



Role of Apomixis in Perpetuation of Flowering Plants: Ecological Perspective

13

Roopam Sharma and Vishnu Bhat

Abstract

Apomixis or asexual formation of seeds involves three major features, absence of meiotic reduction, recombination and fertilisation, and thereby leads to formation of genetically uniform progeny. Though Winkler coined the term ‘apomixis’ in 1908 to describe ‘asexual reproductive process in place of sexual reproduction without nuclear or cell fusion’, the definition of apomixis is now restricted to the formation of seeds via an asexual process. Today apomictic forms are reported in several flowering plant taxa in species of both monocotyledonous and dicotyledonous genera. Although apomixis seems to be a simple phenomenon, several pathways are speculated to achieve it. Also this phenomenon has many subcomponents which should be achieved consistently and simultaneously to ensure formation of seeds (or next generation). There has been much focus on several facets of apomixis including cyto-embryological, molecular and biotechnological aspects. However, the origin of apomixis (independently in several plant taxa) and its ecological and evolutionary significance is still not completely deciphered. Nonetheless, we do understand that polyploidisation and/or hybridisation-associated shifts as well as environmental gradients play a role in establishing apomixis in most of the studied taxa. Further diversification occurs through several processes including mutation, chromosome rearrangements and aneuploidy, residual sexuality and backcrossing. While environmental changes bring about range shifts and secondary contact hybridisation of different ecotypes results in origin of apomictic lineages, apomixis is also an important factor in changing the ecological scenarios. Previously apomictic lineages were considered to be a dead end, but the current understanding treats them as a means of diversification of polyploid complexes and evolution in angiosperms.

R. Sharma · V. Bhat (✉)

Department of Botany, University of Delhi, New Delhi, India

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275

Keywords

Apomixis · Apospory · Diplospory · Parthenogenesis · Autonomous endosperm · Pseudogamous endosperm

Glossary

Amphimixis: or sexual reproduction Amphimixis is the process of reproduction where megaspore mother cells undergo meiosis to form a reduced embryo sac and then form embryo after double fertilisation to give rise to seeds with both maternal and paternal contribution.

Apomixis: Apomixis (asexual seed formation) is a phenomenon in which a plant bypasses meiosis and fertilisation to form a viable seed.

Sporophytic apomixis or adventitious embryony: This variation of apomixis involves the formation of a maternal embryo from one or more somatic cells of the ovule.

Gametophytic apomixis: Those apomictic pathways where a diploid cell divides mitotically and differentiates to form an unreduced embryo sac which eventually gives rise to the maternal embryo.

Apospory: It is the type of gametophytic apomixis where the unreduced embryo sac arises from a somatic nucellar cell which acquires the developmental program of a functional megaspore.

Diplospory: It is the type of gametophytic apomixis where the unreduced embryo sac arises from a megaspore mother cell with suppressed or modified meiosis.

Parthenogenesis: It is the process of spontaneous fertilisation-independent development of the embryo from reduced or unreduced egg cell.

Polyphyletic origin: When a phenotype is derived independently from more than one common evolutionary ancestor.

Polyphenic origin: When multiple forms or phenotypes can arise from a single genotype by differing external conditions.

Geographic parthenogenesis: It is the term used for higher-latitude geographic distribution of asexuals compared to their sexual counterparts.

Sympatric: Two species are said to be sympatric if they occupy the same or overlapping geographic areas.

Syntopic: Two species are said to be syntopic if they can coexist without interference with each other.

Exaptive evolution: A character not selected by natural selection for its current utility.

Polyspory: Polysporic species include both bisporic (meiosis produces only two megaspores, each with two haploid nuclei, and one of them forms functional megaspore; therefore, two haploid nuclei are involved in the formation of embryo-sac) and tetrasporic species (meiosis produces one 4-nucleate megaspore, and all haploid nuclei are involved in the formation of embryo-sac).

13.1 Introduction

Flowering plants have two modes of reproduction: amphimixis or sexual reproduction and asexual reproduction. Asexual reproduction can be achieved by means of vegetative propagation and agamospermy or asexual production of seeds; apomixis and agamospermy are usually used as synonyms (Bicknell and Koltunow 2004). Amphimixis involves fusion of male and female gametes and thus an alternation of sporophytic and gametophytic generations, while the absence of chromosome reduction in the pathway to embryo development is the defining feature of apomixis (Ozias-Akins 2006). Whereas sexual reproduction is a means to develop new genetic combinations, apomixis can help in the maintenance of desired plant phenotypes (Hojsgaard and Hörandl 2019).

All apomictic systems share at least three developmental components (Fig. 13.1): (i) apomeiosis, the generation of a cell capable of forming an embryo without prior (full reductional) meiosis; (ii) parthenogenesis, the spontaneous fertilisation-independent development of the embryo; and (iii) the capacity to either produce endosperm autonomously or to use an endosperm derived from fertilisation (Koltunow 1993). Based on apomeiosis, two main mechanisms for apomixis are recognised: sporophytic apomixis or adventitious embryony and gametophytic apomixis (Nogler 1984; Koltunow 1993; Crane 2001). The simplest pathway for apomixis is to avoid the production of a gametophyte and formation of a maternal embryo from one or more somatic cells of the ovule (sporophytic apomixis). Sporophytic apomixis differs from the gametophytic in that no alternation of generations intervenes prior to embryo development. Gametophytic apomixis encompasses those apomictic pathways where the maternal embryo originates from a diploid egg cell differentiated in an unreduced embryo sac. Gametophytic apomixis further shows classification into two main pathways: in the first case, the unreduced embryo sac arises from a somatic nucellar cell which acquires the developmental program of a functional megaspore (apospory). Alternatively, the embryo sac arises from a megaspore mother cell with suppressed or modified meiosis; here the pathway is termed diplospory. These pathways can be further subdivided into a variety of different developmental schemes described in several reviews (Nogler 1984; Asker and Jerling 1992; Crane 2001).

