Reproduction — a factor of plant evolution

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(Received: March 22, 1988. Revision accepted: August 8, 1988)

Abstract

The process of reproduction (amphimixis and apomixis) represents a major factor of evolution. The facultative apomictic species are the pioneers of evolution. They combine the advantages of amphimixis (high degree of variability and heterogenesis) and apomixis (relative stability and low material expenditure) assuring a rapid rate of adaptive evolution.

Key words: *amphimixis, apomixis, selection, evolution*

INTRODUCTION

The progress achieved as the result of the appearance and spreading of amphimixis is undeniable; the question therefore arises on how to account for the fact that, mainly in plants, we see a return to apomixis.

In eukaryotes, from the primitive to the evolved species, amphimixis has improved concurrently with a change in the gametophyte to sporophyte ratio in favour of the latter. The primitive eukaryotic species multiplied mainly by simple division, according to the sporophyte-sporophyte pattern. The gametophyte appeared latter and its extent in the ontogenetic cycle varied — evolution has aimed at considerably reducing both its size and role in time. Exceptions, as *Bryophyta* for instance, represent dead branches of phylogenesis.

ADVANTAGES OF SEXUAL REPRODUCTION FOR SPECIES SYSTEMS

It is impossible to ignore in evolutionary theories the part played by selection in the dynamics and direction of the evolutionary process. Am-

phimixis has a decisive role in securing individual variability (the field of selection action) and heterosis. It provides for an optimum range of variability through genetic recombination and mutations. All these phenomena depend on the specific circulation of genetic information provided by the formation of gametes and their fusion. The former implies meiosis. Random assortment of chromosomes during meiosis assures formation of 2^n different types of gametes and 2^{2n} different types of zygotes (n = haploid chromosome number). Crossing-over substantially expands the range of variability by restructuring the chromosomes (the manner in which genes are joined together).

Another means of increasing individual variability is mutation. In principle, mutations may affect any cell and, eventually, any organism — monocellular or multicellular. However, mutations (genic, chromosomal, genomic) do not have the same magnitude and, obviously, the same effects on the variability of a population and on the rate of evolution of a species. From another point of view, mutations are two large categories — somatic and germinative. Regardless of their type, mutations are accidental and undirected events (Dobzhansky et al. 1977). Although fortuitous mutations are neutral, tolerable, advantageous or disadvantageous, some authors (Kimura 1968, King and Jukes 1969, Kimura and Ohta 1971, Ohta 1974) have reached the conclusion that the greater the demand from a function and its hereditary support, the more stable it is hereditarily. They believe that evolution is due to neutral mutations. But, the genes responsible for the synthesis of molecules with essential functions in the organism are stable because any mutation is bound to be rapidly eliminated by selection. The more functionally necessary a gene is, the more it is evolutionally stable and the lesser the probability for its mutations to become fixed (Antoși and Gavrilă 1981). Apomicts are considered to be more dependent on mutations (Dobzhansky et al. 1977) while the probability of survival with persistence of mutant genes is considered to be higher in species with sexual reproduction and lower in those in which sexual and asexual reproduction alternate (Charlesworth 1980).

The incidence of mutations is higher in germ cells than in somatic cells. Moreover, the two types of mutations have a different fate even if they have the same rate of occurrence. The role of somatic mutation is similar to that of gametic mutation only if a new individual results from the affected cell, tissue or organ.

Organisms with amphimictic reproduction are reservoirs of alleles produced by mutation. Mainly due to the phenomenon of dominance can the recessive mutations be perpetuated in the population *ad infinitum*. Only in case of homozygosity do lethal and even harmful mutations disappear. Apomictic reproduction precludes any chances for an organism to become homozygous.

