03. Apomixis – classification and significance in plant breeding

Apomixis, derived from two Greek word "APO" (away from) and "mixis" (act of mixing or mingling). It refers to the occurrence of an sexual reproductive process in the place of normal sexual processes involving reduction division and fertilization. In other words apomixis is a type of reproduction in which sexual organs of related structures take part but seeds are formed without union of gametes. Seeds formed in this way are vegetative in origin. When apomixis is the only method of reproduction in a plant species, it is known as obligate apomixis. On the other hand, if gametic and apomictic reproduction occurs in the same plant, it is known as facultative apomixis. The first discovery of this phenomenon is credited to Leuwenhock as early as 1719 in *Citrus* seeds.

Apomixis is widely distributed among higher plants. More than 300 species belonging to 35 families are apomictic. It is most common in Gramineae, Compositae, Rosaceae and Rutaceae. Among the major cereals maize, wheat and pearl millet have apomictic relatives.

Apomixis

Long back, Winkler (1908) defined apomixis as "the substitution for sexual reproduction or another asexual reproductive process that does not involve nuclear or cellular fusion (i.e. fertilization)". Stebbins (1914) and later Nygren (1954) presented an excellent review on apomixis in angiosperms, which can be referred to for greater details. Here, a brief account of apomixis, is furnished only from the point of view of breeding.

Types of apomixis

Mainly four types of apomixis phenomenon are suggested by Maheshwari (1954)

1. **Recurrent Apomixis**

An embryo sac develops from the MMC or megaspore mother cell (archesporial cell) where meiosis is disturbed (sporogenesis failed) or from some adjoining cell (in that case MMC disintegrates). Consequently, the egg-cell is diploid. The embryo subsequently develops directly from the diploid egg-cell without fertilization. Somatic apospory, diploid parthenogenesis and diploid apogamy are recurrent apomixis. However, diploid parthenogenesis / apogamy occur only in aposporic (somatic) embryo-sacs. Therefore, it is the somatic or diploid aposory that constitutes the recurrent apomixis. Such apomixis occurs in some species of *Crepis*, *Taraxacum*, *Paa* (blue grass), and *Allium* (onion) without the stimulus of pollination. *Malus* (apple), and

Rudbeckia where pollination appears to be necessary, either to stimulate embryo development or to produce a viable endosperm.

2. Non -recurrent Apomixis

An embryo arises directly from normal egg-cell (n) without fertilization. Since an egg-cell is haploid, the resulting embryo will also be haploid. Haploid parthenogenesis and haploid apogamy, and androgamy fall in this category. Such types of apomixis are of rare occurrence. They do not perpetuate and are primarily of genetic interest as in com.