Parthenogenesis defined as spontaneous development of an embryo in the absence of fertilisation (diploid parthenogenesis, when the embryo develops from an unreduced egg cell) is the second component of gametophytic apomixis. The third (and last) component for the production of a functional apomictic seed is functional endosperm formation. Though a 2:3 embryo-to-endosperm ploidy ratio (related to the role of differential genomic imprinting on the maternal and paternal contributions) is of predominant occurrence among many species, in apomicts, the embryo-to-endosperm ploidy ratio can differ from normal 2:3 ratio depending on the mechanism of apomixis employed (Ozias-Akins 2006).

Apomixis can lead to the formation of variable progeny types. As discussed, combination of three steps, namely, non-reduction, loss of fertilisation, and parthenogenesis, results in apomixis and genetically identical progenies, but omission of

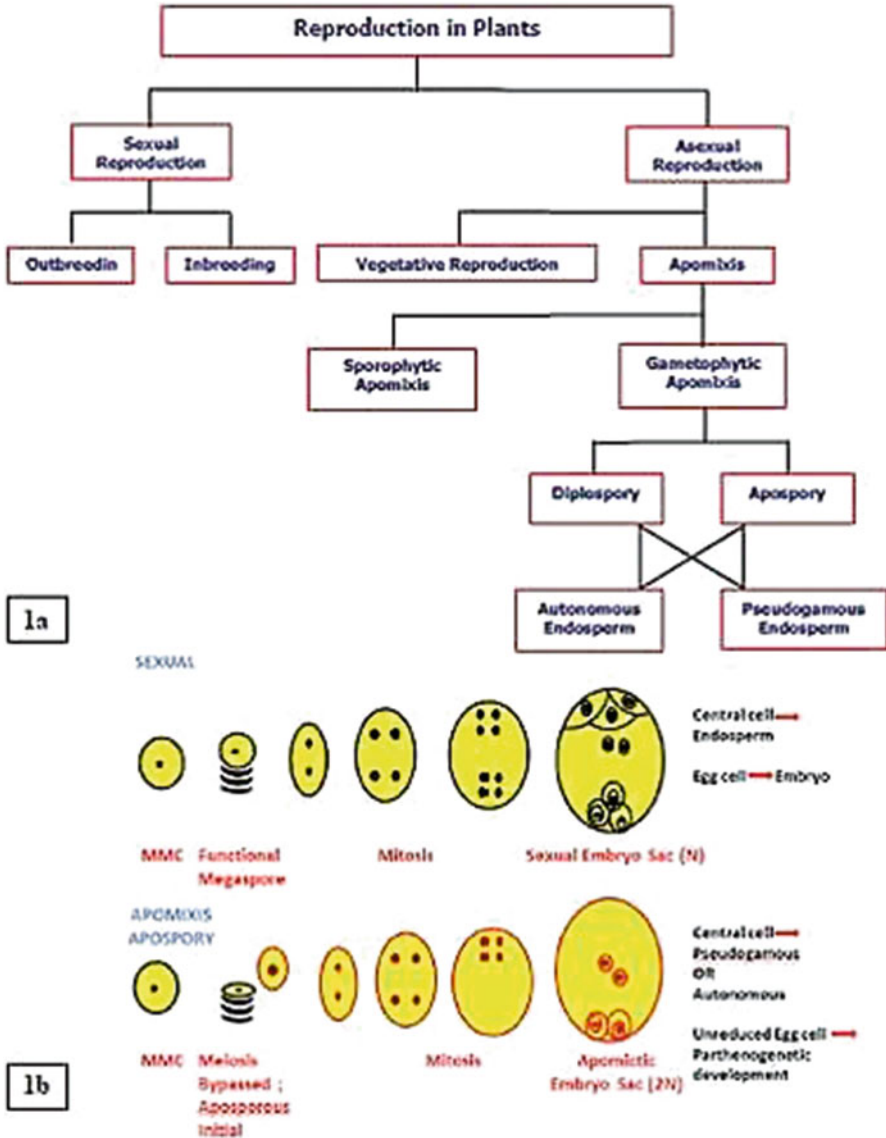


Fig. 13.1 (1a) Types of reproductive strategies in plants; (1b) components of apomixis as shown for apospory: (i) apomeiosis or by-pass of meiotic reduction, (ii) parthenogenetic development of egg cell to form the embryo, and (iii) endosperm development through autonomous or pseudogamous development

any one step is also a possibility in some cases, and therefore, in total four progeny types are possible:

- (a) $n + n$ or (BII) hybrids: normal sexual process; embryo development via fertilisation of two reduced gametes
- (b) $n + 0$: haploid parthenogenesis (gynogenesis or androgenesis); embryo development from one of the reduced gametes
- (c) $2n + n$ or (BIII) hybrids: embryo development from fertilisation of one reduced and one unreduced gamete
- (d) $2n + 0$: apomixis; embryo development from an unreduced gamete

The capacity to autonomously produce embryos from a reduced egg cell indicates that the locus controlling parthenogenesis is not as tightly linked to the genetic locus responsible for apomeiosis. The capacity to form BIII hybrids indicates that the unreduced embryo sac is functionally similar to embryo sacs derived from meiotic reduction in having a capacity to attract the pollen tube and that its egg cell can also successfully participate in the fertilisation process (Koltunow and Grossniklaus 2003).

Another important characteristic feature of apomixis to be considered for understanding the origin and evolution of apomictic reproduction is its facultative nature with co-occurrence of both sexual and apomictic embryo sacs. Rosenberg (1906, 1907) discussed it after observing the coexistence of meiotic and ameiotic structures in the ovules of *Hieracium*. It is essential that the sexual pathway of seed development remains intact in sporophytic apomicts as this is the sole source of endosperm tissue in such apomicts (Briggs and Walters 2016). In gametophytic apomixis also, many apomictic taxa are facultative, meaning that a single individual can produce seeds through both sexual and apomictic pathways. Furthermore, apomicts and their sexual relatives are often sympatric (but not necessarily syntopic) and morphologically difficult to differentiate (Albertini et al. 2010).

On one hand, where climatic fluctuations are thought to create range shifts and secondary contact hybridisation of different ecotypes results in apomictic lineages; on the other hand, development of apomictic genotypes also leads to new ecological scenarios (Hojsgaard and Hörandl 2019). In this chapter, we would be discussing this aspect of apomixis and its implication in propagation of flowering plants.