Heterosis is another attribute of sexual reproduction with important implications in the evolution of species. Amphimictic reproduction facilitates

the coming together of gametes from individuals which have lived in different ecological conditions and have different reaction amplitudes. Although cross-breeding as a phenomenon and particularly the possibility and advantages of its practical use have been known since ancient times (Stebbins 1959), studies on it began only as late as the mid-eighteenth century (Levin 1979). Cross-breeding has been found to be of major evolutionary value, particularly if it is followed by a selective incorporation of genes from one population (and even species) into another, as well as by hybrid stability and fertility. On the other hand, selection may also stop the flow of genes between hybrid off spring and their parents (Wallace 1889, Dobzhansky 1951, Grant 1966) being a way of preventing the waste of gametes. Cross-breeding, especially when it is followed by introgression, results in greater evolutionary flexibility, enhances the capacity of a population to intensively exploit the resources of its habitat, and increase its reaction amplitude much over the limits of the non-hybrid population (Anderson 1948, Anderson and Anderson 1954, Rattenbury 1962). Hybrids have other ecological abilities, requirements and potentialities than their parents, as has been found in the genera *Quercus*, *Aquilegia* and others (Chase and Raven 1975). The fate of hybrids, their role in evolution, depends very much on the way in which they reproduce and produce offspring, as well as on habitat conditions. Opinions on the incidence of hybrid occurrence are different. Some authors estimate that the number of hybrids in *Pteridophyta* amounts to 620, and in the *Gymnospermae* and *Angiospermae* to over 23, 675 (Knobloch 1972). The higher incidence of hybrids in perennial plants is associated with the opportunity they have to better preserve their genotype because they do not interfere with their parents for a long period of time (Jones and Luchsinger 1979).

These are in brief the principal advantages of sexual reproduction, which is the most widespread (Young 1981) and provides for a wide range of individual variation (Case and Bender 1981).

THE DISADVANTAGES OF AMPHIMIXIS AND ADVANTAGES OF APOMIXIS

Living matter is belived to have developed at a very high rate mainly in the past 600 million years (Udriste 1978), that is, after the appearance of sexuality. Darwin himself believed that we must accept the existence of a natural law according to which self-fertilization is harmful and cross-fertilization is highly useful. Consequently we might expect the sexual process to improve permanently and offspring to be produced by the fusion of gametes from different parents as an unavoidable result of the action of natural selection. But, it is not so. Hence, although, theoretically, dioic plants should be the most evolved, there are also monoic plants or plants with hermaphroditic flowers — 95% of flowering plants (Borgia and Blick 1981)

and in which apomixis replaces sexual reproduction. What are the causes and how can we explain these phenomena?

No doubt, amphimictic reproduction offers a number of incontestable advantages to living beings. According to the general systems theory, the pooling of information from two or more systems to a single system implies not only that the two information contents add up, but also that they interact, which results in a new quality — a specific information content. Homozygotes are inferior to heterozygotes because they are less flexible and have a narrower reaction amplitude. In as far as this is possible, plants should be dioecious and the individuals very far apart in order to benefit by highly different ecological conditions. This implies that the pollen of an individual reaches the stigma in the flower of another individual. There are countless such cases in nature and even when plants are monoecious or even have hermaphroditic, morpho-anatomical, physiological, biochemical and genetic mechanisms have evolved that prevent self-fertilization and at the same time favour cross-fertilization (Zuberi et al. 1981, Bull 1981, Bernatzki et al. 1988).

Among the developments which selection has picked out and retained with a view to favour allogamy are those with implications for the easy, rapid and sure dissemination of pollen. In many plant species we find pollen whose structure enables it to float on water (*Rupia*, *Valisneria*), to be carried by the wind over large distances (*Quercus*, *Fagus*, *Betula*, *Rumex*, *Plantago*, *Cannabis*, *Urtica*), or to stick to the body of animals, mostly insects, which take it from one flower to another (*Fuchsia*, *Techoma*, *Verbascum*, *Anemone*, *Dianthus*, *Trifolium*, *Melilotus*, *Ononis*). There are many other mechanisms which favour cross-fertilization, such as a stigma that retains and assures rapid germination of pollen, stamen with oscillating anthers which more easily and shed pollen at the slightest breeze, special flower construction which compels insects etc. There are also much subtler morpho-anatomical changes of other plant parts,— great discrepancies between the length and position of stamens and styles (distily — *Primulaceae*, *Oleaceae*, *Plumbaginaceae*, *Rubiaceae*; tristily — *Oxalis*, *Colchicum*, *Lithrum*), the maturing of stamens and pistils at different times etc. One of the subtlest mechanisms that prevents self-pollination and favours cross-fertilization is genetically determined self-sterility (*Nicotiana*, *Cerasus*, *Trifolium* etc.).

