Genetic systems: an overview

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Abstract

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This paper stresses the fact that different and contrasting genetic systems have evolved in the flowering plants, it also focuses on some of the main elements that build these systems, particularly the level of ploidy and the various modes of reproduction (cross-pollination, self-pollination and asexual reproduction). Since each genetic system moulds the genetic architecture of populations in a different way, each poses specific demands when the planning of conservation is considered.

The genetic systems which characterize plants and animals are the species-specific ways by which their genetic material is organized and transmitted, particularly the various elements that determine the genetic structure of the populations and the amount and patterns of gene recombination, in other words, the factors that determine the balance between immediate fitness and genetic flexibility in populations. Prominent among the elements that determine the genetic system in any given species is chromosome organization, such as the number of chromosomes, the ploidy level, the amount and the localization of crossing-over, sex chromosomes, etc. Not less important is the mode of reproduction each species has evolved — whether it is sexual or asexual, cross-pollinated or self-pollinated, etc. As already stressed by Darlington (1939), who coined the term, the genetic system in each species determines its capability to undergo evolutionary change. Moreover, genetic systems are themselves under genetic control. Furthermore, they evolve. In each population, and in each species, selection acts to maintain — or to change — the genetic system, just as it acts to maintain or to change morphological or physiological traits.

While most animals are diploid, bisexual and cross-fertilized, this basic genetic system is not universal in the flowering plants. About half of the flowering plants are polyploid, not diploid. Bisexuality (dioecy) is relatively rare in plants, and self-incompatibility, rather than sex determination, is largely responsible for ensuring cross-fertilization in plant species. Not less important is the fact that in numerous plants the basic breeding system of cross-fertilization and panmixis, have been replaced by alternative modes of reproduction — such as self-pollination or apomixis. All in all, in contrast with animals, higher plants represent diverse and contrasting genetic systems. Each system moulds the populations into a specific genetic architecture. Each carries substantial evolutionary weight, and each poses specific demands when the planning of conservation is under consideration.

The following elements of the genetic systems should be of particular concern when one tries to formulate strategies for the conservation of the wild relatives of cultivated plants.

Polyploidy

While animals are overwhelmingly diploid, about half of the flowering plants are polyploid. Several estimates of the frequency of polyploids in plants have been made (for reviews see Stebbins 1971, Grant 1981). Estimates vary, depending on the criteria used by different authors for identification of polyploids. Among angiosperms they fall between 35% and 50%. Very likely the amount of polyploids among the wild progenitors of cultivated plants is also of this order.

As already stressed by Stebbins (1971), the diploid and polyploid chromosomal systems are different in their responses to selection, and in their ability to accumulate and maintain genetic variation. Selection operates more effectively in diploids. In contrast, the polyploid chromosome system is more effective in fusion of genetic variation. Through polyploidy, plants can combine adaptive traits that have evolved in two or even several diploid species. Polyploid species also have a better capacity to absorb — through inter-specific hybridization — alien genetic variation. Furthermore, polyploidy is frequently associated not with adaptive radiation and rapid speciation, but rather with genetic fusion. It often results in the build-up of polyploid complexes comprising of (i) diploid pillars and (ii) a large, inter-connecting polyploid superstructure to which these diploids contributed. Frequently, the polyploid forms in such complexes are widely distributed and successfully colonize disturbed or newly opened habitats; while the diploids are ecologically more specific and are restricted to smaller areas. This is the situation in the cross-pollinated cocksfoot grass *Dactylis glomerata* (see the papers by Lumaret 1997, and by Humphreys 1997, this volume), in alfalfa *Medicago sativa*; in the predominantly self-pollinated wheat group *Triticum-Aegilops*, and in the largely apomictic blackberry *Rubus fruticosus* aggregate. In such wild relatives, the whole polyploid complex ought to be the target for conservation. Often, as shown by Lumaret (1997, this volume), the rarer diploid pillars are endangered. They should be of special concern to the conservationist.

Asexual reproduction

Many plant species reproduce not only sexually but also vegetatively. In fact, in numerous plant groups sexual reproduction is largely replaced by asexual propagation; and their populations consist of vegetative clones. By reproducing asexually such plants can fix superior genotypes by producing numerous identical copies, and exploit the immediate fitness of such vegetative clones. In plants, the evolutionarily most successful mode of vegetative reproduction is apomixis (Gustafsson 1946-1947, Stebbins 1950, Grant 1981), where the shift to asexual reproduction remained associated with seed production. But while in sexually reproducing plants the seed's embryo is formed by fertilization, in the apomicts it develops from a maternal cell. Thus in apomicts, asexual reproduction hitchhikes on long established ways of seed dispersal and on seedling establishment. The seeds (the principal means for dispersal in plants), keep their vital function as propagules, ensuring dissemination. Yet instead of spreading sexual embryos, most seeds produced by apomicts contain exact copies of the genetic constitution of their mother plants.

Because asexual plants evade meiosis and gamete formation, they tolerate chromosome combinations which, in sexually reproducing plants, result in meiotic irregularities and seed sterility and are promptly weeded out. In other words, the shift from sexual reproduction to vegetative propagation is often associated with the build up of unbalanced polyploid or aneuploid chromosome complements. Some apomictic groups contain not only tetraploids and/or hexaploids clones — but also triploid, pentaploid, or aneuploid ones. Such meiotically unbalanced chromosomal types maintain themselves (as distinct clones) by avoiding sexual reproduction.