13.2 Distribution of Apomixis Across Taxa

13.2.1 History

Winkler coined the term ‘apomixis’ in 1908 to describe ‘asexual reproductive process in place of sexual reproduction without nucleus or cell fusion’ (Winkler 1908). This definition is very broad, and the definition of apomixis is now restricted to the formation of seeds via an asexual process (Richards 1997). It was Smith (1841) who gave the first description of apomixis in *Alchornea ilicifolia* (syn

Caelebogyne ilicifolia). Since then, apomictic forms have been reported in several hundred flowering plant species of both monocotyledonous and dicotyledonous genera with adventitious embryony, apospory, diplospory, and apospory and diplospory together occurring in 148, 110, 68, and 17 genera, respectively. This number may be an underestimate of the prevalence of apomixis in plants (Hojsgaard et al. 2014).

13.2.2 Distribution

The widespread distribution of apomixis amongst flowering plants and the occurrence of analogous phenomena in other organisms indicate that it has originated *de novo* several times (Albertini et al. 2010). Distributions of apomixis across angiosperms were recently reviewed by Hojsgaard et al. (2014), and an online database has been created for an easy access to updated lists (<http://www.apomixis.uni-goettingen.de>) (Fig. 13.2). According to this report, angiosperms have a general capacity to switch from sexual reproduction to apomixis, which mainly depends on diversity and genomic complexity of the clade (Hojsgaard et al. 2014). Both sporophytic and gametophytic types of apomixis and similarly both diplosporic and aposporic forms of gametophytic apomixis can be present in the same family. The occurrence of multiple types of apomixis in a family, genus, species, and sometimes individual genotype is interpreted as a result of overlapping or intersecting developmental pathways subjected to genotype and environment effects (Ozias-Akins 2006). Though in most cases apomicts within a single genus utilise a similar mechanism to produce asexual seed, members of closely related genera may differ widely in the apomictic mechanisms employed (Bicknell and Catanach 2006). Apomixis occurs sporadically among various clades of angiosperms, and several authors have noted a marked bias in the distribution of apomixis (Asker and Jerling 1992; Mogie 1992; Carman 1997). But in general, it has been found that apomixis biodiversity is paralleled by total biodiversity, i.e. more diverse orders, families (e.g. Asteraceae, Poaceae), and subfamilies contain more apomicts as well. Apomixis is possibly an ancient feature in some major clades particularly in commelinids, fabids, and lamiids (Hojsgaard et al. 2014). Carman (1997) listed 126 apomictic genera, 220 polysporic genera, and 255 polyembryonic genera. Sporophytic apomixis or adventitious embryony was supposed to occur more frequently in tropical than in temperate flora (Naumova 1992), but this view has been contested recently by Hojsgaard et al. (2014), who stated that both the forms (sporophytic and gametophytic) are more prevalent in the tropics in terms of total numbers. Adventitious embryony is more represented in diploid species, while in polyploids, other forms of apomixis are generally more prevalent. Adventitious embryony is found in several agriculturally important species like *Citrus* and mango (*Mangifera indica*) and in orchids. Naumova (1992) published the most comprehensive treatise on adventitious embryony.

As for the gametophytic apomixis, roughly three-fourths of gametophytic apomicts occur in just three families—the Rosaceae, Poaceae, and Asteraceae

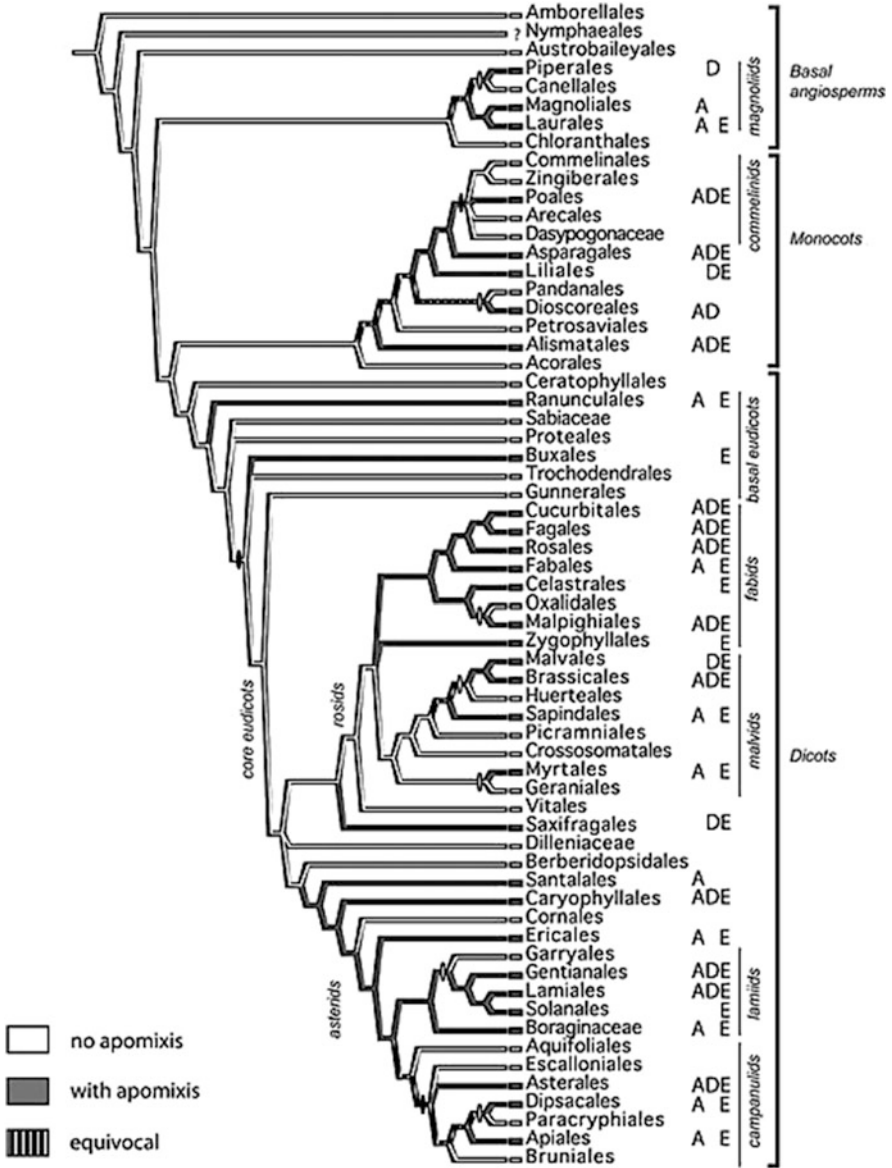


Fig. 13.2 Apomixis among orders of angiosperms. (From: Hojsgaard et al. 2014) (A) Apospory. (D) Diplospory. (E) Adventitious embryony

