Problems of demography in the conservation of wild relatives of cultivated plants

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Abstract

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The importance of the study of demography and population genetic in the conservation of wild relatives of cultivated plants is stressed. The following aspects are analyzed: variation of heterozigosity in small populations; genetic population dynamics and the importance of natural and artificial selection; life form and plant population structure; structuring in plant populations resulting from pollination and seed dispersal mechanisms; breeding systems and polyploidy and thier effects on heterozygosity variation.

The conservation of biological diversity at species level implies the preservation of all the genetic variability relevant to species survival, adaptedness and evolution. Rational conservation requires a knowledge of what populations are like (demography) and of the distribution of genetic variability in and among plant populations (population genetics), two aspects which are intimately interdependent, as it will be further illustrated.

Of the two complementary ways of conserving the diversity of plant species, *in situ* and *ex situ*, many wild and crop species may be conserved *ex situ*, a strategy requiring the collection of samples relevant to most of the genetic variability of a species. For this a knowledge of the genetic structure of species populations is necessary, the main approach being one of population genetics. Demography, however, is sometimes just as important or perhaps even more so, especially for *in situ* conservation, the only available strategy for many, and recommendable for all wild species because of the evolutionary opportunities involved, opportunities which are absent or are totally different in *ex situ* conservation.

Demography can be defined as the statistical study of population growth, especially with reference to the way size, density and life history characteristics govern the expansion or decline of population numbers. In short demography is concerned with population dynamics and with the factors that control population dynamics. But as a geneticist my view on demography is from genetic demography, that is to say, the genetic control of life history factors and the role these factors play in determining the structure of natural populations. How populations expand or decline (demography) and how genetic variability is distributed in and between populations (population genetics) are strongly interdependent so that we can define genetic demography as the integration of both disciplines. It has been argued that too much attention has been paid to genetics in detriment of demography. Brown & Schoen (1992) pointed out that: 'Conservation strategies for individual species populations were based solely on genetic criteria such as the number of individuals needed to avoid inbreeding depression, or the number required to harbor sufficient quantitative genetic variation. to allow future response to selection. However it has been claimed that emphasis on genetics at the population level has led to the relative neglect of basic demography'.

Size, density, spatial distribution and others characteristics are largely determined by quantitative characters such as fecundity, mortality, growth rates, and so on, but as Ritland (1990) has pointed out, the genetic study of quantitative variation in populations from natural environments is rare. Thus most studies of plant genetic demography either involve discrete single-gene characters or electrophoretically marked blocks of genes. Now, DNA markers obtained by restriction fragment length polymorphisms (RFLP) and random amplified polymorphic DNAs (RAPD) have been incorporated into the panoply of genetic markers available (Pérez de la Vega 1993, Thormann & Osborn 1992). In turn, the study of demographic factors such as density, longevity, fecundity, may help in answering questions on the adaptive significance of genetic variation in relation to environments.

In conserving genetic resources of wild species, in particular for *in situ* conservation, some topics are of particular relevance such as population size and distribution. The destruction of natural habitats in Europe, and in many other densely inhabited areas, is endangering many plant species, including most crop relatives, hence the importance of understanding the ecological and evolutionary dynamics of small populations as natural areas become smaller and more fragmented, which would allow us to preserve the *in situ* variability of species and reintroduce them effectively in restored areas.

Small populations

Human activities have disturbed most European habitats in such a way that many species populations have passed through recent bottlenecks or are the result of recolonization events. That fact is of transcendental importance in conservation strategies, both in collecting samples for *ex situ* conservation and in *in situ* conservation, since from the genetics point of view they can be considered small populations. Even if genetic sampling error (genetic drift) has not fixed the population for a particular allele, it decreases allele richness and increases both inbreeding and population differentiation. Populations reduced to a very small size may lose up to 90% of their average heterozygosity, although the loss in allelic diversity may be much greater. Demography is particularly relevant in this case. If most alleles in the initial population are rare, the number of alleles remaining in the population will be most affected by the minimum population size, but if a population remains small over long period of time more common alleles will be lost as consequence of allele frequency random fluctuations (Barret & Husband 1990). Heterozygosity decreases by 1/2N in each generation (where N is the number of breeding individuals in a population) and therefore, after the initial disturbance, inbreeding will be increased significantly only if the population remains small for a number of generations. The rate of increase of the population during the recovery phase (r) will determine the length of time the population remains small following a bottleneck, and consequently, r plays a major role in predicting the further lose of genetic variability during the recovery phase (Nei & al. 1975). This represents an example where demographic factors determine, to a great extent, the genetic effect. Repeated founding events in space or time coupled with drift in small populations have other effects; differentiation among population is increased, and this fact is of major significance in sample collection and in *in situ* conservation.