3. Adventive Embryony

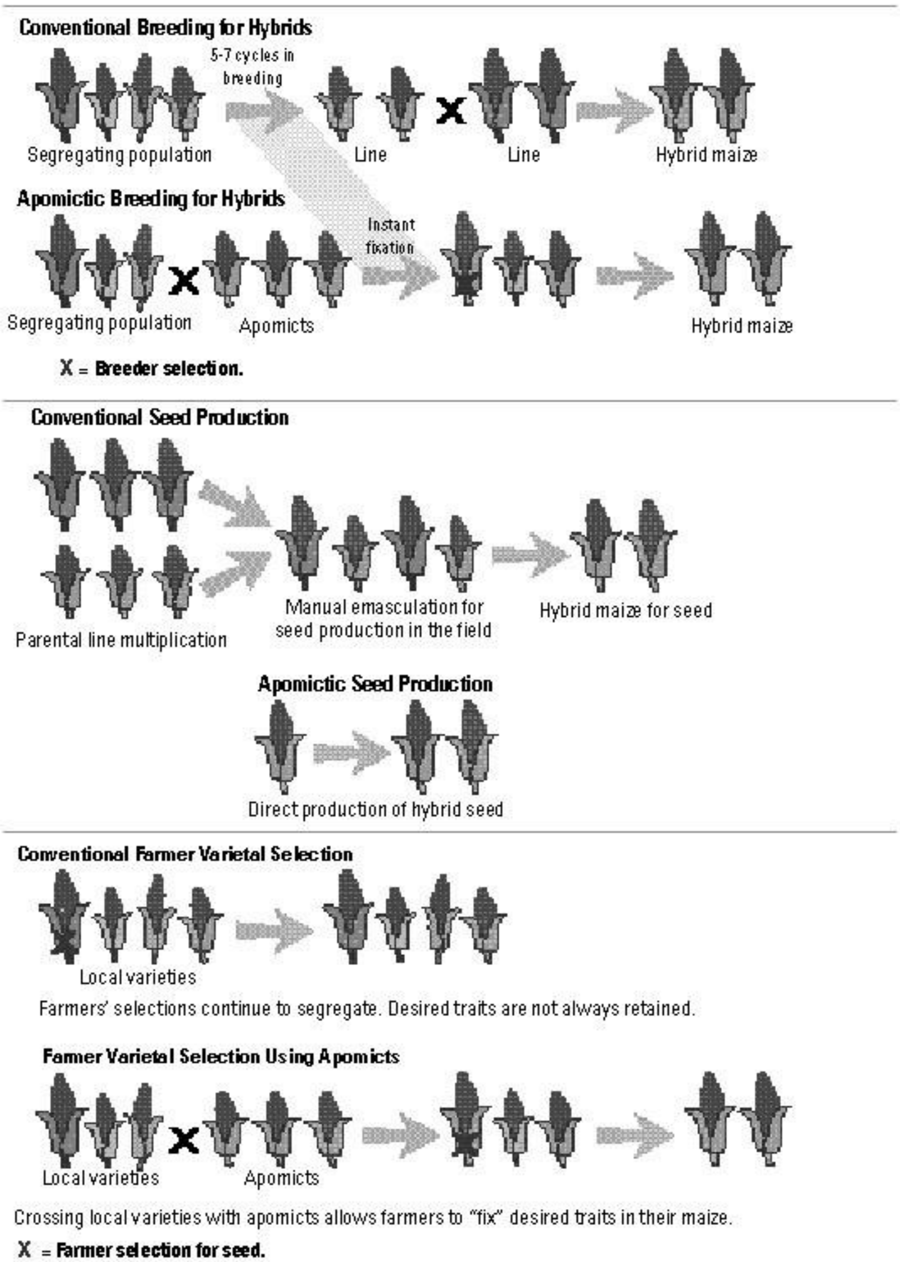
Embryos arise from a cell or a group of cells either in the nucellus or in the integuments, e.g. in oranges and roses. Since it takes place outside the embryo sac, it is not grouped with recurrent apomixis, though this is regenerated with the accuracy. In addition to such embryos, regular embryo within the embryo sac may also develop simultaneously, thus giving rise to poly-embryony condition, as in *Citrus, Opuntia.*

4. **Vegetative apomixis**

In some cases like *Poa bulbosa* and some *Allium*, *Agave* and grass species, vegetative buds or bulbils, instead of flowers are produced in the inflorescence. They can also be reproduced without difficulty. However, Russian workers do not group this type of vegetative reproduction with apomixis. Now, different apomictic phenomena in each of the recurrent and non-recurrent apomicts are considered in relation to the development of the embryo sac or embryo.

Advantages of apomixis in plant breeding

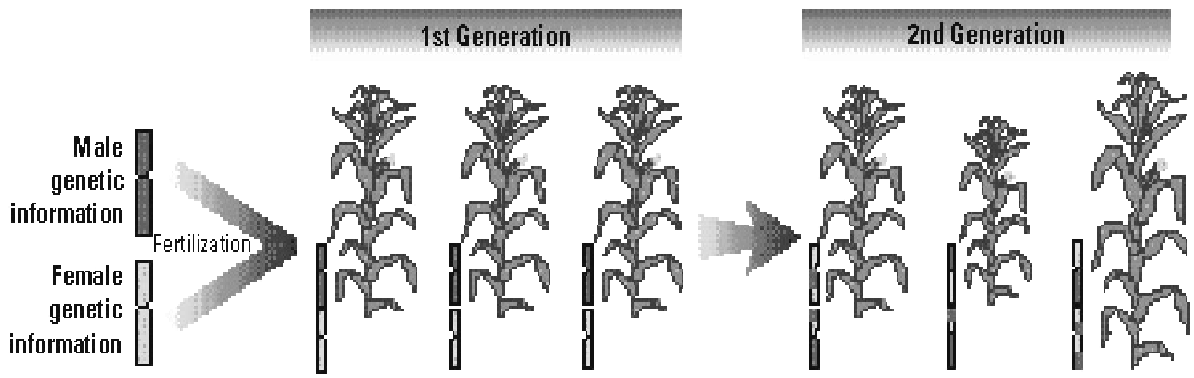
The two sexual processes, self-and crossfertilization, followed by segregation, tend to alter the genetic composition of plants reproduced through amphimixis. Inbreeding and uncontrolled out breeding also tend to break heterozygote superiority in such plants. On the contrary, apmicts tend to conserve the genetic structure of their carriers. They are also capable of maintaining heterozygote advantages generation after generation. Therefore, such a mechanism might offer a great advantage in plant breeding where genetic uniformity maintained over generation for both homozygosity (in varieties of seIfers), and heterozygosity (in hybrids of both seIfers and outbreeders) is the choicest goal. Additionally, apomixis may also affect an efficient exploitation of maternal influence, if any, reflecting in the resultant progenies, early or delayed because it causes the perpetuation of only maternal individuals and maternal properties due to prohibition of fertilization. Maternal effects are most common in horticultural crops, particularly fruit trees and ornamental plants.