(Richards 1986; Asker and Jerling 1992). However, as discussed earlier, it might be because these are quite large and genomically complex families. Such patterns of distribution of apomicts may also reflect the presence of certain predisposing characteristics (cytological characteristic like massive nutritive nucellus in *Citrus*)

(Koltunow et al. 1995) or genetic characteristic like apparent linkage group in species like *Tripsacum dactyloides*, *Pennisetum squamulatum*, *Paspalum simplex*, and *Erigeron annuus* (Grimanelli et al. 2001) which make them amenable to the developmental and genetic changes characterising apomixis. With recorded taxa, apospory is found to be more frequent than diplospory (Hojsgaard et al. 2014). Since most gametophytic apomicts are polyploids, other factors like the higher frequencies of neopolyploids in temperate to arctic regions (Brochmann et al., 2004) may also make gametophytic apomicts more frequent in these regions.

Though parthenogenesis has been widely recorded in flowering plants (Asker and Jerling 1992; Hojsgaard et al. 2014), it occurs in most species at a low level. In comparison, the rates of parthenogenesis in the native apomicts like *Hieracium aurantiacum* and *H. piloselloides* are very high, 97.6% and 98.0%, respectively (Bicknell et al. 2003). Though as discussed before, there is a possibility of development of $n + 0$ progeny through haploid parthenogenesis (gynogenesis or androgenesis), parthenogenesis has been more frequently studied as a component of apomictic development pathway. In fact, the geographical distribution of apomicts and sexual lineages has been labelled as *geographic parthenogenesis* (discussed later).

13.2.3 Variability in Endosperm Development

Autonomous endosperm development (endosperm – initiated autonomously without any contribution from male gamete) is of usual occurrence among the apomicts of Asteraceae and more common among species showing diplospory and adventitious embryony (Albertini et al. 2010). Pseudogamous (fusion of one of the sperms with the central cell to give rise to the endosperm and the degeneration of the other sperm without fusion with the egg cell) development of endosperm requires a pollination stimulus to occur and is more common in aposporous species, including the families Rosaceae and Poaceae but rare in the Asteraceae family. In endosperms for pseudogamous species, the expected level of the $4(n)$ maternal:1(n) paternal ratio is often altered by the variable number of polar nuclei involved, the extent of their fusion, and the number and ploidy level of the male gamete(s) which operate in fertilisation. Thus, in many cases, the required 2:1 maternal-to-paternal ratio of the endosperm is maintained (Albertini et al. 2010). On the other hand, relaxation in the typical 2:3 embryo/endosperm ploidy balance requirement is also a norm in many apomictic plants (Matzk et al. 2000), for example, in the apomict *Poa pratensis* where two unreduced polar nuclei fuse with a sperm nucleus resulting in an embryo/endosperm ploidy ratio of 2:5. Other patterns of endosperm balance displayed and tolerated by apomictic species have been previously reviewed (Koltunow and Grossniklaus 2003). In *Tripsacum dactyloides*, a wide variety of maternal:paternal (m:p) ratios support functional endosperm development (Grimanelli et al. 1997). In *Paspalum notatum*, it was found that the crosses between sexual diploid and tetraploid plants result in seed abortion, whereas apomictic plants tolerate a wide range of m:p ratios (Quarin 1999). This demonstrates that a tolerance for unbalanced embryo:endosperm ratio is closely related to apomictic reproduction (Koltunow and

Grossniklaus 2003). In the case of sporophytic apomicts, usually an endosperm formed as part of the sexual process nourishes the somatic embryos. Such an endosperm is derived from fertilisation of two reduced polar nuclei with reduced male gamete, which results in the typical 2:3 embryo: endosperm ploidy ratio and normal development (Bicknell and Catanach 2006). It has been found that apomicts with autonomous endosperm formation tend to produce less viable pollen and, in some cases, are male sterile (Meirmans et al. 2006; Thompson et al. 2008). Exceptionally, *Commiphora wightii* is a sporophytic apomict, and most of the populations are made up of exclusively female plants (Gupta et al. 1996). Even when one or two male plants are present, in the population there is no pollination. Manual pollinations result in pollen germination, but the pollen tubes do not grow beyond the upper part of the style (Gupta et al. 1998). Thus, apomicts for this species do not require pollination stimulus for apomictic embryo formation and show autonomous endosperm development. In rare cases, even though neither the embryo nor the endosperm is fertilised, still apomicts require pollination to stimulate seed development (Bicknell et al. 2003). Reduced pollen acts as a means for gene flow from apomictic to sexual genotypes, for example, from apomictic tetraploids to sexual tetraploids in *Rubus* (Sochor et al. 2015; Šarhanová et al. 2017; Dickinson 2018). Therefore, its involvement in reproduction might be a way to maintain the apomictic genes in the long run.

13.2.4 Classification System

In apomictic plants, numerous morphologically or physiologically distinct yet interfertile varieties are found growing true to type from seed, for example, *Alchemilla*, *Hieracium*, *Pennisetum*, *Poa*, *Potentilla*, *Ranunculus*, *Rubus*, and *Taraxacum* (Bicknell and Catanach 2006). Apomixis forms a reproductive barrier at the level of genera or species. These separate apomictic genotypes are called as agamospecies, and their collection is referred to as an agamic species complex. Diverse pathways of reproduction in apomixis can give rise to varied levels of ploidy, leading to formation of an 'agamic complex' (Asker and Jerling 1992). Since there is no involvement of gametes in sporophytic apomixis, they do not form agamic complexes. Typically, apomictic lineages are confined to the terminal branches of phylogenetic trees (van Dijk and Vijverberg 2005).

