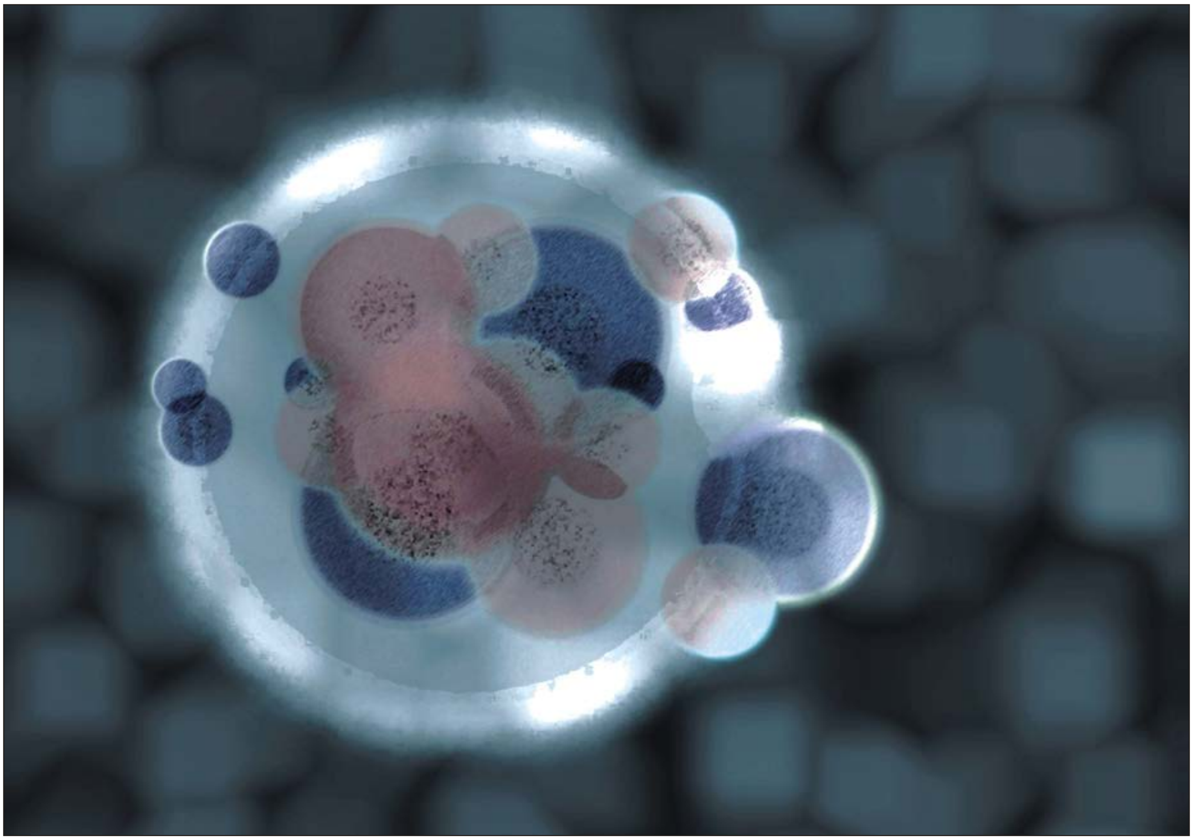

Journal of Biological Sciences

ISSN 1727-3048

science alert

ANSInet
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Journal of Biological Sciences 9 (8): 788-795, 2009
ISSN 1727-3048

A New Alternative for Plant Breeding, Biodiversity and Environmental Sustainability: Apomictics

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Abstract: Aim of this study is to explain of the apomixes, utilization in the plant breeding and to indicate its importance in terms of biodiversity and environmental sustainability. Etymologically, apomixis comes from the Greek apo (= away from) and mixis (= act of mixing). Botanically, apomixis is a kind of biological reproduction process without fertilization and meiotic division. These types of plants produce with genetically identical seeds to their female parent. It is uncommon in the wild and rare in cultivated crops. If it is possible to exploit or harness this type of reproduction, then produce new cultivars more quickly and cheaply. Similarly, the breeding process will be significantly accelerated in related seed companies, furthermore, farmers and growers would be able to reduce costs in their production input/s in terms of, for example, the purchase of hybrid seed, time saving and the size of labor force, etc. or reach a maximum yield potential level. In spite of the many potential advantages, according to some researchers the development of commercial apomictics is making slow progress. However, other research from a multidisciplinary approach to apomictics indicates that all potential obstacles could be overcome in commercial production in the near future. With this contribution, thousand million persons who dye from hungry could be saved and their basic and vital requirements could be met.

