Summary

Division the cells of blood cords in gradient ficolls is an most optimum method for the further cultivation in vitro. Phenotyping cultures of the cells of blood cords shows the expantion a hemopoietic stem cells.

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THE PHENOMENON OF APOMIXIS IN SOME MONOCOTYLEDONES
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In present article a short review of apomixis in Poaceae family and the description of the recent advances in the molecular and genetic characterization of apomicts has been done and apomixis using for breeding,,biotechnology and gene engineering purposes.

Apomixis is an asexual mode of reproduction in which an ovule develops into a seed without involving meiosis and fertilization. It is now used synonymously with 'agamospermy' meaning asexual reproduction by seeds or seed apomixes. This mode of reproduction is reported in more than 400 species belonging to 40 families [1].

For many years, apomixis was studied only by a small group of interested botanists and plant breeders. However, because of its tremendous potential for agriculture:rapid development of new hybrid varieties, economic hybrid seed production, propagation of hybrid seed, resistance against pathogens, handling propagation material.

In this case apomixis research has attracted much more attention during the last few years. If apomixis could be introduced into sexual crops, it would greatly simplify breeding schemes and allow the fixation of any genotype, including that of F1 hybrids. Apomixis technology could play a major role in feeding the growing population of our planet provided that it will be freely accessible to all users, especially resource-poor farmers in developing countries, requiring innovative approaches for technology generation, patenting, and licensing.

Current apomixis research focuses on elucidating the genetic basis and molecular mechanisms that control apomictic reproduction. Two major complementary approaches are being pursued: first, to identify genes controlling individual elements of apomixis in well-defined sexual model species and second, to unravel the genetic control of apomixis in natural apomicts. For nearly two decades, the genetic control of apomixis had been elucidated in very few species. Recently, however, inheritance studies for several natural apomicts have been published that shed new light on the genetic control of this important developmental process [2].

Phenomenon of apomixis

In sexual reproduction meiosis reduces the chromosome number of the megaspore mother cell to form reduced megaspores, one of which develops into an embryo sac containing the female gamete (the egg cell). In most plants these embryo sacs have eight nuclei and are described as *Polygonum* type The fusion of two unique haploid gametes, derived from the random assortment of the genetic material occurring during meiosis, results in the generation of diploid and genetically diverse progenies. In contrast, in apomictic reproduction, the embryo develops autonomously an unreduced cell having the same set of maternal chromosomes and giving rise to plants that are clones of the mother plant [2].

Apomictic plants are the result of either one of two types of development, sporophytic or gametophytic. In sporophytic apomixis or adventitious embryony, embryos are formed directly from unreduced cells of the nucellus, or inner integument, while the developmental pathway of meiotic embryo sac is maintained. Gametophytic apomixis is characterized by apomeiosis. Meiosis is either altered or totally bypassed, and as a consequence, an unreduced female gametophyte, or embryo sac, is formed. There is no fusion of male and female gametes and the egg cell develops autonomously, by parthenogenesis, generating an embryo that keeps the same set of maternal chromosomes. Apospory and diplospory are different types of gametophytic apomixes. In diplospory, the megaspore mother cell bypasses or fails to achieve meiosis, but through mitoses forms an embryo sac with all unreduced cells distributed as in the meiotic embryo sac of the *Polygonum* type. In this case, the sexual process is completely compromised. In apospory some nucellar cells, called aposporous initials enter in mitosis directly and unreduced embryo sacs are formed. Sexuality and apospory can occur simultaneously in the same ovule. If fertilization of the central cell is necessary to form the endosperm, the system is regarded as pseudogamous, if not, it is autonomous [3].