13.3 Origin of Apomixis

13.3.1 Polyphyletic Origin

Since gametophytic apomixis has scattered distribution at the ordinal level (Fig. 13.2), apomixis is believed to have originated independently on several occasions (Hojsgaard et al. 2014). When occurrence of apomixis is superimposed on current phylogenetic tree, multiple independent origins as well as recurrent changes from facultative apomixis to obligate sexuality are observed (León-

Martínez and Vielle-Calzada 2019). Another fact supporting polyphyletic origin of apomixis is that the two main variants of apomixis, i.e. apospory and diplospory, do not appear to have a common ancestor (Briggs and Walters 2016; Albertini et al. 2019). The same genes might result in different forms of apomixis, and Bicknell et al. (2000) had also indicated allelic nature of two different forms of apospory in *Hieracium*. Nevertheless, apospory and diplospory are considered likely to be nonhomologous (van Dijk and Vijverberg 2005).

This repeated de novo evolution of apomixis is difficult to explain, as it would require highly specific changes in two conserved and molecularly complex processes, i.e. meiosis and syngamy. Also, to maintain viability, these mutations should occur simultaneously (Mogie 1992; Neiman et al. 2014). Apomeiosis without parthenogenesis would cause elevated ploidy in each generation which would be deleterious. On the other hand, mutants with haploid parthenogenesis would be weak and have recessive mutation load. Therefore, this phenomenon is easier to explain in species where apomixis is a single-locus trait. In species like *Poa pratensis*, a complex 5-locus genetic model has been postulated which includes single, unlinked genes for initiation of apospory, apospory prevention, parthenogenesis initiation, and parthenogenesis prevention, as well as a megaspore development gene (Matzk et al. 2005). In such cases, it becomes difficult to explain de novo origin of apomixis. Also, in *Potentilla puberula*, genetic contribution from at least one apomictic parent has been found to be necessary for the formation of new apomictic genotypes, and penta- and hexaploids derived from sexual backgrounds did not show apomixis and hence do not support de novo origin of apomixis (Nardi et al. 2018). Here, it has been suggested that perenniality and outcrossing may bring the required traits in the species, which then get clubbed together through chromosomal rearrangements (van Dijk and Vijverberg 2005).

13.3.2 Mutation Theory

Mutation theory considers that generation of new alleles through accumulation of mutations may lead to new genotypes via occasional sexual outcrossing (Muller's ratchet; Muller 1964; Asker and Jerling 1992; Majesky et al. 2012). The theory assumes that a combination of pre-existing tendencies for features like haploid parthenogenesis and relaxed 2 m:1p requirement for endosperm development along with dominant apomeiotic mutations would lead to apomixis (Mogie 1992; Carman 2001a). As discussed above, this theory would be easier to explain in species where apomixis is a single-locus trait, as it is difficult to assume that the alleged mutations required for all the three components of apomixis should occur simultaneously. Also, this theory falls short in explaining the variability in facultative nature of most apomicts (Carman 2001a). In some studies, it has been found that in the absence of some critical alleles at separate loci, major apomictic locus is also defective. Alternatively, certain genetic backgrounds have been found to induce apomixis even after lacking major apomixis-conferring linkage groups (Carman 2001a). These occurrences undermine mutation-based theories for apomixis.

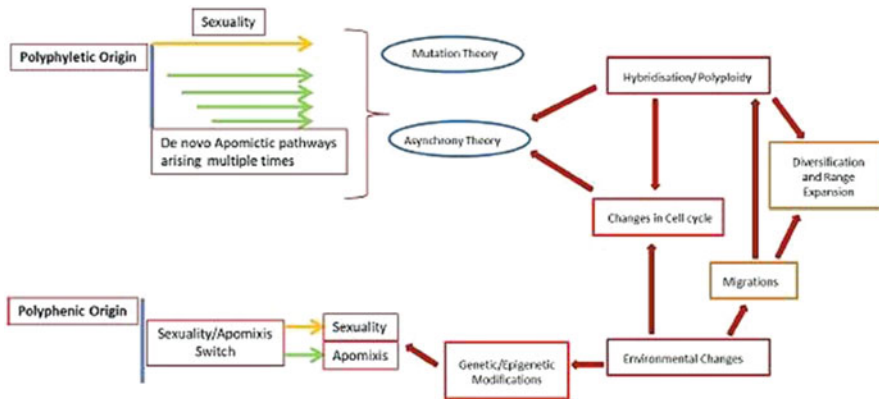


Fig. 13.3 Theories regarding origin of apomixis

13.3.3 Hybridisation-Derived Floral Asynchrony Theory

Carman (1997, 2001b, 2007) suggested that apomixis could result from temporal deregulation of alleles involved in demarcation of reproductive fate of cells. This deregulation may occur due to the hybridisation of divergent alleles. This is referred to as *hybridisation theory*. This has also been supported recently through transcriptomic profiling of apomixis in *Boechera*. This study showed that several genes conserved across both sexual and apomictic systems are heterochronously expressed in apomictic reproduction and could also be linked to parent of origin effects (Sharbel et al. 2009; Tucker and Koltunow 2009). According to this theory, asynchrony in megasporogenesis and embryo sac development in hybrids are the main cause of apomixis. It proposes that hybridisation of two such divergent ecotypes leads to heterozygosity which gets stabilised through polyploidisation and this multilocus heterozygosity leads to apomixis. Further, intergenomic recombinations, mutations, and other chromosomal aberrations may lead to embryological events leading to reversion to sexuality or other anomalies. There are further controls in the form of rate of divergence among developmental programs, variability in expressivity of the genes involved, nutritional status, and epigenetic conditions (Carman 2001a).

Although it is difficult to provide a general theory for de novo origin of apomixis, it is clear that apomixis has evolved several times during evolution of angiosperms and several interrelated factors seem to play an important role (Fig. 13.3), including hybridisation, polyploidisation, and environmental factors (Hojsgaard and Hörandl 2019).