Key words: Apomixis, biodiversity, environment, plant breeding, reproduction

INTRODUCTION

Apomixis is a natural process that allows clonal propagation by seed, resulting in off-spring that is genetically identical to the mother plant and if can be exploite, this process will be a new milestone and the beginning of a new era for plant breeding (Adolfsson and Bengtsson, 2007) and seed production, since it allows the immediate fixation of desired genotype, including F_1 hybrids without any segregation in off-springs (Anonymous, 1994; Grossniklaus *et al*., 1998; Ulukan, 2007). In nature, apomixis is widespread but infrequent biological phenomenon. It occurs in arround 10% of the 400 families of flowering plants, but only in 1% of the 40,000 species that make up those families. Many wild plants and some families such as Alliaceae, Apiaceae, Asterceae, Brassicaceae, Compositae, Orchidaceae, Plumbaginaceae, Rosaceae, Rutaceae, Solanaceae, Urticaceae and certain tropical forage grasses have apomictic plant species (Ramulu *et al*., 1999; Spillane *et al*., 2001; Kaushal *et al*., 2004; Ozias-Akins and van Dijk, 2007). According to Ozias-Akins (2006) apomictics (only) preserve the maternal genotype by parthenogenetic embryo development so they maintain their heterozygosity and epistasis and they produced by cloned seed and enable them to reproduce asexually (Dresselhaus and Colombo, 2001) with their viable pollens. Plant breeders are very interested in their advantage(s) in terms of propagation and reproduction of them and this issue will be discussed later. On the one hand, apomixis pecularity could also be transmitted through the more common mechanism of sexual reproduction. Generally, this phenomenon does not occur naturally but there are some exceptions such as some citrus fruits (*Citrus* spp.), major field crops [rice (*Oryza* spp.), wheat (*Triticum* spp.), rye (*Secale* spp.) barley (*Hordeum* spp.)]. On the other hand, apomictic relatives that can be crossed with eachother. Furthermore, commercial hybrid production systems are available and this has made a major impact through the simplification of the hybrid seed production (Şehirali and Özgen, 2007) in some important field crops such as maize (*Zea mays* L.), sorghum (*Sorghum* spp.) and millet (*Pennisetum glaucum* (L).R.Br.). According to study results, the increase in yield with the fixation of hybrid vigor of inbred crops such as wheat (*Triticum* spp.) and rice (*Oryza* spp.) by apomixis was observed to be 15.0 and 35.0%, respectively (Asker and Jerling, 1992). The aim of this article is to make general evaluation on the usage possibility (ies)-exploitation (s) of the apomictics in the plant breeding, their impacts on biodiversity and environment and to make some recommendations and suggestions on breeding and seed production processes, biologically.

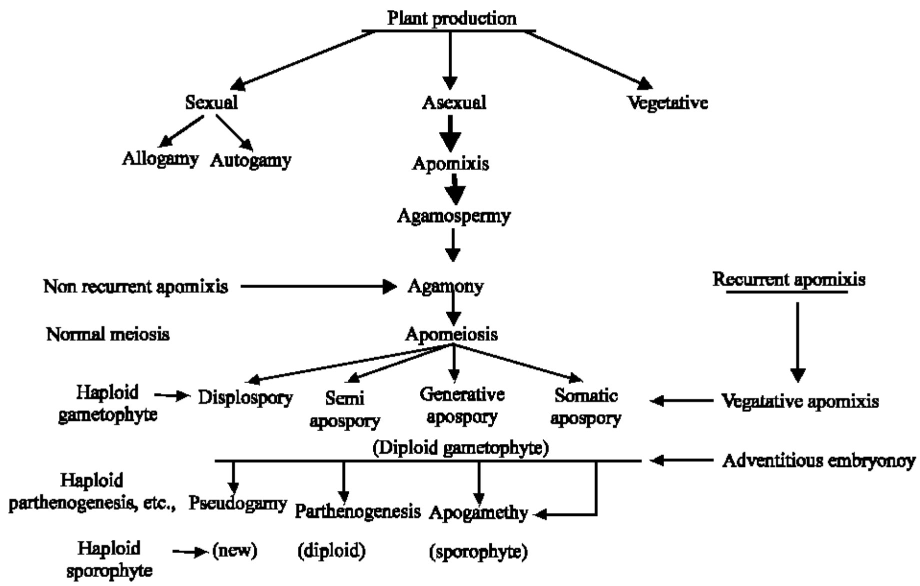

Fig. 1: Reproduction modes in the plants (Modified from Spillane *et al*., 2001; Şehirali and Özgen, 2007)

