis to occur, in addition to buffering against deleterious mutations in gametes and somatic cells (Bicknell *et al.* 2000, Grimanelli *et al.* 2001, Sharbel *et al.* 2009). For example, the *Anachyris* subgenus of *Paspalum* has at least three sexually self-incompatible diploid species, as well as apomictic tetraploid representatives of autopolyploid origin (Hojsgaard *et al.* 2008), suggesting that apomictic alleles are present in diploids and that their expression depends on ploidy level (Quarin *et al.* 2001).

Genes involved in natural apomixis. Interspecific hybrids or specific hybrids within agamic complexes are widely studied in the context of segregation of apomixis (apomeiosis, parthenogenesis and functional development of endosperm; Fiaz *et al.* 2021). Although the genes controlling the various components of apomixis have already been identified, the genetic mechanism of asexual reproduction is complicated in nature and is still not sufficient to explain the entire apomictic phenomenon (Fiaz *et al.* 2021, Niccolo *et al.* 2023). Therefore, knowing the genes controlling the sexual pathway may be another way to develop apomixis (Fiaz *et al.* 2021). Many specific genes that act on parthenogenesis control have been described, such as *ASGR-BABY BOOM*-like (*ASGR-BBML*), *BABY BOOM1* (*BBM1*), *LOSS OF PARTHENOGENESIS* (*LOP*), *PARTHENOGENESIS* (*PAR*) genes from apomictic dandelion that triggers embryo development in unfertilized egg cells. Others like Somatic Embryogenesis Receptorlike Kinase (*SERK*) and *MSP1* control somatic embryogenesis. On the contrary, some genes, depending on their homozygous or heterozygous condition, can promote sexuality or apomixis, such as the *APOLLO* gene (Fiaz *et al.* 2021, Hojsgaard & Hörandl 2019, Underwood *et al.* 2022).

Genetic analysis of apomixis inheritance in cereals, grasses, and related genera, *i.e.*, *Tripsacum*, *Pennisetum*, *Panicum*, *Bracchiaria*, and *Paspalum*, detected a single chromosome responsible for inducing apomixis. However, the transfer of such chromosomes has been difficult (Mieulet *et al.* 2016, Fiaz *et al.* 2021).

In Asian apomictic citrus fruits, a minimum inverted repeat transposable element (MITE) in the promoter region of CitRWP was found to confer an apomictic phenotype responsible for dominant citrus polyembryony. This insertion was estimated to have arisen in the early Pleistocene in an ancestral population and spread to other mandarins, oranges, grapefruits, and lemons (Wang *et al.* 2017, Wu *et al.* 2021). Interestingly, repeat transposable element (MITE) insertion in the promoter was also identified in dandelion and hawkweed (Underwood *et al.* 2022).

Finally, Niccolo *et al.* (2023) extensively reviewed the expression of genes between sexual and apomictic conditions. They found a differential gene expression between both groups concerning several endogenous effectors (such as small RNAs, epigenetic regulation, hormonal pathways) that may contribute to the appearance of apomixis.

Synthetic apomixis. Apomixis can potentially preserve hybrid vigor in economically important plant genotypes for multiple generations, and synthetic apomixis has been suggested to fix hybrid vigor. As described above, the emergence of apomixis requires three modifications of the sexual pathway to ensure the growth of viable and apomictic fruits: 1) the bypassing of meiotic cell division, 2) the parthenogenetic establishment of an embryo, and 3) the successful development of the endosperm (Barke *et al.* 2018, Fiaz *et al.* 2021). Hojsgaard & Hörandl (2019) noted that hybridization could only affect a component of apomixis, such as the formation of an unreduced embryo sac. Still, the

other two steps corresponding to parthenogenesis and the endosperm formation would remain unaffected. d’Erfurth *et al.* (2009) managed to create a genotype called *MiMe* (“Mitosis instead of Meiosis”) as a first step to identify the genes related to apomixis and then try to generate synthetic apomixis genotypes. For example, “apomeiosis” involves the omission or deregulation of meiosis, resulting in a mitotic-like division that prevents ploidy reduction. Three features distinguish meiosis from mitosis: (i) a succession of two rounds of division after a single replication, (ii) pairing and recombination between homologous chromosomes, and (iii) cosegregation of sister chromatids in the first division. By identifying and bringing together three genes that modified these characteristics (*OSD1*, *ATSP11-1*, and *ATREC8*), they created a genotype in which mitosis replaces meiosis without affecting subsequent sexual processes. Later, Mieulet *et al.* (2016) showed that additional combinations of mutations can turn *Arabidopsis* meiosis into mitosis by replacing *SPO11-1* with other recombination initiation factors (*PRD1*, *PRD2*, or *PRD3/PAIR1*) and that a combination of three mutations in rice (*Oryza sativa*) efficiently turns meiosis into mitosis too. They also identified the functional homolog of *OSD1* in rice (*OsOSD1*), suggesting that it could be identified in other cereals.