Most apomictic plants are able to keep genetic flexibility in their populations by retaining some ability for sexual reproduction. In some genera (e.g. *Crepis, Rubus, Crataegus, Poa*) this genetic system has had a considerable evolutionary success; and the adoption of apomixis led to the build up of enormous agamic complexes (Grant 1981), comprising hundreds of morphologically distinct apomictic forms or agamospecies. Again, in conservation of apomicts one has to consider their unique genetic structure (numerous and frequently highly heterzygous clones) and their origin (derived from sexual forms, frequently products of interspecific hybridization and polyploidization). Understanding how a given agamic complex evolved, and knowledge of the distribution and the ecological specificities of its main asexual as well as the sexual forms, is a prerequisite for planning effective conservation.

Relatively few crops are apomicts and/or have apomictic wild relatives. Prominent among them are blackberry *(Rubus fruticosus)* and several of the *Citrus* fruits such as oranges and mandarins.

Self-pollination

Self-pollination (more correctly, almost full self-pollination) is a common breeding system in plants, particularly in annual species.

While populations of cross-pollinated plants are usually characterized by wide genetic polymorphism, considerable heterozygosity and reshuffling of the genes (recombination), in every sexual cycle, selfing brings about drastic reduction of recombination and the splitting of the population into homozygous, true breeding lines. The units of selection in selfers are therefore different from those in cross-pollinated plants. While in outcrossers the genes are recombined in each sexual cycle, and the alleles are selected on base of their individual general preformance, selfing moulds the variation present in the population into homozygous, true breeding gene combinations (genotypes), and structures their genetic variation in tightly kept multilocus gene combinations (see also Pérez de la Vega & García 1997, this volume). Thus, in selfers, the units of selection are not the individual genes but rather the various homozygous genotypes. Competition is between different inbred lines. In populations of selfers, genetic polymorphism is maintained by co-existence of different homozygous lines; and genetic flexibility is maintained by rare crosses between lines, crosses which result in recombination and production of numerous new homozygous combinations.

Self-pollination is a very common breeding system among the wild relatives of grain crops. In fact, the majority of the World's principal cereals and pulses are selfers; and so are their wild progenitors.

Molecular genetic tests performed in stands of predominately self-pollinated wild relatives of cultivated plants such as wild barley *Hordeum spontaneum* (Nevo & al. 1979), wild wheat *Triticum dicoccoides* (Nevo & al. 1982), and wild oats *Avena barbata* and *A. hirtula* (Pérez de la Vega & García 1997, this volume), showed how varied the populations of these wild cereals can be; and how tightly associated are given multilocus genotypes (inbred lines) with definable micro-niches, soil types and climatic conditions.

Safeguarding cross-pollination

While self-pollination and apomixis are rather common in plants, cross-fertilization is the basic and the most widespread breeding system among the angiosperms. Among others, it characterizes practically all the wild relatives of fruit trees and the forest trees. Also many of the ornamentals, several of the vegetables (e.g. cabbage, asparagus) and some of the grain crops (e.g. rye, maize) are cross-pollinated.

In animals, cross-fertilization is brought about mainly by sex determination and sex dimorphism (50% males : 50% females). In plants, sexual dimorphism (dioecy) occurs as well, but only in a small fraction of the species. Instead, most plants have remained hermaphroditic, but evolved a whole battery of devices to prevent selfing and safeguard cross-fertilization, even though their flowers usually contain both anthers and pistils.

In the flowering plants, the most widespread mechanism to assure cross-fertilization is self-incompatibility. Darlington & Mather (1949) estimated that about half of the angiosperms use this genetic device to safeguard cross-fertilization. It is the main mechanism that assures outcrossing in the *Cruciferae, Leguminosae, Rosaceae, Compositae, Liliaceae* and *Gramineae*, i.e. the families that rank among the richest in cultivated plants. Several systems of self-incompatibility have evolved in plants (Nettancourt 1993). Each seems to have originated a relatively long time ago, and each characterizes a large group of plants (a whole family, or even a series of families). The majority of the self-incompatibility systems in plants are governed by a single, multi-allelic, gene-locus (S), and in some families (such as grasses and *Liliaceae*) by two such gene-loci. Rarely one finds systems governed by several self-incompatibility genes. Finally in several groups of plants, self-incompatibility is not poly-allelic but di-allelic; and it is not associated with hermaphroditic flowers but reinforced by floral polymorphism such as distyly or tristyly.

The efficiency of the poly-allelic self-incompatibility systems depends on the number of the S alleles present in the populations. The larger the number of S alleles, the better are the chances that pollination will take place between individuals possessing different self-incompatibility genotypes, and thus result in seed production. In species where self-incompatibility was extensively studied (such as the Rosaceous fruit trees and clovers), dozens of S alleles were detected in the tested populations. For this reason, when conservation of self-incompatible species is planned, maintenance of numerous S alleles in the protected populations has to be a prime goal of the conservationist.

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