Seed development occurring without fertilization is called apomixis and occurs naturally in some crop plants (Fig. 1) (Van Dijk and Van Damme, 2000; Şehirali and Özgen, 2007) and it is mainly seen in polyploid plants, because it was the apomictic mutants that survived in the course of evolution (Kumar, 2006). Scientists have classified this phenomenon into two basic sub-classes according to whether unreduced cells give rise to a mega-gametophyte (= gametophytic) or to an embryo (= sporophytic) and the usefulness in the plant breeding (Spillane *et al*., 2001; Kaushal *et al*., 2004; Ozias-Akins, 2006). In spite of the fact that apomoxis eliminates practically all of the potentially negative processes associated with sexual reproduction, adventitious embryony retains an important physiological characteristic of the sexual process and other types of agamo-spermy which is the ability to produce the distinctive characteristics of the seedling. To identify the apomictics by determing the location of the gene, researchers are using many advanced recognition and characterization biological tests and techniques such as cyto-embryological/cytological or histological tools, some DNA-Molecular Markers (RFLP, RAPD, AFLP, SSR, etc.) (Estrada-Luna *et al*., 2002; Ozias-Akins, 2006). Genetic studies on the apomictic mechanisms are difficult to conduct and frequently they reach a dead end because of the lack of the necessary crosses and backcrosses for the tests on the segregated progenies. Similarly, if the plants reproduced by facultative apomixis, it is difficult to understand the inheritance of them (Hanna, 1995) thus, apomixis controlled genes have not yet been found in major cultivated plants (especially in the Poaceae family). However, these genes can probably be found in wild species or related crop cultivars. As a result of the study, it was understood that apomixis's heritage pathway was under the control of qualitative inheritance. This point is very clear and progress is being made in understanding the genetic control of apomixis in various cultivated plants (Ozias-Akins, 2006; Ozias-Akins and van Dijk, 2007). The simple structure of the genetic control of the apomixis makes it easy to improve the potential for manipulating the reproductive mechanism and transferring it to other plants. In terms of this aspect, certain successful examples were obtained in *Brachiaria* spp., *Eragrostis* spp., *Panicum* spp., *Paspalum* spp., *Pennisetum* spp. and *Tripsacum* spp. (Kaushal *et al*., 2004). Developments in advanced biological molecular marker techniques/tools and technological facilities had been achieved to transfer desirable apomixis genes into non-apomictics. Similarly, use of mutagenic agents, for example Ethyl Methanessulfonate (EMS) (Şehirali and Özgen, 2007), may be another valuable source for the production of mutant genes for apomictic reproduction. Parthenogenesis, apospory and other types of apomixis reproduction have been considered by some scientists as weird (Dresselhaus and Colombo, 2001; Adolfsson and Bengtsson, 2007). Whatever it is, development of apomictic plant reproduction will give or reproduce stable apomictic cultivars releases for the farmer(s)/grower(s) in a big possibility. If pseudogamous diploid progeny can be induced in large numbers as complex hybrids; true breeding homozygotes will easily be produced, thus, long processes for fixing the valuable new combinations obtained from intra or inter varietal hybridizations could be eliminated. However, to be able to understand and explain the appearance of apomixis in cultivated plants, three factors must be defined clearly, namely they are hybridization, polyploidy and related genetic factors.