Another critical relationship between demography and small population genetics is the effective population size. In populations, N is rarely equal to the effective size, N_e, which is the appropriate parameter for finite population model calculations. Factors such as gene flow over long distances, sub-structure within populations, non-random mating, variable population size, etc., affect the disparity between N_e and the real census of individuals (Heywood 1986). Unfortunately there are few studies in which N_e and N have been compared in plant populations.

The inheritance of demographic factors with clear ecological significance is not well understood. Although, there are examples of quantitative characters under relatively simple control, most life history traits are probably under complex polygenic control. If the genetic variance of polygenic traits is due to additive allele effects, it should decrease in proportion to $1/2\ N_e$ after a bottleneck of effective size N_e; but if the variance is at least partly due to epistatic and/or dominant effects, the genetic variance will not change following a simple relationship with N (Lande 1980, Barret & Husband 1990).

In small populations the effect of genetic drift on genetic variability can be compensated by genetic flow (migration) in a ratio proportional to 4Nm (where m is the migration rate). Single migration events can have a great influence in maintaining variability in small populations; although, in natural conditions, migration from neighbouring populations is a repetitive process which occurs in a non-regular way in time and space. This fact introduces a great deal of uncertainty in predicting gene flow effects in nature. The impact of gene flow during recolonization depends on whether the migrants founding new populations are from the seed bank of the same population, from the closest population or from several populations with different gene frequencies. This points out the importance of a buffered life strategy where natural seed bank composition and survival compensate for population catastrophes. According to Barret & Husband (1990), under certain circumstances, in populations experiencing frequent colonization and extinction, an increase in the frequency of colonization increases the genetic diversity within populations. It is also possible that interpopulation migration plays a larger role than drift in colonization dynamics. Unfortunately, as stated by Barret and Husband, migration between populations is one of the least tractable problems of population genetics.

To sum up, although the theory of finite populations is well developed, it remains for the experimental geneticist and ecologist to determine the importance of demographic factors and the significance of the theory itself for natural plant populations.

Finally, it is worth mentioning Lande's (1988) list of fundamental demographic factors that determine the survival of small populations:

(1) Populations declining below a given number of individuals, or a threshold density, can lose viability so that recovery becomes impossible (the ALLEE effect). This could be of special importance to open-pollinating species, particularly if self-incompatibility systems are involved. Low density and/or the reduction in the number of incompatibility alleles can reduce fertility to levels endangering population survival (Fig. 1). Quoting Lande 'Theory and empirical examples suggest that demography is usually of more immediate importance than population genetics in determining the minimum viable sizes of wild populations'.

(2) Stochastic demography. Individuals of a given age or stage of development have differential rates of survival and reproduction, being affected similarly by environmental factors. This is particularly relevant for populations of perennial species if cohorts are too young or too old for their optimal rate of reproduction.

(3) The edge effect. The importance of this effect lies in the progressive isolation of habitats which become surrounded by unsuitable ecological areas that hinder genetic flow and seed dispersal.

(4) Extinction and colonization. They are determined by fluctuating environments which can make some habitat patches temporarily unsuitable, thus rendering populations extinct. Patches sooner or later again become colonizable, a fact exploited by some opportunistic annual species, so that widely distributed populations persist through a balance between local extinction and colonization.

Population dynamics: selection

Population dynamics from a genetical point of view is the study of the dynamics of allele and genotype frequencies. These frequencies are in turn controlled by the interaction among the different forces acting on populations (mutation, migration, selection, genetic drift) and also by the breeding system. If the breeding system is known and if it can be assumed that all the forces moulding population except selection have negligible effects on genotypic frequencies, then the fitness of genotypes can be estimated from data at the same stage of life cycle in successive generations or at different stages of life cycle. These techniques, which integrate genetics and demography, have been widely applied in both predominantly self-pollinating and predominantly outcrossing species (see review by Ennos 1990). Directional changes in populations are mainly attributed to selection. When selection acts to favour the same genotypes, it can contribute to a decrease in genetic variability, but if it acts differentially in different life cycle stages or seasons or if it opposes the effects of other forces such as inbreeding it can maintain a high degree of polymorphism in populations. To summarize the results obtained from the application of these techniques I would like to quote Ennos (1990): "We can say that the application of demographic genetic analysis (for both inbreeding and outcrossing species) has proved a powerful technique for detecting and measuring selection in plant populations. It has demonstrated that relative fitness is not constant for any particular genotype, but can vary with the life cycle stage, season, and frequency of the genotype in the population. The approach, however, has limitations. In inbreeding populations where selection has often been detected, differences in fitness cannot readily be ascribed to the effects of particular gene loci because of the correlated multilocus structure of the genome".