Synthetic apomixis achieved with *MiMe* has disadvantages, such as doubling ploidy in each generation, generating low fertility, and a limited apomixis induction rate in rice. These problems have been solved with the heterologous expression of the dandelion *PAR* gene, effectively producing clonal seeds with fixed genotypes, which remained stable during the three generations analyzed (Song *et al.* 2024). The same expression of dandelion *PAR* in lettuce (*Lactuca sativa*) egg cells induced haploid embryo-like structures without fertilization (Underwood *et al.* 2022, Song *et al.* 2024). Recently, the *MiMe* system could be established in inbred tomatoes through mutation of *SISPO11-1*, *SIREC8*, and *SITAM* (Wang *et al.* 2024).

The genetics, genomics, and epigenetic modifications that promote apomixis in flowering plants are widely studied. In contrast, studies on apomixis induced by gene editing techniques, *i.e.*, CRISPR/Cas9, are in an early stage, as only a few reports have been published, like those done with rice (Fiaz *et al.* 2021). Genomic alteration employing genome editing technologies (GETs) like clustered regularly interspaced short palindromic repeats (CRISPR)/CRISPR-associated protein 9 (Cas9) for reverse genetics has opened new avenues of research in the life sciences, including for rice grain quality improvement (Fiaz *et al.* 2019). As has been done with rice, the disadvantages presented with the *MiMe* and with CRISPR/Cas9 have been attempted to be solved with the “fix strategy” (hybrid fixation) with genes that promote the development of the “auto endosperm,” which can solve the problem of low fertility (Fiaz *et al.* 2021). Circumventions of key imprinting and/or dosage barriers in the endosperm will facilitate the engineering of apomixis technology (Spillane *et al.* 2004).

Evolutionary relationships between hybrid, polyploid, and apomictic species. When sexual and apomictic plants coexist in sympatry, hybrid swarms can form; for this reason, apomictic groups represent a complex reticulated network of sexual species, stable apomictic lineages and their hybrids with a large variation of genotypes and phenotypes. This variation complicates the taxonomic denomination of such apomictic lineages (Majeský *et al.* 2015, Majeský *et al.* 2017, Hamston *et al.* 2018). In the review by Kolař *et al.* (2017), it was found that many species contain odd-ploidy cytotypes (3×, 5×, 7×, 9×), which may play an important role in polyploid evolution as mediators of gene flow and recurrent polyploid origins. They also found that species in which odd-ploidy cytotypes are dominant exhibit strong if not exclusive, asexual modes of reproduction, and although their hybrid origin has only been confirmed occasionally, asexual reproduction would facilitate their establishment (Paun *et al.* 2006, Robertson *et al.* 2010). Apomixis is generally associated with ploidy (4× or more). However, there are genera where apomixis occurs in diploids and triploids, such as *Boechera* (Dobes *et al.* 2007). Diploid apomictics can infect asexually through haploid pollen (Mau *et al.* 2021). In genera such as *Pilosella*, *Taraxacum*, *Rubus*, *Boechera*, and *Ranunculus*, a higher gene flow between apomictics and sexuals has been documented (Sarhanová *et al.* 2017). *Boechera* and *Alchemilla* are genera that show complex evolutionary relationships due to reticulate hybridization and apomixis. Interspecific hybridization is widespread in the former, and sexual species tend to hybridize between them. Apomictic hybrids may also be backcrossed with sexual individuals. *Alchemilla* presents unresolved taxonomic relationships and a complex taxonomy, although it has many taxa almost exclusively apomictic and only a few with sexual reproduction (Majeský *et al.* 2017).

One consequence of the interaction among distinct cytotypes is the production of intermediate cytotypes (*i.e.*, triploids), generally at low frequencies. However, triploids may promote the coexistence of multiple cytotypes through a triploid bridge, so understanding the role of triploids is crucial to understanding the dynamics of mixed-cytotype populations (Moura *et al.* 2020). It is known that triploids are found more frequently where diploids of different species are sympatric and where diploid hybrids occur (Burgess *et al.* 2015).