MATERIALS AND METHODS

This study was carried out at the Department of Field Crops, Faculty of Agriculture, University of Ankara, during 2009, Ankara, Turkey. The development of apomixis in the plants has two important effects in terms of evolution. First, a species group gives rise to innumerable microspecies or clonal species through the perpetuation by apomixis of sexually sterile hybrid derivatives, the genetic and morphological barriers between the male and female parents (Asker and Jerling, 1992); second the genetic analysis of them provides to researchers certain handicaps because of their ploidy levels, lack of sexual progeny, lethality, accurate identification and classification of the progeny. According, to the simple inheritance hypothesis, one or two dominant genes control apomixis (Asker and Jerling, 1992). And it is well fitted in the Mendelian segregation ratio (1:1) for apomictic plants in sexual progenies that are hybridized from sexual and apomictics reproduction. When the apomixis, governed by a dominant gene or a simple inheritance pathway in the plants, all are heterozygous for their reproduction and their usage is very easy in the plant breeding programs. (Sexual×apomictic) hybridizations result in both sexual and apomictic F_1 genotypes and one half of the F_1 plants are sexual and the reminder are apomictics. Afterwards, all plants obtained from one half of the sexual F_1 plants can be discarded or used in hybridizations with other apomictics to produce new (apomictic) hybrids and sexual plants with the new gene combination. Furthermore, by using sexual plants in the crosses with improved apomictics from other hybrids in each generation, the possibility of developing superior apomictic hybrids increases in advanced generations. So, F_1 apomicts with desired biological and agronomic trait(s) produced from the hybrid can be selected and they can be re-used as desired in any kind of breeding programs. Moreover, at the end of these procedures, doing progeny and stability tests for these genotypes is not necessary to understand if they are obligate apomictic or not and the obtained superior genotypes can be released as cultivars. These released cultivars are apomictic hybrids (either in terms of F_1 and or subsequent generations) under related conditions. On the other hand, if the apomixis phenomenon is controlled by a recessive gene, all F_1 sexual plants will be heterozygous in hybrids between sexual plants and apomictics. Thus, the breeding strategy will change in process of time. If the inheritance pathway works in the way mentioned above, breeding procedures will be rather complex and they can change according to the particular plants (or parents and hybrids), their genetic background and effective gene numbers. In any commercial plant breeding program, if a male sterile line use for the apomictic undesired apomictic traits can be easily eliminate from those materials (male sterile A, male fertile B, maintainer lines, R-lines etc.) to develop the quality and quantity. Generally, the main trend is to determine or select the superior apomicts cultivar release (Stebbins, 1941) in the hybrid populations after that stage as candidates besides certain cytological, biological-biochemical, histological, histo-chemical and advanced tests. Unfortunately, despite all efforts, no clear apomixis gene(s) has/have been clearly identified or isolated or successful transferred to the cultivated plants, furthermore it may vary, except for some minor successful attempts at the academical level within the same genus.

AS AN EFFICIENT TOOL IN THE PLANT BREEDING

There are three types of breeding approaches in apomixis:

- Introgression (transfer of the apomictic genes from wild relatives by interspecific hybridizations)
- Mutagenesis application(s)
- Molecular biology and genetic engineering techniques (Kaushal *et al*., 2004)

And basically there are three main and important plant breeding methods (mutation breeding, selection and backcrossing and cloning) are valued for apomictics (Fig. 2) and the remainder techniques are combinations of these methods (Ulukan, 2009a). It is clear that many angiosperms but apomictic plants exhibit genetic variation (Adolfsson and Bengtsson, 2007) in terms of sexual versus apomictic seed production, but there are few scientific findings on the extent of this in natural populations (O'Connel and Eckert, 1999). They are produced through seed, but their embryos are developed from the cells in the ovary without fertilization; so they are genetically similar to their mothers. During this stage, mutation breeding technique has an important place. As known, mutation agent applications have pleiotrophic effects because they turn on the genes that normally remain re-pressed, including those epigenetically/silenced via DNA methylation