Association between apomixis, polyploidy and polyembriony is recorded for many species. Apomicts are generally polyploids, tetraploidy being the commonest level and very few diploid apomicts existing in nature. The reason for this association is still not understood [4]. Besides apomixis, anomalies involving ovule development can result in polyspory (bispory and tetraspory) and polyembryony. In polyspory ovule development is disrupted, but reduced egg cells are formed and require fertilisation. Polyembryony refers to the formation of multiple embryos in one ovule and some authors consider adventitious embryony as a form of polyembryony. In polyembryony embryos may result from - the presence of multiple embryo sacs in an ovule, - synergids or - the cleavage of the cells produced by the zygote and not from unreduced cells of the nucellus as defined for adventitious embryony. In contrast, in some reviews on polyembryony and apomixis, the term apomixis was restricted to gametophytic apomixis and adventitious embryony was regarded as polyembryony [5]. Based on cytological, phylogenetic and genomic data, he suggested that apomixis; polyspory and polyembryony have a common origin that is the asynchronous expression of duplicate genes in polyploids. Until now, induction of polyploidy in sexual plants by application of suppressors of cell division could not elucidate the association between apomixis and polyploidy.

In *Paspalum*, facultative apomicts were generated by duplicating the chromosome number of previously sexual diploids after colchicine treatment [6], while in *Brachiaria brizantha* tetraploids derived from duplicating sexual diploids maintained their sexuality [7].

In apomicts, pollen formation often occurs normally in anthers generating viable reduced pollen. Apomicts able to generate at least part of its progeny by sexuality are regarded as facultative. Progenies from facultative apomicts segregate into maternal (apomictic) and non-maternal or aberrant (derived from sexuality) classes. Apomictic plants bearing fertile pollen can be used to pollinate sexual or facultative apomictic plants to transfer genetic characters to their offspring. Even so, a frequent limitation of crosses between sexuals and apomicts is ploidy number. Apomictic species are organized in agamic complexes, where individuals of different ploidy levels exhibit characteristic reproductive modes. While diploids are sexual, polyploids express apomixis. Considering that new apomictic polyploids can eventually be originated from diploids by sequential steps of 2n + n hybridization, it is clear that this peculiar strategy allows the maintenance of a certain degree of variability among polyploids, even when they are apomictic [8].

Identification of apomixis

Czapik discussed the parameters on how to detect apomixis in angiosperms. From geographic distribution and morphological features in the field to cytological and embryological observation, there are many ways to identify and to confirm the occurrence of apomixes [2].

Plants that reproduce strictly by apomixis do not segregate; the progeny is identical to the mother plant. Therefore, in the field, the observation of non-segregation of maternal phenotypic characteristics is an indication of apomixis. In the case of autonomous apomixis, one can observe the occurrence of seed set in plants that had their female flowers isolated or, that had their stigmas and anthers excised from the flowers. This is not possible for pseudogamous apomicts because, although there is no need for fertilization to trigger embryo development, it is still necessary to form the endosperm and a viable seed. Apomixis can be evidenced more accurately by analysis of the segregation of biochemical and molecular markers.

Isozymes and RAPD (Random amplified polymorphic DNA) markers are useful for detecting precociously the mode of reproduction in hybrids, as shown in *Poa pratensis* [9]. In cereals, polyploidy and unbalanced meiosis are present in mainly members of the section of grass, corroborating the hypothesis of apomixis previously built by the observation of a pronounced morphological influence of the maternal parent. Indeed, analysis of RAPD markers showed no inheritance from the male parent [6]. To our knowledge a definitive study of the embryology of this plant has not yet been performed. RAPDs were also successfully applied to the analysis of apomixis in different segregant population of *Paspalum notatum*, an important grass for turf and forage. In tetraploid populations of *Aronia* [10], the mother parent and the offspring showed identical RAPD profiles. In the savanna grass, *Hyparrhenia diplandra*, highly variable micro satellites were used to show the occurrence of facultative apomixis with rare events of sexual reproduction [11]. In *Brachiaria*, GISH (genome *in situ* hybridization) and FISH (fluorescent *in situ* hybridization) probes were used to distinguish maternal and paternal chromosomes for hybrid verification and a suspicion of apomixis was discarded [12].

Many cytoembryological characteristics of apomictic plants can be used as circumstantial indicatives of apomixis. Gametophytic apomicts are generally polyploids, while related sexuals are diploids. Chromosomes counting in root tips and estimation of DNA content by flow cytometry are largely employed to determine ploidy [13]. Though a direct correlation of apomixes and polyploidy is not established, polyploidy can indicate a possible presence of apomixis.