Hybridization in completely apomictic populations requires that fertile pollen and reduced egg cells are produced by natural apomicts (Tas & Van Dijk 1999). In *Taraxacum*, the male meiosis of triploids is predominantly reductional, leading to more than 90 % infertile gametes. Still, the pollen of tetraploid hybrids was reduced and is diploid (Baarlen *et al.* 2000). However, both can form new triploid apomictic lineages (Mártonfióvá *et al.* 2007). Triploids can arise in two ways: from the fertilization of unreduced eggs by reduced sperm or through the fertilization of reduced eggs of diploids by reduced sperm of tetraploids (Baarlen *et al.* 2000, Dickinson *et al.* 2007).

In *Boechera*, some apomicts produce predominantly unreduced pollen, with considerably high quality, and other triploid lineages are apomictic and produce large quantities of non-functional pollen, but with artificial crosses, they were able to produce tetraploid offspring which have low frequency in natural populations (Tas & Van Dijk 1999, Dobes *et al.* 2007). It is necessary to know the function of these tetraploids in *Boechera* since in *Taraxacum* they help to generate new triploid lineages (Schranz *et al.* 2005).

In the case of *Pilosella*, the quality of pollen depended more on the cytotype than on the reproductive mode or its hybrid origin since pollen of lower ploidies $3\times$ and $5\times$ was of lower quality, and this improved as the ploidy increased (Rotreklová *et al.* 2016). In *Amelanchier*, the percentage of apomictic seeds increased according to ploidy in di, tri, and tetraploids (Burgess *et al.* 2015).

If pollen is not needed to form the endosperm, as in many Asteraceae, triploid apomictic lineages can be established quickly, as in *Erigeron*, *Hieracium*, and *Taraxacum* (Hojsgaard & Hörandl 2019). On the contrary, an important barrier to gene flow between cytotypes is the likely deviation from the normal $2m:1p$ genome ratio (maternal genome: paternal genome) during endosperm formation, as has been suggested for *Ranunculus* (Hörandl & Temsch 2009, Paule *et al.* 2011). However, in brambles, they seem to have a relaxed pressure to maintain the normal endosperm equilibrium number $2m:1p$, which can vary up to $8m:1p$ or sometimes have autonomous development (Sarahanová *et al.* 2017).

The most studied apomictic species complex with reticulate relationships is the *Ranunculus auricomus*, which comprises approximately 800 apomictic microspecies traditionally grouped into four morphological groups (Majeský *et al.* 2017). It is known that apomixis introgression into sexual populations is limited by ploidy barriers in the *R. auricomus* complex and, to a lesser extent, by mentoring effects. Therefore, apomixis introgression could only occur if sexuals had the same ploidy level as apomictics and if in interploidal crosses, there was a relaxation of endosperm balance or autonomous endosperm production (Hörandl 2009).

All apomictic plants appear scattered at the tips of phylogenies and are thought to be evolutionarily young even though the estimation of their ages is biased by possible reversals from apomixis to sexuality (Pellino *et al.* 2013). For example, *Limonium dufourii* is a triploid apomictic species that could be considered a dead-end because it is self-incompatible and highly sterile; as a consequence, it presents a strong genetic population differentiation (Palop-Esteban *et al.* 2007). However, although lineages have low fertility, they are not necessarily doomed to extinction because perennial plants can persist for several years (Schranz *et al.* 2005).

Obligate apomixis and the formation of unreduced male gametes as an evolutionary advantage for the propagation of apomixis help to escape from meiotic sterility because of interspecific hybridization (Matzk *et al.* 2003). For some tetraploids, the gametophytic apomixis, pollen fertility, and SC (self-compatibility) will combine to improve their fecundity and increase their abundance (Dickinson *et al.* 2007). Meiosis and pollen production are expected to be more stable in tetraploids, and diploid pollen will be available for pseudogamy (Hojsgaard & Hörandl 2019).