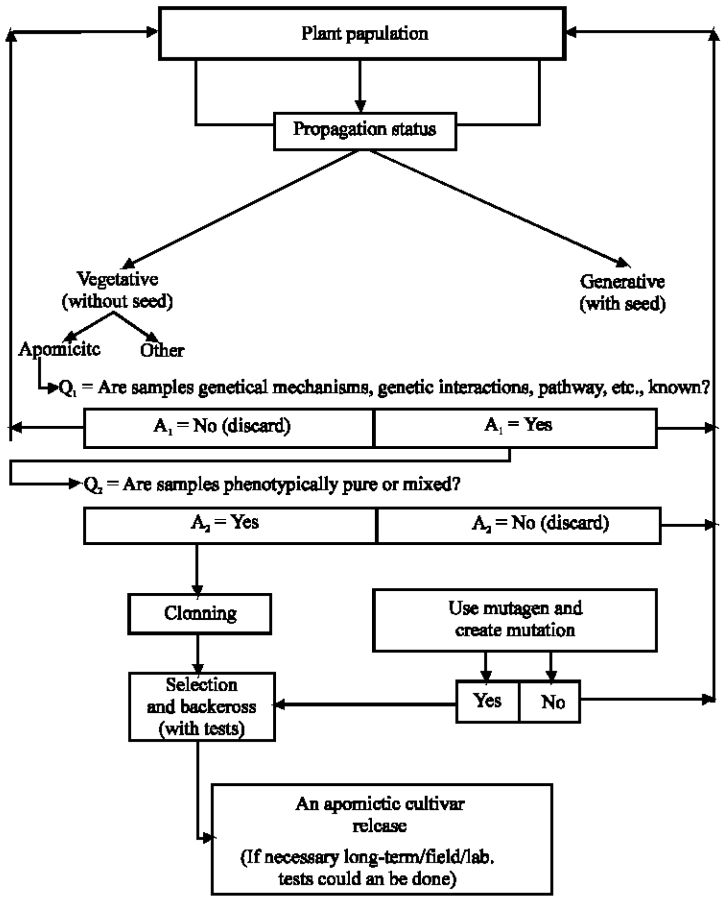

Fig. 2: Follow chart for the apomictic breeding methods (Modified from Bashaw, 1980; Şehirali and Özgen, 2007).

(Kumar, 2006). So, this method (mutagen agent application(s)) is used for developing a new cultivar from the wild forms, cultivar(s) and population(s); after selecting according to desirable characters phenotypically. But, in some plants, for example Kentucky bluegrass, (*Poa pratensis* L.) the apomixis trait is optional and apomictic seed amount is equal to the sexually produced amount. Likewise, the sexuality degree only varied between 1-50% or more in them. In addition, obtained research findings showed that, sexuality degrees could be affected from the internal factors such as the plant age and some external factors (temperature, water, light, time, etc.). So, a plant species can be totally apomictic in an environment but may not be in another environment. Nevertheless, to be able to find and maintenance apomictic plant species is possible if these breeding methods are used properly (Fig. 2). It is well known that apomictic plants produce through seed but they do not have insemination. So, they do not show any segregation in their off-spring.

Agricultural scientists would dearly love to convert these plants to apomixis: making embryos that are genetic clones of themselves rather than the product of sexual reproduction with its inevitable gene reshuffling and after 20 years of study, an apomictic corn (maize) has been produced, but it does not yet produce enough viable kernels to be useful commercially. Basic aim of the plant breeding which will be carried out for the apomictics is to obtain genetic recombinations and identify them among the progenies as superior/true-breeding apomictics at the level of suitable cultivar status. For this, obligate apomictics can only be used as male parent (they are genetically recombined and comprise chromosomally reduced male gametes) in all kind of plant breeding programs and they are generally called gorgeous and opportunist due to the remarkable polymorphism of the complexes, also being considered as heterotic, aggressive (frequently) and competitive (Bashaw, 1980). However, these plants (apomictics) are adapted to flora and they have taken great advantage of conditions and they have adjusted themselves to changes in the biotic and abiotic stress factors over a long period. This phenomenon usually happens in the polyploid plants and it may be necessary at the level of tetraploidy or higher levels (Ramulu *et al*., 1999); but, they have been most valuable genetic tools for the plant breeders in the 21st century (Asker and Jerling, 1992). In addition, cultivating apomictic plants would reduce the costs of hybrid production and it would be possible to produce virus-free plants, particularly in Citrus (*Citrus* spp.) crop plants. This trait will allow to breeders to create perfect and precisely engineered plants which combine agronomically desired traits in one genotype (Ramulu *et al*., 1999; Ulukan, 2009a, b). Producing by apomixis to determine the hybrid seeds could lead to impressive time and cost savings. Some attempts were made to produce apomictic cereals but with very limited success and generally, no apomictic cereal cultivars has/have been released up to now. As mentioned above, it can be said that these topics still wait for a successful solution (Kaushal *et al*., 2004). According to research results, it is estimated that with the introduction of apomixis trait to the rice (*Oryza* spp.) crop plants the total annual gain will be US$ 2.5 billion in the world (Grossniklaus *et al*., 1998). The implications of the apomixis-led acceleration of the plant breeding could be dramatic; lower costs and much reduced time requirements will change the face of the plant breeding and related sectors and farmers or growers. Similarly, if apomixis and plant genomics can also be combined, rapid and uniform delivery of quality crops to the products' end-users in terms of food, fibre, pharmaceuticals, plastic or as raw material will be possible. If public attention is drawn to this topic, it will likely result in a general decrease of seed and seedling prices. But, one or a few seed/seed(ling) companies controls the apomixis, their potential effects will be disseminated immediately, directly or indirectly. However, poor farmers in developing countries, could be negatively affected in two ways, firstly, they could not use and secondly they could save these seeds (Dresselhaus and Colombo, 2001). It is not necessary to wait for rich farmers longer to be able to get or access new hybrid seed for every growing season in order to ensure sufficient agricultural production. This point is particularly very important in undeveloped countries. The apomixis phenomenon may increase access of farmers to hybrid seeds, but can not let them take the control of the seeds. These farmers have to learn how to obtain faster breeding procedures, to take control of their local agro-environment conditions and to obtain cheaper seed of more adapted varieties for their production. This is wholly possible and depends on whether apomixes is accessible to those who want to use it. In addition, the superiority of vegetative reproduction by seed has a major impact not only on vegetatively reproduced but also on seed-propagated (generatively) crops and in terms of avoiding of phyto-sanitary threats in unfavorable seasons or conditions (Ramulu *et al*., 1999).