Apomixis occurs in the female part of the flower, the ovary and more specifically in the ovule. The morphological characterization of ovule development is a traditional way to predict apomixis by detecting meiosis failures, abnormal pattern of callose deposition, presence of aposporous initials, presence of more than one embryo sac in an ovule, formation of typical or irregular embryo sacs, polyembryony, presence of embryos in ovules before fertilization, etc. These characteristics can be observed by light microscopy using microtome sections or clearing methods. Both procedures can be used to establish the development of ovules, embryo sacs and embryos and to detect signs of apomixis. The nucellar or integumentary origin of the adventitious embryos can only be claimed after embryological studies [14].

Clearing methods, such us described by Herr (1971) or Young *et al.* (1979) are very useful for rapid screening of numerous samples [15]. They are faster and easier than sectioning and staining because nuclei and walls of reproductive cells can be observed in intact pistils and ovules, previously incubated in methylsalicylate, with interference contrast microscopy. For example, they have been employed to analyze natural apomicts and their hybrids with sexuals in diplosporous autonomous apomictic in large segregant F_1 populations of *Paspalum* sp. [16, 17]. Clearing methods can also be used in combination with aniline blue to detect callose deposition during megasporogenesis, which can to some extent be related to apomixis or sexuality. Abnormal callose deposition was found during apomictic megasporocyte development in *Poa pratensis*, in aposporous *Panicum maximum*, *Pennisetum squamulatum* and *Brachiaria brizantha* [18, 19]. The cell wall morphology during megasporogenesis showed deficiency in callose deposition in facultative diplosporous apomictic *Elymus rectisetus* and it was used to classify the hybrids between *Elymus rectisetus* and *Triticum aestivum* L. [20].

Occurrence of polyembryony can be an indicative of apospory or adventitious embryony and has to be determined by embryological methods or during seed germination. But, polyembryony does not necessarily imply apomixis. Alternatively, diploid plants can result from zygote cleavage or haploid plants can result from development of one or more synergids or antipodals and from more than one embryo sac in the ovule. Isozymes or molecular analysis of seedlings can determine their zygotic or adventitious origin.

Genetic of apomixis

In this chapter, we will concentrate on the genetic bases of gametophytic apomixis, in which the embryo originates from an unreduced gamete, because it is the type of apomixis better studied so far.

Nogler considered that probably the basic determinants of apomixis could have been originated by mutation and most of the other genes involved in the process would probably be similar to those implicated in sexuality. More recently, apomixis has been accepted as a result of a rearrangement of the developmental programs that constitute the normal sexual pathway. It is a heritable trait whose genetic control in many species still remains unclear [21].

Despite its broad distribution within the angiosperms, apomixis is not very common in the major crops. This condition forced studies in the field to be performed in wild species that are polyploids, highly heterozygous and genetically poorly characterised. In grasses, inheritance analyses are carried out normally on segregating F1 progenies originated from crosses between sexual and apomictic progenitors. Families of this type are generated using natural sexual diploids or, if available, sexual polyploids (natural or artificially generated) as mother plants and apomicts as pollen donors. Backcrosses (F_1 sexual x sexual progenitor or F_1 apomictic x sexual progenitor) and F_2 (F_1 sexual x F_1 sexual or F_1 sexual x F_1 apomictic) are also recommended to confirm the results [22]. Progenies are then classified as apomictic or sexual by cytoembryological methods or progeny tests.

Detailed descriptions about the genetic control of apomixis in several species can be found in previous works [23]. Genetic analysis in *Panicum maximum* indicated the trait was under the control of a simple dominant factor. In these works, apomeiosis and parthenogenesis were shown to co-segregate strictly, suggesting that these two components rely on the same genetic control, or that parthenogenesis is a pleiotropic consequence of apomeiosis. However, the complexity of the apomictic process has lead to often conflicting interpretation of results in different species. In a way to simplify the analysis, most studies concentrated in the inheritance of apomeiosis (apospory or diplospory). In the grasses, after the pioneer work in *Panicum* studies in *Pennisetum*, *Brachiaria*, *Maize-Tripsacum* hybrids and *Paspalum* agreed in indicate that both apospory and diplospory were controlled by one dominant locus [3, 23-27]. Although in *Paspalum* and *Pennisetum* a strong distortion in the transmission of apospory was observed [3, 24].