Comparison between sexual species and apomictic polyploids. Another type of study compared the process of meiosis and mitosis between organisms with variation in ploidy level and reproductive mode, which presumably have under-

gone hybridization processes or, in the best of cases, have been confirmed (Baarlen *et al.* 2000, 2002). In *Ranunculus*, megasporogenesis (egg formation) and microsporogenesis (pollen grain production) were compared between diploid and polyploid hybrids, finding that hybridization affects the meiosis of megasporogenesis to a greater extent than microsporogenesis (Barke *et al.* 2020). In *Taraxacum officinale* unexpectedly high levels of genetic variation have been found in the apomictic populations. Meiosis was compared between sexual diploid and apomictic triploid plants to find mechanisms that could account for the high levels of genetic variation in the apomicts. The authors found a low level of chromosome pairing and chiasma formation at meiotic prophase I in the microsporocytes of the triploid apomicts and an incidental formation of tetrads in the megasporocytes of the apomicts (Van Baarlen *et al.* 2000).

A sympatric population of sexual and apomictic cytotypes of *Paspalum* contains a higher level of genetic variation than ploidy-uniform populations, which highlights hybridization as a process that increases the genetic variation of apomictic cytotypes and creates new apomictic lineages (Majeský *et al.* 2017). Likewise, repeated backcrossing of apomictic derivatives with parental *Sorbus* taxa is responsible for generating new apomictic taxa (Robertson *et al.* 2010).

In dandelion contact zones, hybridization between apomictic and sexual plants generates greater genotypic and morphological diversity of apomictics, and the accumulation of somatic mutations was found (Majeský *et al.* 2015). In *Boechera*, the diploid apomicts showed high heterozygosity as a result of the combination of disparate genomes, suggesting that most are of hybrid origin and that hybridization allows the transition to gametophytic apomixis (Beck *et al.* 2012). Polyploidy may favor the rapid accumulation of changes in a short period because more possible mutational sites are available (Pellino *et al.* 2013). New highly heterozygous species arise from interploidy crosses and can be perpetuated with apomixis or with a more or less mixed mating system (Dickinson *et al.* 2007).

Facultative apomicts retain the ability to reproduce sexually and produce viable pollen, and therefore, their genotypic variability is often comparable with that of their sexual relatives (Sarhanová *et al.* 2017). It is proposed that occasional sexuality and recombination could generate high levels of genetic variation within populations and help to differentiate apomictic populations. However, this does not apply to *Limonium dufourii* due to its self-incompatibility and high sterility, showing a range of moderate to high genotypic diversity (Palop-Esteban *et al.* 2007).

The divergence between diploids and hexaploids can be attributed to Muller's ratchet (accumulation of mutations in asexuals) since apomicts have been shown to generate appreciable amounts of genetic variation through non-meiotic processes (Paule *et al.* 2011). Therefore, we expect generally elevated levels of heterozygosity in apomictic individuals relative to the ancestral sexual lineages (Lovell *et al.* 2013). To analyze the origins of genetic diversity in polyploids, it is necessary to compare the polyploid taxon with its presumed parents or to compare multiple sets of progenies. Neither of these methods is feasible in *Limonium dufourii* because its parental species are unknown, and it cannot reproduce sexually (Palop-Esteban *et al.* 2007).

Due to the non-recombinant nature of apomicts (Lovell *et al.* 2013) and considering apomictic taxa as "young taxa," most of the genetic diversity in obligately polyploid apomictic taxa is obtained at the time of species formation through hybridization (Palop-Esteban *et al.* 2007).

Finally, many other study systems could improve the understanding of the evolution of these three phenomena. For example, in the genus *Fuchsia*, *F. microphylla* and *F. thymifolia*, which are gynodioic shrubs described as diploid, female flowers produce fruits under conditions of isolation from pollinators; however, there is a lack of molecular evidence confirming the presence of apomixis (Cuevas *et al.* 2014). It is worth mentioning that both species coexist sympatrically, and hybridization between these two species has recently been confirmed, making it a good model for monitoring polyploidy and apomixis in hybrid individuals (Cervantes-Díaz *et al.* 2024).

In conclusion hybridization is commonly recorded without the emergence of polyploidy and apomixis. However, this does not exclude the possibility that they accompany it because these last two phenomena are scarcely evaluated in most angiosperms. In the case of the so-called "apomictic species", this classification can often depend on the evaluated sample size, as well as the technique used for its identification, because in many cases, apomictic species are not obligate but rather facultative, along an asexual-sexual gradient. However, polyploidy and apomixis are strongly related because both phenomena imply a dysregulation of the sexual reproductive pathway. The hypotheses

that try to explain the conjunction of these phenomena included study cases that support them and, in other cases, do not because of the high diversity of possibilities in the few species studied. Therefore, future studies should expand to succeed in finding a general pattern.