Yet, this does not mean that the most specialized sexual reproduction, which implies the pooling of hereditary information from distinct and distant individuals, has no shortcomings which selection has not discovered. This is the reason why, alongside sexual reproduction developed to perfection, the plant kingdom has retained other modes of reproduction, considered “primitive” and fairly recently it has developed asexual mechanisms in some of the highest species of angiosperms.

To cover a certain distance, pollen needs a carrier. When this carrier is missing or disappears, pollination is impaired. On the other hand, the

transport must be as fast as possible, because pollen cannot germinate unless it retains certain biological properties' and the stigma can catch pollen and ensure its germination during a certain period only. If something changes in the normal conditions of environment (temperature, humidity) pollination too is thwarted. These difficulties decrease in the following order: self-fertilization, monoic plants, hermaphrodites, apomicts. Apomictic reproduction predominated in the north, in arid zones etc., while amphimictic reproduction is found in the more southern regions, with a milder climate. In lower plants, where germ cells move exclusively through water drops, asexual reproduction occurs mainly in dry weather (Whittier 1968). Conifers benefit by it in the very harsh climate of Scandinavia (Bergström 1969).

Another drawback of sexual reproduction is the great expenditure of material and energy to guarantee fertilization (Botnariuc 1976). Raò et al. (1978) found that although 90% of the pollen produced in the stamens of *Sorghum* is viable, only 60% can germinate. So, from the onset, over 35% of the material for whose production energy was spent is wasted. This wastage of reproductive material is much smaller, and sometimes even nonexistent, in apomictic reproduction. In the species with alternating sexual and asexual reproduction the cost of meiosis is much smaller than in those multiplying exclusively by sexual reproduction (Charlesworth 1980, Băra and Ghiorgă 1980). A diminution of the reproduction apparatus, to such an extent that plants become true vegetal eunuchs, was recorded in other circumstances too. According to Harper (1977), when density exceeds a certain limit, the development of individual plants and the efficiency of reproduction are greatly impaired.

Plant improvement and selection experts have obtained hybrids of outstanding value in terms of yield, resistance to disease and bad weather, precociousness etc. After a short time a highly valuable hybrid begins to decline and then soon is no better than its parents or becomes even inferior. Why? Meiotic division offers unlimited possibilities of recombination of the genetic material, implicitly resulting in an immense variability of the offspring. Consequently, the succeeding hybrid generations will be highly non-uniform. Panmixis enormously increases the chances that extremely diverse individuals, in terms of value, meet and accordingly expand the range of individual variability.

The deterioration of a population that has undergone selection, or of a hybrid's offspring, may be limited by autogamous reproduction and in particular by apomixis. Stabilizing hybrids by a sexual mechanism is not as reliable and common as by asexual ones (Levin 1979).

Hence, if cross-breeding produces a highly valuable individual, it will be possible to multiply it for a long time, without alterations due to genetic recombinations, exclusively by means of apomixis. This is how the greatest advantage of sexual reproduction — securing the hybrid vigour of the offspring — is annulled due to certain characteristics of this type of

reproduction. What is more, there are authors (Müntzing 1966) who consider that individuals produced by apomixis proved to be more resistant, more vigorous, than those resulting from sexual reproduction.

REPRODUCTION STRATEGIES WITH EVOLUTIONARY VALUE

Everybody agrees that recombinations and mutations are the sources of hereditary variations. Modifications too play an important role in selection, but, because they are not inheritable, they will not be taken into consideration for the moment.

The possibilities of securing individual variability steadily decreases from allogamy to autogamy and to apomixis. Obviously if sex had implied disadvantages, it would have been rapidly lost in the species with sexual and asexual reproduction (Manning and Jenkins 1980). Yet selection "assessed", stabilized and perpetuated all modes of reproduction.