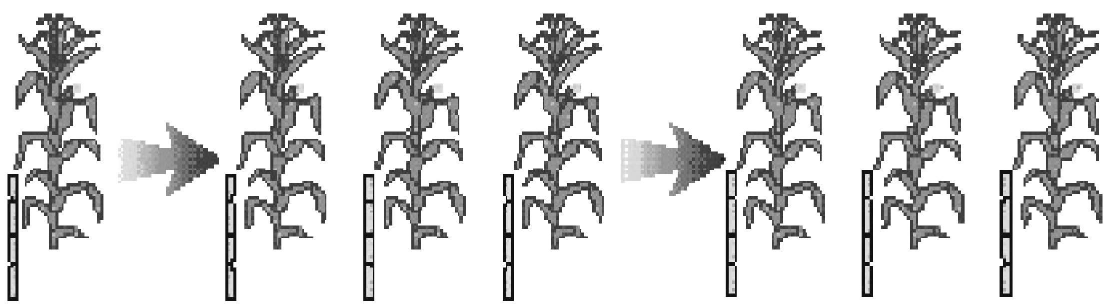
Thus, in short the benefits of apomixis, insofar as their utility in plant breeding is concerned, are:

1. Rapid multiplication of genetically uniform individuals can be achieved without risk of segregation.
2. Heterosis or hybrid vigour can permanently be fixed in crop plants, thus no problem for recurring seed production of F 1 hybrids.

3. Efficient exploitation of maternal effect, if present, is possible from generation to generation.
4. Homozygous inbred lines, as in corn, can be rapidly developed as they produce sectors of diploid tissues and occasional fertile gametes and seeds.



Sexual Reproduction: Hybrid maize that has been produced through sexual reproduction displays identical genetic makeup. The depiction of the second generation represents the use of seed recycled from hybrids, a common practice in many developing countries, and its varied results.



Apomictic Reproduction: Hybrid maize that has been produced apomictically (asexually) also displays identical genetic makeup in the first generation, but it *retains* its genetic composition and characteristics through the second generation and beyond.

Exploitation of apomixis in crop improvement

The use of apomixis in crops in a follow-up process, after a variety or hybrid is evolved, as reflected by the benefits it renders. Therefore, our aim in this section is to deal with only apomixis as a tool to plant breeding. With a view to exploit apomixis in sexual crops, it needs to detect and identify an apomictic phenomenon, occurring spontaneously in any plant, or, to incorporate it artificially, perhaps through hybridization between apomicts and amphimicts.

Detection of apomixis

Positive evidence for the presence or absence of apomixis can be obtained only from an intensive screening of a large number of plants in a variety/hybrid. The screening involves a careful and systematic tracing of steps for the development of embryo-sac and embryo, through microtomy of ovule, right from megaspores to embryonic development. as such, therefore, it is a most tedious job requiring a lot of patience and persistence indeed.

It should however be noted that it is only recurrent apomixis, namely diploid forms of apospory / parthenogenesis / apogamy / adventive embryony and vegetative propagation which are beneficial for plant breeding purposes. The simple reason being that it is these which produce viable diploid embryos without fertilization and thus can continue to perpetuate over generations. Nonrecurrent apomixis are of academic use.