A fine characterisation of the inheritance of apomixis in tetraploid *Tripsacum dactyloides*, a wild relative of maize, showed that diplospory segregated in a non-mendelian fashion [26]. Linkage maps for the segment controlling diplospory in tetraploid apomicts were used to compare the same linkage group in diploid sexual plants. The data show that recombination is strongly suppressed in the segment that controls apomeiosis, which therefore behaves as a single genetic unit. This unit represents 40 cM on the map developed for sexual

Tripsacum; this block probably contains several hundred genes, of which an unknown number would participate in apomixis [27]. A similar structure was found in *Pennisetum* where several markers belonging to an apospory specific genomic region (ASGR) co segregate strictly linked to apospory. This ASGR resulted partially hemizygous and showed a strong restriction in recombination [28]. Experiments using *in situ* hybridisation with markers completely linked to apospory in the species confirmed that a single chromosome is sufficient for the transmission of apomixis (and molecular markers linked to it) and showed that ASGR is located at the end of a single metacentric *P. squamulatum* chromosome [29].

In *Paspalum notatum* and *Panicum maximum* numerous molecular markers segregating completely linked to apospory were also detected [17, 30]. These particular distribution of markers in both species suggested a strong restriction in recombination around the apospory locus because it is unlikely that a small genomic region became saturated with markers while the rest of the genome do not. In *P. notatum* the chromosome block carrying the locus for apospory (in which numerous markers are completely linked) contains repetitive elements and could actually span for a segment of 25-30 cM (about 40 Mpb for the species). This particular chromosome segment showed also preferential chromosome pairing (disomic inheritance), while the rests of the genomic complement have a polisomic behaviour [30].

The lack of recombination associated with the control of apomeiosis can be associated with a strategy for avoiding dispersion of factors that need to co-segregate strictly if apomixis is to be determined [26].

Attempts to map apomeiosis with common molecular probes in several species, including *Tripsacum, Brachiaria* and *Paspalum,* all forage grasses, have shown the genomic regions that controls the trait are distinct (i.e. non-homologous) among those species [16, 31, 32]. However, the region is conserved within the three species of the genus *Paspalum* [33]. This means that apomixis, in its various forms, probably arose in different grass species through the action of different genetic loci [34]. Moreover, in particular cases, this gene(s) appeared to be associated with some lethal factor affecting part of the female or male gametes [16].

Although it is the case for most apomicts studied, there are some exceptions. In the triploid *Erigeron annus*, diplospory and parthenogenesis are controlled by independent loci [34]. In *Poa pratensis* a recent analysis involving several segregating populations from inter-crossing and selfing of obligated and sexual and facultative apomictic plants proposed that five major genes control apomixis in the species. Differences in expressivities and interactions among them would be responsible for the inheritance and the wide variation of the mode of reproduction. In this system also apomeiosis and parthenogenesis segregated independently [35].

Apomixis and applied approaches

With the advances of biotechnology an interest in apomixis increased. Gene transfer between plants, independently from sexual compatibility, is already a reality and the control of apomixis by genetic engineering is a challenge to different research groups around the world [36].

In floriculture, vegetative propagation of individuals is desirable as it is a way to keep low genetic variability in the propagated culture. There are several methods *in vitro* techniques as: vegetative propagation such induction of adventitious buds, grafting, and female gametophyte culture [37, 38]. Micropropagation brings great commercial advantages and success stories about the utilization of tissue culture technology are numerous. In fact, micropropagation and the production of clonally uniform plants has become an industry all over the world involving axillary branching and somatic embryogenesis. There are still some ornamental plants in which a vegetative propagation method is not fully established, and with a limited multiplication rate. One can imagine the impact of transferring apomixis to commercial plants [39]. Its controlled use can bring a direct advantage, such as fixing and cloning through seeds elite genotypes and hybrids. Cloning by seed cultures that are actually vegetatively propagated is of floricultural interest since it can be used to restrain viral diseases, once viruses can accumulate in the plants diminishing yield and quality. Another advantage of bringing apomixis to elite genotypes and hybrids is to allow small farmers to propagate their own seeds. As a result, commercial production will be simplified, with a subsequent decrease in cost. Another expected benefit of apomixes is the possibility of fixing locally adapted varieties. Their ability to survive under local stresses like extreme climate conditions or under pathogen pressure would be fixed and used in propagation. In addition, breeding of natural apomicts is very difficult because of the impossibility of making crosses and incorporating a new trait as a consequence of this mode of reproduction. Study of apomixis can be envisaged to find a way to control the expression of genes responsible for apomixis. This would allow the transmission of the male progenitor characteristics to the progeny. In this way, at least in theory, interfering in the expression of one or a few genes, apomixis could be silenced, allowing recombination, and re-expressed in improved hybrids.