On the other hand, stabilized apomixis is considered to help enhance fitness by fixing and reproducing advantageous genotypes (De Wet and Stalker 1974). A remarkable number of assertions seems to contradict previous opinions. Nyárády (1933), Rousi (1956), Băra and Ghiorghită (1980), Asker (1985) and others noted a marked, and sometimes incredibly great variability in the most diverse species with different mechanisms of asexual reproduction. Without reporting all the data collected on individual variability by the above-mentioned authors and by others for various asexually reproducing plant species, we point out the fact that evolution of a biological process, i.e. individual variability, takes into account only certain aspects of the process, not the process as a whole. For example, not infrequently the apomictic *Ranunculus auricomus* group was earlier considered to be stable. But a thorougher analysis reveals new aspects. A comparative study carried out in populations of this species and of related sexually reproducing species showed individual variability, regardless of the types of reproduction. *R. auricomus*, for example, has a comparatively short flowering period, extending over some 20 days (on a population scale). The related species, *R. repens*, has a very long flowering period, sometimes as long as 4 or 5 months. Even one and the same plant, while shedding some mature nutlets, which fall to the ground and even germinate, forms flowers that are only budding. Hence, there is a comparatively great difference between the June and the September seed, and this will influence the plants of the next generation. To wit, the plants will live in entirely different environmental conditions, they will have to face different pressures of natural selection. The first conclusion that may be drawn is that the offspring of *R. auricomus* are much more uniform than those of *R. repens* in terms of age and competitiveness of the immediate offspring. Proceeding with

the experiment, we found that while in *R. auricomus* the germinating period of nutlets extended over more than a year, in *R. repens* it was much shorter, more uniform.

Hence, offspring of both species emerge over a certain period of time and the various plants live in different conditions of the biotic and abiotic environment which ultimately represents a way of survival, a way of ensuring a certain type of variability. In generalizing, one may ask what can the mechanisms providing for variability in apomictic species be, given the fact that high individual variability has been found in many of them?

Ordinarily, when we say that recombination occurs only in meiosis, we think mainly of the hereditary characters determined by chromosome genes. However, heredity is an attribute of the whole cell, with all its components (mitochondria, plastids etc.). Following the discovery of mitochondrial heterogeneity and of the possibility of their genetic recombination, the view that "mitotic division results in the formation of two identical daughter cells" must be abandoned. The formation of two identical daughter cells, having at least the same mitochondrial composition, from a mother cell is impossible. Consequently, even two individuals produced by mitotic division of a single cell may differ, not to speak of individuals (apomicts, of course) resulting from two cells of different origin. In fact, another error often made when assessing variability is to consider mainly morphological variability and to ignore biochemical, physiological, genetic, behavioral and other forms of variability.

The source of variability in some apomictic species is semiheterotypical meiotic division (Petrov 1964). But other means of securing variability in such species have also been reported. For example, studies carried out on *Ranunculus cassubicus* have demonstrated that embryo sacs were produced both by reduction division and apospory. A similar situation occurs in adventive embryogeny, where one and the same plant carries several offspring, some originating in the embryo sac, others in nucellar cells etc. One can readily see that these individuals are fairly diverse.

Mitosis, which precedes the apomictic appearance of embryos, may often be aberrant and the resulting individuals will differ in the number of chromosomes and, consequently, have other morphological or functional characters, as noted by Skalińska (1959), Müntzing and Müntzing (1943) etc.

Another process which may be responsible for individual variability, and which is not specific to apomicts but may also involve sexually reproducing plants, is modification. It leads to great phenotypical diversity, which is not subject to hereditary transmission. However, because the pressure of selection depends on a number of biotic and abiotic factors, which, in turn, may greatly vary, a modification may very well have great selective value at one time or another. The individual thus escapes from a blind alley, it can perpetuate and contribute to the perpetuation of the species.

By securing individual variability — the initial material on which natural

selection works, asexual reproduction is involved in many ways in the evolution of species. The most important aspect of this involvement will be discussed now.