13.3.4 Polyploidisation and Hybridisation

Apomicts differ from their sexual relatives not only in reproductive mode but also in ploidy (for most cases). Many wild apomictic species are characterised by hybridity and polyploidy (Richards 2003). Whereas odd ploidy levels (e.g. triploidy, pentaploidy) are often reliable predictors of the presence of apomixis, tetraploidy is the most common ploidy level among apomicts (Asker and Jerling 1992). An evolutionary correlation between vegetative reproduction and polyploidy has been reported in the central European flora (Herben et al. 2017). It is still unclear as to the relative contributions of hybridisation and polyploidy to asexual lineage origin and evolution, as both phenomena can have diverse regulatory consequences causing coordinated deregulation of the sexual pathway (Albertini et al. 2010). Two theories on the basis of cause and effect have been proposed; with one of them suggesting that polyploidy stimulates the development, penetrance, and maintenance of apomixis, and the other proposes that apomixis stimulates the formation and proliferation of polyploids (Bicknell and Catanach 2006). Functional roles for polyploidy in apomicts have been hypothesised to include epigenetic gene deregulation (Koltunow and Grossniklaus 2003), ploidy-dependent gene expression (Cervigni et al. 2008), ectopic gene expression resulting from genome asynchrony (Carman 1997), and restoration of hybrid fertility through allopolyploidy-induced sequence elimination (Rieseberg and Willis 2007). On the other hand, there are species which appear to express apomixis without any signs of hybridity or polyploidy. In *Paspalum*, the presence of apospory in otherwise sexual diploid plant species has been reported (Ortiz et al. 2013; Hojsgaard and Hörandl 2019). Diploid apomicts are also reported following the experimental manipulation of several polyploid apomicts (Bicknell 1997; Kojima and Nagato 1997), but in almost all reported cases, the identified diploid apomict was weak and pollen sterile. These findings indicate that polyploidy is not an absolute requirement for the expression of apomixis, but in most systems, it may act to enhance the expression or promote the transmission of the trait (Bicknell and Catanach 2006). There is also a possibility that apomixis promotes polyploidy, and complexities associated with polyploidy were evolved following the establishment of apomictic reproduction and thus may be secondary with regard to its genetic control (Ozias-Akins and Van Dijk 2007). In any case, polyploidisation has often coincided with major evolutionary transitions and adaptive radiation of species and hence might play a role in spurts of adaptive speciation. It can provide new gene functions by supporting genetic redundancy and combining with other processes like recombination, gene mutation, transposon activity, and chromosomal rearrangement, which can act as drivers of diversification, speciation, and ultimately species evolution (Alix et al. 2017).

Apomicts in nature also often appear to have a hybrid origin (Šarhanová et al. 2017). As discussed before, Carman (1997, 2001b) proposed that hybridity itself is the cause of apomixis, and a combination of hybridity and polyploidy can lead to the disjunction of key regulatory events during critical stages of megasporogenesis, megagametogenesis, and fertilisation. Hybridisation among distantly related taxa is also an easier possibility with higher ploidy. A possible hybrid origin may also

explain the apparent puzzle of apomixis resulting from the summation of several components, each of which on its own would confer a selective disadvantage to the plant (Mogie 1992). Here, residual sexuality of apomicts is supposed to play a major role in reducing the mutation load of semi-lethal heterozygosity resulting from hybridity in asexual reproduction (Klekowski Jr 1988; Niklas and Cobb 2016). Also, polyploidy may help to mitigate hybridisation-associated genome shock (Hegarty et al. 2006) and thus facilitate fixation of the hybrid (Soltis et al. 2010; Mason and Pires 2015).

13.3.5 Epigenesis

Epigenetic effects linked to hybridisation and/or polyploidisation can also affect expressivity of the different reproductive pathways (Grimanelli 2012) as reported in *Hieracium* (Koltunow et al. 2000; Krahulcová et al. 2011). It was found that DNA methylation in reproductive cells induces apomeiosis-like phenotypes (García-Aguilar et al. 2010). As discussed below, environmental changes also affect the frequency of apomixis and point to the role of epigenetic factors in apomixis. This epigenetic model unites the mutation and hybridisation theories because epialleles can behave genetically like mutations, and epigenetic changes in gene expression have been documented after hybridisation (Lee and Chen 2001). The epigenetic control model also provides answer to the very improbable simultaneous origin of apomeiosis, parthenogenesis, and functional endosperm formation in apomictic plants (Mogie 1992).

13.3.6 Environmental Changes

In *Ranunculus kuepferi*, spontaneous formation of apomictic seeds was found albeit at low frequencies in otherwise sexual, diploid wild populations. It was shown that these diploid populations are not hybrids, as they are geographically distant and isolated from each other as well as apomictic tetraploids (Cosendai et al. 2013; Schinkel et al. 2016). Here the important factor was suggested to be environmental effects like cold shocks and frost treatments during development which increased frequencies of apomictic seeds in warm-adapted, diploid *R. kuepferi* (Klatt et al. 2018). Even a small increase in the frequency of apomictic seeds is strong enough to make an impact through evolutionary time periods (Hojsgaard and Hörandl 2019). At the same time, whether stress will increase or decrease the frequency of sexual reproduction depends on the involved genotype and the type and severity of stress itself. *Boechea* pistils exposed to short-term stress (H_2O_2) as well as long-term stress (drought, sugar starvation, and BRZ) bring shifts from apomeiosis to meiosis. On the other hand, pharmacological treatments of glucose, epiBL, DTBA, and 5-azaC were able to induce apomictic reproduction in the sexual plants of *Boechea stricta* (Gao 2018). Other examples where environmental cues have been able to switch on the residual sexuality include *Boechea* under drought or heat stress

(Mateo de Arias 2015), *Ranunculus* under extended photoperiods (Klatt et al. 2016), *Eragrostis curvula* under drought or culture stress (Rodrigo et al. 2017). Thus, the frequency of apomeiosis in facultative gametophytic apomicts is affected by several environmental factors, such as temperature, photoperiod, soil salinity, and drought stress (Albertini et al. 2019). Environmental changes are likely to confuse cell cycle in plants; for example, nonconductive photoperiods have been known to cause abortion of meiosis (Moss and Heslop-Harrison 1968; Carman 2001a). This indicates that metabolic status of ovules is an important factor for sex/apomixis switch (Albertini et al. 2019). At the metabolic level, apomeiosis is postulated to occur in response to shifts in redox homeostasis (Gao 2018; Sherwood 2018). Such shifts could be a result of hybridisation and polyploidisation (Kirk et al. 2005) and might result in induced epigenetic changes to permit apomictic development in some cases (Albertini et al. 2019).