Few studies have proposed to corroborate whether interspecific hybridization can promote the emergence of apomixis and polyploid. Still, it is evident that once these lineages are established, they can continue to hybridize with their own parents or with other taxa, generating more lineages. In this way, the complex relationships established between these systems make it difficult to recognize “species” to such an extent that most authors prefer to refer to their study populations with terms such as “taxa, lineages, complexes or sections”. It is important to note that for this reticulated evolution to occur, apomictic hybrids, whether polyploid or not, must produce some proportion of viable pollen that will be their only way to contribute to generating new lineages.

Some evolutionary routes related to the three phenomena assessed in this review are presented in [Figure 1](#). For example, when a reduced gamete (species A) joins with an unreduced gamete (species B), a polyploid hybrid is instantly formed because of the divergence of the parent genomes. In another case, we see that diploid species A could become autotetraploid ($4\times$); therefore, apomixis could develop. Finally, if two diploid species, A and B, hybridize, they can give rise to a diploid hybrid that can suffer irregularities in meiosis, leading to the appearance of apomixis, which depends on whether pollen is required to form the endosperm and could lead to the formation of polyploid or diploid apomictic hybrids. In the event that diploid hybrids do not become apomictic immediately after hybridization, they can increase their percentage of unreduced gametes that, when fusing with gametes of some other species, would give rise to a polyploid hybrid that could develop apomixis.

Related to hybridization, apomixis, and polyploidy, there are other important factors to consider, such as the 2:1 genetic contribution (maternal: paternal) in the formation of the endosperm since it has been shown that when this ratio is disrupted, the seed’s viability is reduced. In addition, it has been reported that many species lose self-incompatibility by developing an apomictic capacity, which many consider to be an evolutionary “*cul-de-sac*” destined to extinction due to a lack of genetic variation. Finally, we concluded that the knowledge of these three phenomena is

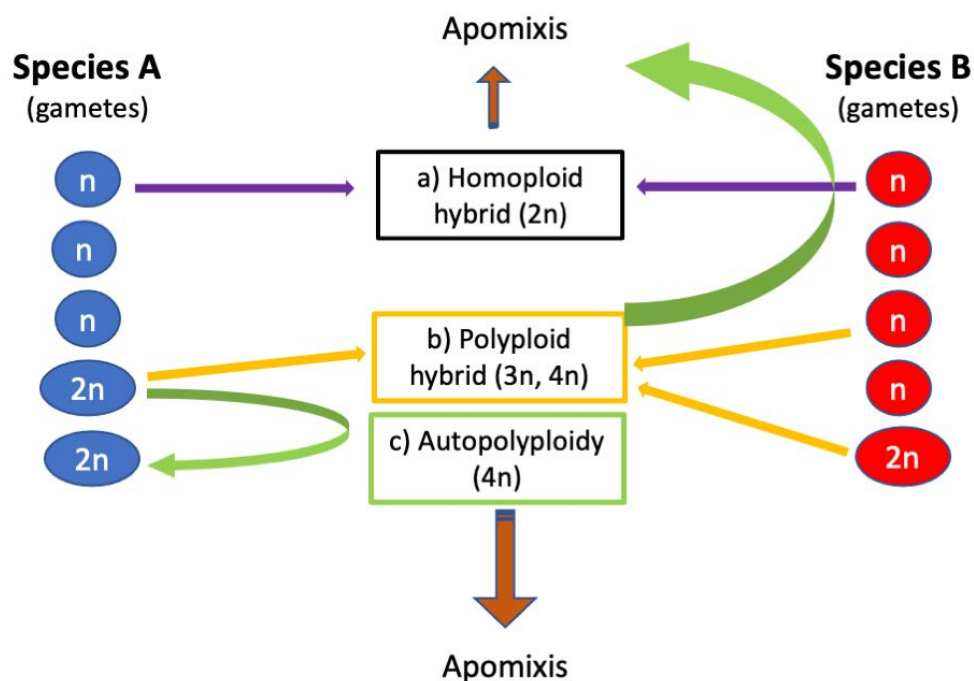


Figure 1. Different routes from two diploid species ($2n$) and the production of haploid (n) or non-reduced gametes ($2n$) and their relationship with the emergence of hybridization, apomixis, and polyploidy. Although apomictic diploid species are also known, these usually present a history of hybridization and polyploidy in their previous lineages.

still very limited due to the difficulty in detecting them and their enormous variation, their potential for combination, and the numerous orders in which they can occur in plants. However, the development of metagenomics will most likely bring significant advances in the short and medium term.

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