Many plant species are characterized by facultative apomixis. One and the same species, sometimes even one and the same individual, is capable of amphimictic and apomictic reproduction. The former provides it with a whole range of advantages deriving from recombinations and mutations in the gametes, and all these advantages, including heterosis, are preserved with more chances of persistence through the latter type of reproduction. The opinion is going around that the future of evolution belongs to the species with facultative apomixis, which can combine the advantages of variability offered by the alternation of gametophytic and sporophytic generations, and those of stability offered by sporophyte-sporophyte perpetuation. These species are the pioneers of evolution in the plant kingdom. They conquer new habitats, new ecological niches, for this type of reproduction has great chances of being used in practice.

From Darwin to date, the theory of natural selection has been modified so as to reflect the progress taking place in various fields of biology. Now it is the population, not the individual which is considered the object on which selection acts. The special interest in this topic is reflected by the studies presenting evidence that the rate of evolution increases much when selection acts on regulating and modifying genes (Milkman 1960, Rendel 1967, Wagner 1981), that selection is a feed-back mechanism (Hahlweg 1981) and reduces the number of similar components, while contributing to the specialization of the extant ones (Saunders and Ho 1981).

Amphimixis and apomixis have been subjected to the action of selection, which has maintained, but also constantly improved and diversified them. From our point of view, as humans, the difference between the two types of reproduction consists, for the species concerned, in the ensuring individual variability, the preservation of heterozygotism and vitality, the maintenance of an optimum population size, the achievement of integrality, the provision of material for the production of offspring, the capacity to colonize a new habitat, determining the behavior in constant and changing environmental conditions etc.

To find out why species of a higher organization revert to a type of reproduction in which the alternation of generations is sometimes lost, we must consider the question in the light of systems theory and methods.

Reproduction is a means of ensuring the circulation of information, its transmission from generation to generation, or from individual to individual within the same population or species. In apomixis, population integrity is no doubt preserved (Botnariuc 1976), but genetic information does not circulate between two individuals of opposite sexes and offspring is no longer produced by the pooling of two sets of information.

Individual systems are subsystems of population/species systems. The law of natural selection is specific for systems on this level of organization. Essentially, this is a cybernetic process, implying that the population receives a stimulus, is subjected to pressure from the external biotic and abiotic environment and must respond to that pressure. The system on the next higher level is informed about the nature and magnitude of the response and, by acting once again on the population, "tells" the population if the response was appropriate or not. The population takes note of this "assessment" and responds accordingly. So the entire activity of the population system is self-regulating, of the feed-back type, and it runs in two circuits: environment-phenotype and genotype-phenotype (Hahlweg 1981). The individuals in a population will ultimately be "evaluated" as positive or negative by selection. They will have to bear the consequences of the transmission of information pulses between population and biocenosis/ecosystem.

Individuals must keep two attributes of the information system in equilibrium. They must preserve the information content in a form unaltered in the highest possible degree, and maintain redundancy at an optimum level. These two attributes are closely connected to the process of reproduction. In general, the information content of living systems is well protected from the action of external factors. Nevertheless alterations take place fairly often and reproduction is sensitive to the occurrence of disturbances. The chances for novelties arising and being perpetuated differ greatly between haploids and diploids (Lewis and Wolpert 1979). A novelty in a haploid may cause its disappearance. In diploids, due to allelism, the mutation persists. The subsequent duplication of the chromosomes and genes will lead, through crossing-over, to insertion of the new genes in the old ones in the tandem, and this results in a permanent enrichment of the genome.

In practice, the genetic message is the chromosomes which are protected by the karyolymph, nuclear membrane, cytoplasm, cell wall, organism. When the genetic message is transmitted from one individual to another through germ cells, it may be easily altered. Amphimictic reproduction disregards one of the principles of information theory — preserving unaltered the information content. This drawback was compensated for by redundancy: every individual produces many germ cells. But this leads to excess redundancy and to an additional and sometimes useless expenditure of material and energy. In this respect, Horovits and Beiles (1980) found that plants develop dioicism as a means of making the best use of pollen by rendering some of it redundant and facilitating its abolition in a sector of the population.