Grasses from the Poaceae family are largely used as ornamental plants in parks and gardens. They maintain soil fertility, create a habitat for wildlife and provide recreational space for sport and leisure while

contributing to the general landscape. Grasses cover 26% of the world's total land area and because of their economical importance, apomixis in grasses has been far more studied than in any other group of species [40]. Several grass genera of ornamental importance contain apomictic species such as: *Calamagrostis*, *Eragrostis*, *Panicum*, *Paspalum*, *Pennisetum* and *Poa*. Breeding such species is restricted in many cases to the selection of superior genotypes from the natural populations. Because of this, collection of germplasm is one of the most important points to take in account. After that, determination of the reproductive mode of each accession as well as the chromosome number is needed. After field evaluation, cultivars are obtained directly by multiplying the desired genotypes by seed. For instance, in *Poa pratensis* (Kentucky bluegrass), a pseudogamous facultative aposporous apomictic is used as a turf grass; cultivars can be originated by a single plant selection and multiplication or selection in F1 progeny [41].

Basically, two groups of procedures have been considered for transferring gametophytic apomixis into sexual species: 1) wide hybridization between a sexual plant and a wild apomictic relative; 2) genetic transformation of sexual cultivars with genes considered to control the onset of the character. The first approach has already been attempted in several species, generating apomictic backcross plants with additional chromosomes and a high degree of seed abortion [39]. The second one still remains hypothetical.

The first proposal aiming to introduce apomixis from wide crosses was applied nearly 40 years ago, by hybridisation of tetraploid maize with tetraploid *Tripsacum dactyloides* [42]. Similar attempts produced intra-specific hybrids of maize-*Tripsacum* that reproduce by apomixis. However, as hybrids obtained after a series of backcrosses are completely male sterile, progress in recovering the maize genome is strongly associated with the degree of facultativeness and hence to some expression of sexuality.

The lack of such plants is at present challenging this strategy. An additional difficulty observed is the strict requirement of a 2 maternal:1 paternal genome ratio necessary to develop the endosperm and set viable seeds in maize. In spite of these problems, significant advances have been achieved as a result of these works. The *Tripsacum* chromosome carrying the genes for apomixis was identified and compared with its syntenic region in maize [42]. Moreover, a segregation-distorter factor promoting the elimination of the apomictic alleles when transmitted by haploid gametes was proposed to explain the relationship between apomixis and polyploidy. Likewise, a program initiated at the end of the seventies attempting the introgression of apomixis into pearl millet (*Pennisetum glaucum*) from *P. squamulatum* is still being carried out [43]. The transference of apomixis gene(s) in a breeding program was successfully performed in guinea grass (*Panicum maximum* Jacq.). "Natsukaze" was the first apomictic hybrid cultivar generated from crosses between a sexual plant and an unidentified tetraploid apomictic line through open pollination [44].

Genetic transformation of sexual cultivars with genes controlling the expression of the apomictic character is considered as a technical alternative. It opens future perspectives dependent on the identification of this kind of genes. In the last few years molecular marker technologies and molecular biology approaches have produced a considerable amount of new knowledge that could be useful for the future isolation of genes related to the trait [45]. Several markers co-segregating with apomixis in grasses such as hybrids maize-*Tripsacum*, *Pennisetum*, *Brachiaria*, *Paspalum* and *Panicum* have been reported [26, 31, 46, 47]. Markers linked to the trait are useful for studying the transmission of apomixis and for attempting any of the map-based cloning strategies. Efforts to disclose the component of the genomic region associated with apomixis using this approach have revealed its complex nature. In *Pennisetum squamulantum,* SCAR markers tightly liked to apospory were used for isolating the corresponding BACs clones [24]. Classes of BAC clones grouped by apomixes linked

SCAR markers did not overlap, indicating that building a contig spanning the apomixis locus likely will require multiple walking steps [24]. Thus, because the characteristic of the region involved (long chromosome segment with restriction in recombination and the presence of repetitive elements) cloning the critical genes involved in apomixis could represent an enormous effort.