The trait of apomixis has also been described as a threshold trait. This feature along with asynchrony and environmental variation might explain the facultative nature of apomixis (Carman 2001a). It also explains multiple phenotypes with each phenotype defined by different threshold.

In some genera, apomicts show a tendency to inhabit regions at higher latitudes affected by the last glacial period (Bierzuchudek 1985; Hörandl et al. 2008). Changing environmental conditions require rapid adaptation and hence show selection for recombination-based reproduction (Peck 1993, 1994; Lively and Morrani 2014). The “Fisher-Muller” population-genetic theory and, subsequently, several theories put forward the notion that sex/recombination though expensive helps in rapid adaptation to changing environment (Muller 1932; Fisher 1999; Brukhin and Baskar 2019). Once the adaptation to altered environment is achieved, selection works against sexual reproduction. It has been found in *Eragrostis curvula* (cultivar Tanganyika) that different stress conditions increased the expression of sexual reproduction and when the stress stops the reproductive mode shifts back to the apomixis original level (Rodrigo et al. 2017). Large-scale migrations of plants during periods of climatic oscillation may also result in widespread secondary contact hybridisation and resulting hybrids would show better fertility after polyploidisation (Stebbins 1985; Hewitt 2004; Hojsgaard et al. 2014). Thus, new genotypes might develop through hybridity and polyploidisation, which might lead to apomictic genotypes that are better adapted to the changed climate.

13.3.7 Polyphenic Origin

Some authors assume asexual reproduction to be an ancestral condition, as prokaryotes lack the meiotic ability (Niklas and Cobb 2016). Sexual reproduction probably evolved shortly after eukaryotic origin and, therefore, preceded the origin of the angiosperms (Cavalier-Smith 2001; van Dijk and Vijverberg 2005). While considering all kingdoms of living organisms, ancestral forms were supposed to largely maintain adapted gene complexes through asexual reproduction while retaining a capacity for producing genetic variants through sexual reproduction. It

is considered that over the course of evolution of land plants, asexual reproduction decreased due to evolution of seed habit and woody, self-supporting stems (Niklas and Cobb 2016).

As discussed before, it is commonly postulated that apomixis across the eukaryote kingdoms evolved from sexual reproduction by genetic or epigenetic modifications causing deregulation of events associated with sexual reproduction (Carman 1997; Grimanelli 2012; Neiman et al. 2014), but there is another point of view where apomixis is considered to be anciently polyphenic with sexual development. According to this view, apomixis and sexuality are determined through genetic or epigenetic modifications controlling the molecular capacities for apomixis or the apomixis switch. The view of polyphenic development is supported by several angiosperms showing inclinations towards cyclical apomixis. Other indications come through observations like origins of apomixis among related genera, facultative nature of most angiosperm apomicts, and environmental role in determining the frequency of apomixis (Albertini et al. 2019).

Due to multiple independent origins of apomixis across various plant taxa and varied pathways known for apomictic reproduction, it is difficult to provide a single theory delivering conclusive evidence for its origin and maintenance within angiosperms. Nevertheless, we can conclude that hybridity, ploidy, and environmental adaptation are some of the factors affecting the process. At the level of cell, the actual switch to sexuality/apomixis might be a sum total of how these factors affect the cell cycle.

13.4 Ecological and Evolutionary Significance of Apomixis

13.4.1 Evolutionary History and Adaptive Value

It has been concluded that apomictic, polysporic (species showing bispority or tetraspority), and polyembryonic species have a similar phylogenetic distribution, which shows their evolutionary relationship (Carman 1997; Carman et al. 2011; León-Martínez and Vielle-Calzada 2019). Though various reproductive developmental mechanisms share a close evolutionary history, the evolutionary relationship between asexuality and their component reproductive processes like unreduced gamete formation have not been dealt in detail. It might also be because individual components of apomixis are represented in much lower frequencies due to their deleterious effect in standalone capacity, but when clubbed together, they provide adaptive potential to taxa. Hence, it is generally not possible to study those separately. The formation of unreduced gamete is considered the most important part of apomictic development. Though it is still unclear if unreduced gametes can be considered as means of exaptive evolution (i.e. having a use not selected by evolution) and evolvability (the capacity to generate adaptive genetic variation), there are several factors like occurrence of unreduced gamete formation across several lineages of organisms, presence of heritable genetic variation within and between species for unreduced gamete production, the involvement of unreduced

gametes in hybridisation events, and the production of unreduced gametes in response to stress which suggest that they could be a part of mechanism for evolutionary speciation (Mason and Pires 2015).

Adaptive value of sexuality and apomixis is still a much-discussed issue (Mirzaghaderi and Hörandl 2018). Meiosis is mainly thought to provide benefit of DNA repair (Hörandl 2009; Hörandl and Hadacek 2013; Mirzaghaderi and Hörandl 2018). Recombination can have positive effects by combining desirable characters but at the same time can also have negative effects on the fitness of populations by altering desired characteristics and requirement of a sexual counterpart to complete the reproductive life cycle (Niklas and Cobb 2016; Brukhin and Baskar 2019). Large population sizes and frequent mutations are required to make sexual reproduction profitable (Crow and Kimura 1965; Brukhin and Baskar 2019). Therefore, it is strange that so many plants still reproduce through sexual means. On the other hand, apomixis traditionally leads to limited gene flow but has been recently associated with increased diversity and diversification of angiosperms (Hojsgaard et al. 2014). Though theoretically unreduced gamete formation should be detrimental, reproductive stability through gametophytic apomixis can provide necessary selective force under stressful environments (Kreiner et al. 2017a, b; León-Martínez and Vielle-Calzada 2019). Factors like fixed heterozygosity, potential hybrid vigour, buffering of inbreeding depression, uniparental reproduction, benefits of reproduction through seeds like seed dormancy, and better dispersal are supposed to be responsible for the ecological and evolutionary success of apomicts (Hörandl 2006). Yet the apomicts are quite rarer than sexuals, and it might be due to low probability of getting together all necessary components to avoid meiosis and create a functional apomict (Brukhin and Baskar 2019).