AS A GUIDE TOOL IN THE BIODIVERSITY AND ENVIRONMENTAL SUSTAINABILITY

Potential advantages:

- Due to their hybrid vigor power, all apomictics have the potential of maximizing the crop production as food (dry matter), forage and fiber yield through the fixation of hybrid vigor (Ramulu *et al*., 1999)
- The rapid generation and multiplication of superior forms through seed, the reduction in cost, time and labor force for the plant breeding
- The avoidance of complications in sexual reproduction, not requiring pollinators, pollination and cross-compatibility and the avoidance of viral transfer in plants especially in vegetatively propagated plants (Bicknell and Koltunow, 2004)
- Expanding the usage possibility (ies) of wild relatives could be directly integrated into the plant breeding programmes. In apomixis technology, fixation of any desired genotype with a certain propagation type is possible (Spillane *et al*., 2001)
- The genotype of every apomictic is fixed in the F_1 generation and each one is derived from a cross has a potential of being the cultivar and maintenance of their elite genotypes is easy and efficient and there is no need for isolation criteria to produce high quality seed or seedling
- The main advantage of apomixis over sexual reproduction is the possibility of selecting individual plants with the superior characteristics, propagating them clonally by seeds and sowing true breeding seeds in crops such as potato (*Solanum tuberosum* L.) (Ramulu *et al*., 1999)
- Seed propagation by apomixis will greatly reduce storage and transport expenditures, losses, disease-virus spreading risks, shipping and planting costs especially for the farmers and growers
- High yielded varieties is the improvement and enrichment of the security of food supply and makes greater autonomy for specific environments in developing countries (Bicknell and Koltunow, 2004)

Due to the fact that genetic and biological bases are still little understood (Mogie, 1992) and not clear, its impacts on the biodiversity are open to speculation, even contradictory to some degree. Use of the apomictics for cultivar development in any plant breeding programme would increase genetic diversity. The introduction of *apomixis* into crops plants (especially to the field crops) will alter the genetic diversity of both cultivated forms, their wild and non-apomictic relatives. At this point, some researchers have different opinion that the low rate of apomixis in nature might be the result of extinction brought about by its long-term disadvantages (Dresselhaus and Colombo, 2001). According to the research, there is another danger for apomictics in that they can be damaged by the natural selection process and biodiversifiying. Environmental conditions are able to negatively influence apomictic expression in some plants (especially under stress conditions). Similarly, sudden environmental changes, new pests or diseases have a negative impact, as well. But, despite of all these negativeness, apomictics have wider ecological survival range and their tolerance ability to stress factors than their sexual diploids because they have larger and wider distribution area. Furthermore, although it is not clear this survival may be related to the ability to escape from predators and pests; greater colonizing ability and the fact that often hybrids have greater genetic variability. Positive and negative impacts can be grouped as follows (Asker and Jerling, 1992; Ramulu *et al*., 1999; Dijk and van Damme, 2000; Estrada-Luna *et al*., 2002; Adolfsson and Bengtsson, 2007; Şehirali and Özgen, 2007; Ulukan, 2008, 2009a, b):

Positive effects:

- Each apomictic plant derived from the hybridization (sexuals×apomictics) is potentially a unique cultivar or a hopeful candidate regardless of heterozigosity or homozygosity genetic background of the parents
- When the genes which was/were responsible for the apomixes introduced into a sexual species, all germplasms within a species have a potential as a parent of a new hybrid and this was determined as F_1, too
- The maintenance of elite genotypes is easy and efficient, so there is no need for isolation criteria to produce a high quality of seed
- The planting of true breeding seeds from the apomictic reproduction has many advantages over the tuber propagated crops
- Seeds will reduce the spread and transition possibility of diseases and viruses by propagated especially by tubers
- Asexual reproduction by passing all of their genes to offspring has some benefits in stable environments; but not in unstable environments and they pass half their genes to off-spring but produce more off-spring at a lower average energy cost and do not have to depend on neighbors or wind or insects for pollination and do not contract sexually Transmitted Diseases (STDs)
- Apomictics produce no wasted offspring with biologically bad or risky genes
- Sexual reproduction causes variation (Adolfsson and Bengtsson, 2007; Ulukan, 2009a) and produces seeds, asexual reproduction has rapid reproductive rate and off-spring are not as fragile as seedlings
- Seed propagation by apomixes reduces the storage, shipping and planting costs
- A number of apomictic genotypes can be mixed together in various combinations to enhance genetic diversity to accomplish a specific goal

Negative effects:

- Apomixis is a very complex trait, but it is governed by genes that behave individually. So, these genes have the negative effect on the fitness, community and viability
- Either the apomixis segregations or inheritance pathway can be changed (particularly at the plant base). According to studies, intermediate parhtenocarpic apomictics have deleterious effect owing to slow but harmful mutations which accumulate in their structures
- Off-spring has biologically useful genes which can be functioned in a particular environment
- Genetic variability is extremely low in the populations in asexual propagation
- Many natural apomictics are triploid and their meiotic division are rather unbalanced in the flowers, so the males are sterile
- They carry potential risks which differ for each apomictics. Compared with other transgenes, apomixis transgenes have endogenous effect for uncontrollable physiologic reactions, meiotic division etc. and demographically dissemination limiting etc
- The superior cultivars will occupy most of the fields covered with a particular crop using apomixis in plant breeding. These fields will be more uniform than monocultural applications, but these cultivars will be more fragile and susceptible to pests and diseases
- There is a danger for the apomixis mechanism spreading to wild populations and the impact on genetic diversity, environment, biodiversity and plant evolution

- Apomixis is limited to polyploid species, which are relatively few in number in the nature
- If it becomes feasible to transfer an apomixis supergenes into wild diploid plants, they can be easily be created
- Their competitive advantages may be affected by genetic erosion this is valid for many wild and non apomictic relatives
- One of the important threats to the farmers is the potential use of Terminator to Traitor Technologies or Technology Protection System (TPS)

RESULTS AND DISCUSSION

Apomixis is currently receiving increasing attention from the scientific and industrial sectors and it is an excellent material for experiments on the effect of the environment on the genotype and natural selection. On the basis of apomictic populations, the relative ages of different flora(s) can be estimated. Those which are young have a large proportion of apomicts, while the olders specimens have the sexual members with different seceral agamic complexes. Therefore, apomixis is not a major factor in evolution; however, it is important in increasing the polymorphism and the geographic distribution of the cultivars where it is found. For the apomictic plant breeding in commercial terms, many universities, national and international institutes, state and private research centers and multinational seed organisations are investing on this topic such as University of Harvard, University of Georgia, CSIRO, CIMMYT, USDA-ARS, IRD, CNR, NIVOT, CPRODLO, CIAT, IRRI, NIOO-KNAW, Advanta, Dupond, Limagrain Group, Novartis, Sudwestdeutsche Saatzucht, Deutsche Saatveredelung Lippstad, etc. In all over the world (Asker and Jerling, 1992; Dresselhaus and Colombo, 2001; Kaushal *et al*., 2004). All multidisciplinary approach of using both sexual model species and apomictic breeding techniques will be make easy the isolation of key the genetic factors controlling apomixis in the near future, but, still low seed setting, low male fertility or low fertility level are the most important constraints (Ulukan, 2009a). And if these hindrances could be overed in terms of biologically and agronomically with the multidisciplinear approach, new horizons will be open for the world beyond the humanity (Ulukan, 2009b).

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