Apomictic reproduction does away some of these drawbacks. Alteration of the information content occurs less frequently, diminishes the redundancy and the useless expenditure of matter and energy. Redundancy, however, occurs on another level — that of the population. Asexual reproduction over a long span of time involves the risk of uniformity, of filling the population with an

unlimited number of copies of the same phenotype. A uniform population is useful in a stable and uniform environment. On the other hand, evolution implies first of all non-uniformity. A uniform population would represent a blind alley of evolution. The deadlock is broken by the optimum, cybernetic association of the two aspects implied in the transmission of any set of information: redundancy and the stability of the information content. The most dynamic species are those in which these two aspects successfully complement each other, associating the two types of reproduction: amphimixis and apomixis. They are the facultative apomicts. One and the same individual, depending on the living conditions, produces offspring by sexual or by asexual mechanisms.

If it lives in harsh conditions, it will no doubt derive advantages from asexual reproduction which often enables it to increase its reproduction rate two-fold (Young 1981). If environmental factors remain more or less constant, the pressure of selection diminishes, the species with facultative apomixis are at a great advantage, for their individuals multiply rapidly, have great vigour, are well adapted to habitat conditions, extend quickly, colonize new areas. The fact that this association of sexual and asexual reproduction is found in many young, still non-stabilized, species provides firm evidence that it may initiate new directions of evolution and diversification. Actually, insufficient individual variation is the only disadvantage of asexual reproduction focused on in most specialist opinions. However, this opinion may be disputed because many species with strictly apomictic reproduction display a high polymorphism. Because individual variation need not be very high all the time, and the pressure of selection diminishes in certain conditions, a uniform population has more advantages and lower energy and material expenditures than a highly polymorphous one. The structure of a population at a certain moment is the outcome of the action of selection at the previous moment and, hence, if living conditions remain constant, the individuals adapted to the existing conditions will be favoured even if the pressure of selection does not fall. Therefore, if a population has the same composition in the following generations due to apomixis, it benefits by adaptations.

If the pressure of selection rises again, as a result of changing environmental conditions, a greater variability becomes necessary and the population may resort to amphimixis which provides it with the polymorphism it needs. This cybernetic process, based on feed-back, can ensure the perpetuation and continuous improvement of species.

A graphical representation of the situation analysed so far may take the form of a diagram where the time in which selection works with various intensities is recorded on the Y-axis and the degree of variability of a species ensured by the two types of reproduction, on the X-axis. Obviously the other characteristics that matter for the present analysis (phylogenetic age of the species, individual heterosis, integrality etc.) are assumed to be similar.

Admitting that variability is optimal at the borderline between amphimixis and apomixis (the former ensures a higher than optimum variability, the latter a lower one) facultative apomixis achieves the chances implied in both types of reproduction. When the pressure of selection is enhanced, the environmental conditions being extremely non-uniform in time and space, only part of the individuals will survive (depending on the type of selection: disruptive, stabilizing or directional), usually those produced sexually. In such instances the population resorts to sexual reproduction in order to ensure the required degree of individual variability.

If the pressure of selection decreases, great variability becomes meaningless. Under such conditions, it is much more economical for the population to perpetuate individuals with characters suited to the concrete environmental conditions. In view of its other advantages, asexual reproduction is more useful.

Like every diagram, this one (Fig. 1) too has shortcomings. It cannot represent the phenomenon in its entire complexity, because natural selection implies many more factors, but it shows that this is a feed-back process.

Fig. 1. The dynamics of reproduction-variability correlation under selection pressure

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Rozmnażanie — czynnik ewolucji roślin

Streszczenie

Zjawisko rozmnażania (amfimiksja i apomiksja) jest zasadniczym czynnikiem ewolucji. Fakultatywne gatunki apomiktyczne są pionierami ewolucji. Łączą one korzyści amfimiksji (duży stopień zróżnicowania i heterozji) i apomiksji (stosunkowa stabilność i mało istotny wydatek reprodukcyjny), zapewniając szybką ewolucję przystosowawczą.