13.4.2 Geographic Parthenogenesis

It is a term used to refer to different geographic distributions of sexuals and apomicts. Apomicts and their sexual relatives can be sympatric, but apomicts usually have larger geographic ranges due to species-specific factors (Hörandl 2006; Kirchheimer et al. 2018; Albertini et al. 2019). Thus, apomicts provide effective spread for their genotypes through space and time. Also, apomicts usually occupy higher altitudes and latitudes compared to their sexual relatives, but this distribution might be more related to glaciation events (Sochor 2016). Due to reasons like residual sexuality and increased heterozygosity (due to role of hybridisation and polyploidy), apomictic populations can exhibit as high genotypic diversity as well as higher allelic diversity which might provide expansion of ecological niche and increased flexibility to environmental changes. Evidence based upon genetic markers also supports this view. This may be the major reason why apomictic polyploids like *Taraxacum* spp. (Van Dijk 2003), *Hieracium pilosella* (Houliston and Chapman 2004), and *Cortaderia jubata* (Okada et al. 2009) serve as successful colonisers of new habitats especially of disturbed habitats. This has also been hypothesised to be the case for putative woody apomicts from New Zealand as

well (Molloy 2019). Apomixis itself leads to wider range expansions, and coupled with sexuality, it seems to be a source for novel geographically isolated lineages that have a capacity to further diversify by ecological and allopatric speciation (Hörandl and Hojsgaard 2012).

But like origin of apomixis, geographic parthenogenesis also cannot be explained fully through ploidy and differential hybrid origin, as seen for single ploidy level in *Rubus ser. Glandulosi* (Šarhanová et al. 2012; Sochor 2016). Another hypothesis for specific geographical distribution of apomict may be related to their inability to evolve in response to pathogen evolution, which might be higher at lower altitudes or latitudes, “Red Queen” hypothesis (Bell 1982; Verhoeven and Biere 2013; Lively and Morrani 2014). During host–parasite coevolution, cross-fertilisation is favoured over uniparental forms of reproduction. A continual environmental change seems to be the requirement for the long-term maintenance of sexual reproduction, and antagonistic coevolution with parasites seems to provide that constant source of environmental change (Lively and Morrani 2014). Another important point to consider here is that the study of distribution of geographical parthenogenesis is also not complete enough to draw any strong conclusions.

13.4.3 Role in Speciation

Despite having advantages of reproductive assurance, apomixis is much less common than sexual reproduction. Apomixis requires combination of several developmental processes and is often associated with infertility (Lloyd 1988). Though apomixis provides short-term advantage, extinction rates of apomicts are expected to be higher (van Dijk and Vijverberg 2005). It was used to be considered as an evolutionary dead end due to absence of genetic variation and adaptability to changing environments especially evolving pathogens (Levin 1975; Bell 1982) and accumulation of deleterious mutations (Muller 1964; Kondrashov 1982; van Dijk and Vijverberg 2005). However, this perception has now changed based on observations that there is much genetic variability in agamic complexes (Carman 1997; Whitton et al. 2008; Hörandl and Hojsgaard 2012). For example, a recent study with agamic complex of *Rubus* showed that this complex dates to last interglacial period and the apomicts helped to combine gene pools of the preglacial diploid ancestors and of recent sexuals from their region. Therefore, apomicts serve to preserve and spread genetic diversity (Sochor 2016). It might be possible because “apomixis genes” can escape extinction through transfer to new clones via hybridisation and can be maintained through sexual gene pool which might predate the splits of related genera. This may be responsible for the common origin of apomixis among related genera. Other factors like facultative sexuality and allelic divergence can also help reduce mutation accumulation of apomictic lineages (Hojsgaard and Hörandl 2015a). Through NGS sequencing, Lovell et al. (2017) found increased sequence diversity in apomictic populations. A positive correlation of number of genera per subfamily, family, and order with number of apomicts shows that apomixis might be working as a springboard for diversification

(Hojsgaard et al. 2014; Hojsgaard and Hörandl 2015b). Moreover, it might be a combined effect of apomict-sexuality ability of agamic complexes working in creating a higher diversity and removing harmful alleles at the same time (Hojsgaard and Hörandl 2015b; Brukhin and Baskar 2019). Apomixis causes rapid ecological differentiation through limited genetic cohesion and rapid range expansion (Brukhin and Baskar 2019).

An *Expanded Transition Theory* has been given by Hörandl and Hojsgaard (2012) to summarise the evolution of apomixis and its role in speciation, which supports Carman's (1997) hypothesis. The process is supposed to start with polyploidisation and/or hybridisation-associated shifts to facultative apomixis which further get diversified through mutation, chromosome rearrangements and aneuploidy, residual sexuality, hybridisation, and backcrossing. Reduced gene flow and mutation accumulation creates locally adapted genotypes. This diversification results in the range expansions of agamic complexes. These may get further complexed through reversal to sexuality which leads to allopatric speciation and eventual evolution of new genera. Thus, apomixis may facilitate diversification of polyploid complexes and evolution in angiosperms (Hörandl and Hojsgaard 2012).

13.5 Conclusion

It is clear that apomixis along with polyploidy provides effective avenues for range expansion and ecological plasticity, but further studies are required to discern the role of apomixis in the reticulate evolution and diversification of angiosperm genera. Embryological studies may help in better assessment of distribution of apomixis at the species level, while genome sequencing studies might help to dissect the role of hybridisation and polyploidy in perpetuation among apomicts. And further population-level assessments are needed to understand the distribution patterns of apomicts.

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