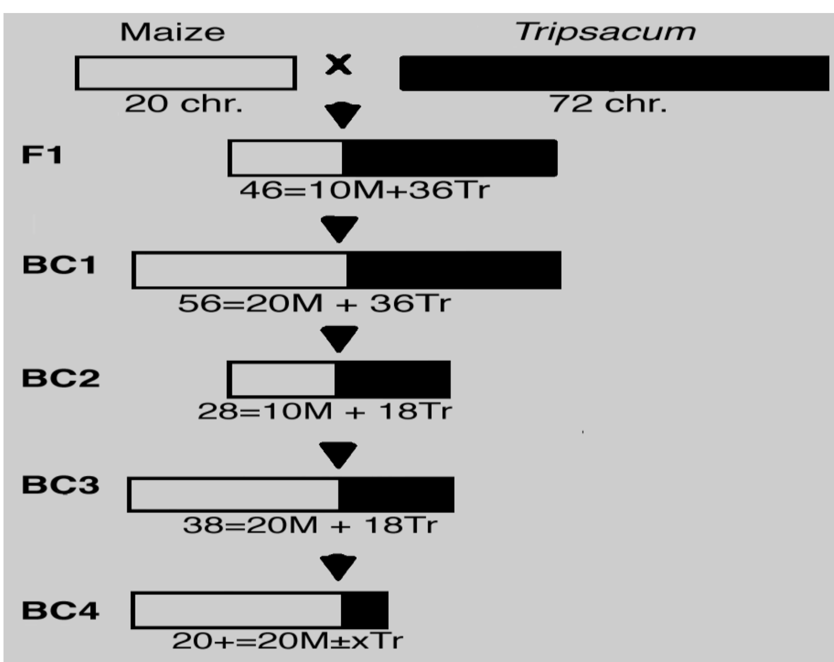
Maintenance of apomixis

Once an apomict plant is detected its inheritance should promptly be studied by crossing a half or few flowers with the pollen obtained from normal plants and going through the segregation pattern in F2 and onward generations. The remaining flowers may thoroughly be checked and seeds collected on maturity. The true nature of such plants would become distinct only after progeny tests. A true apomictic plant will automatically produce mother apomictic progenies which can be maintained without difficulty.

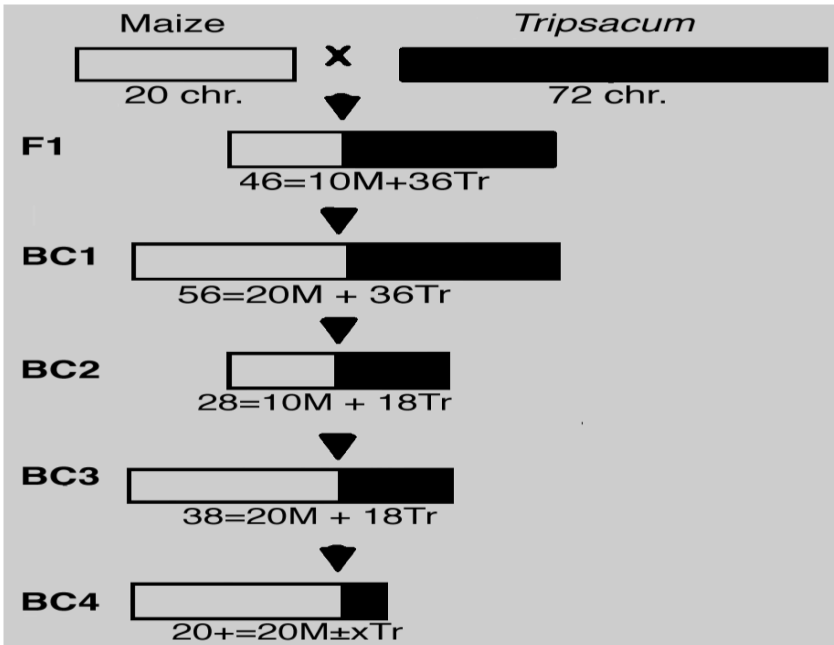
Transfer of apomixes

With regard to transfer of apomixis, substantial evidence is available for the hybrid origin of many of the apomicts. Nevertheless, there is no evidence at all the hybridization by itself can induce apomixis (Stebbins, 1950). Situation is further aggravated by the unstable nature of apomicts since there is every likelihood of the breaking down of interacting gene complexes conditioning apomixis, as stated earlier. Therefore, possibilities of introducing apomixis in non-apomicts are the least but not totally absent.

The CIMMYT Apomixis Project was launched in 1989 with the goal of transferring the naturally occurring, untapped trait of apomixis to maize, an achievement that could dramatically and directly improve farmer productivity in the developing world. Building on decades of IRD



(formerly ORSTOM) apomixis research, project scientists are working to create apomictic maize. A hybrid between maize and its wild relative *Tripsacum* is being backcrossed in pursuit of a true apomictic maize variety. This long-term strategy has provided very encouraging results. It was found that all *Tripsacum* chromosomes can be transferred into addition lines and that about 10% of these plants also show maize-*Tripsacum* translocations, suggesting that 20-chromosome recovered maize plants with small *Tripsacum* DNA segments can be produced from the backcross series.



Production of Maize-*Tripsacum* addition lines: Four backcross generations are required to produce addition lines from maize-*Tripsacum* F1 hybrids.