The complexity of the genetic control of the trait is challenging the strategies for transferring apomixis to sexual crops by genetic engineering methodologies, since the gene responsible still has to be cloned and validated and probably it would be necessary to manipulate several factors that segregate independently.

Recent works focused on gene expression studies have reported the isolation of mRNA transcripts specific to flowers or ovaries at different developmental stages in several apomictic grasses such as *Pennisetum ciliare*, *Brachiaria*, *Paspalum notatum*, *Panicum maximum* and *Poa pratensis* [26, 31, 46, 47]. Several cDNA sequences showed homologies with genes of known functions as *asg-1*: a gene similar to *rd22* of *Arabidopsis thaliana* which is induced in seed by drought; *arp1*: from *Poa notatum* similar to kinesin KatD of *Arabidopsis thaliana*; *arp2* y *arp3* homologous to a SGT protein and an aldehyde dehydrogenase, respectively; *PpSERK*: from *Poa pratensis* similar to SERK [48]. *ASG-1* expression in *Panicum maximum* and *Paspalum notatum* seems to be restricted to immature pollen grains and embryos of sexual and apomicts

but specific to aposporous initial cells in ovules [49]. In *Brachiaria brizantha*, a pseudogamous apomictic, cDNA specific from the developmental steps of aposporous and sexual ovaries showed homologies with myosin, exonucleases, a super-family of RecB, kinase MAP, aquaporin, a protein translocator factor and the ribosomal protein 60S [35, 50]. *In situ* localization of the differential cDNA points to specific moments of the apomictic ovary development (unpublished results). Expression analysis of this type followed by characterisation of the possible biological role of the detected RNA transcripts can lead to the identification and cloning of genes involved in the early steps of apomictic development and may also contribute to isolate the trigger of apomixis itself.

Other procedures such as fine mapping around the apo-locus, transposon tagging and mutagenesis are currently being developed and can have an important role in detecting apomixis-related genes. For instance, approaches to generate apomictic mutants from sexual plants have not succeeded in recreating the character but allowed the identification of genes involved in the control of particular developmental steps that are characteristic of apomixis, such as the proliferation of endosperm in the absence of fertilization.

Conclusion

Much work is being done in the world towards developing new improved ornamental plants from seeds. Many of the new varieties are hybrids.

Cloning by seeds can be a tool for their breeding, eliminating segregation in the progeny. This practice can become available as a result of advances in apomixis research. Incorporating genes for apomixis can also contribute to developing new cultivars from varieties that are locally adapted, increasing the diversity of ornamental plants. This chapter aimed to introduce the many ways to identify apomixis, its incidence in Poaceae family plants and the present state of knowledge in the field. The characterisation of the phenomenon will be improved with the advent of large-scale genomic analysis and high throughput gene discovery. Though numerous questions about gene action, function and regulation of apomixis still remain to be answered, a promising scenario is open for the near future. Our understanding of the molecular bases of apomixis has greatly increased in recent years, supported by the development of powerful molecular biology technologies and the interest in apomixis showed by research institutions and scientists. Many of the results obtained so far have already contributed to the breeding of apomictic species, many of which are important natural resources, and will contribute to programs aiming at the generation of improved and asexually seed-propagating crops.

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Тұжырым

Мақалада дара жаңғақ өсімдіктер туыстастарындағы апомиксис құбылысы туралы зерттеулердің қысқаша шоулы келтірілген, апомиксистің молекулалық-генетикалық сипаттамасының соңғы кездегі жетістіктері және апомиксисті селекция мен биотехнологияда қолданауды қарастырылған.

Резюме

В статье дан краткий обзор состояния исследований явления апомиксиса у однодольных растений, приводятся последние достижения в изучении молекулярно-генетических характеристик апомиксиса, а так же его использования в селекции и биотехнологии растений.