Genetic variability and its distribution within a plant species is also affected by the history of the species in question. In crop species, two kinds of evolutionary histories can be distinguished: natural history and human-directed evolution.

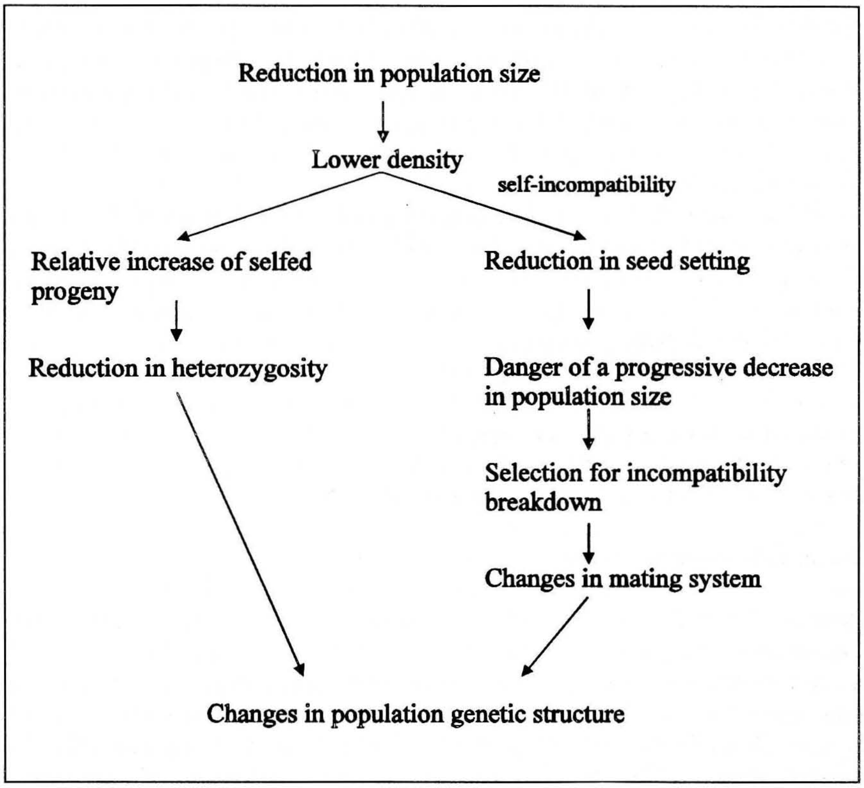

Fig. 1. Relationships between the reduction in population size and changes in the population genetic structure, in open-pollinated species with and without self-incompatibility systems. In species with self-incompatibility systems the reduction in population size can lead to a loss of incompatibility alleles.

Domestication and cultivation imply selective directional changes, seed exchanges, new introductions, adaptation to new environments and so on, many being unknown and unpredictable. In both types of evolution, populations have occasionally passed through bottlenecks. But, while wild populations passes through bottlenecks that are most probably due to accidental reductions of population size, cultivated forms are most probably subjected to founder effect and bottlenecks caused by selection.

Selection reduces the number of lineages in populations, thereby reducing the effective population size. Many crop species have obviously been subjected to strong artificial selection, which, in many cases of horticultural plants, has probably been carried out on relatively small populations. The combination of selection and small effective population size is probably the cause of both the relatively low level of genetic variability in some of these species and the differentiation between populations, as is the case of the morphological diversity among populations of horticultural and ornamental plant species. Miller & Tanksley (1990) reported a good example of low level of genetic variability within accessions and high differentiation among accessions in the cultivated tomato, pointing out that the lower diversity of modern cultivars may reflect breeding methods, often single-seed descent or pedigree selection, together with the genetic bottleneck undergone during their introduction to Europe. Although 'European' species have not suffered such a drastic colonization process, horticultural and ornamental species have been subjected to similar breeding methods, so a low level of variability and high differentiation are to be expected, particularly among inbreeding and asexually reproducing species.

Most of the population genetics selection models are based on the assumption of discrete non-overlapping generations. This demographic rule does not apply in many plant species. It has been proposed (Ellner & Hairston 1994) that temporally fluctuating selection can indeed contribute significantly to the maintenance of genetic variation when the effects of overlapping generations and age-specific or stage-specific selection are considered.

Life form and plant population structure

Another important aspect of genetic demography is the relationships between life form, growth strategies, reproductive system, etc., and the genetic structure of plant populations. Hamrick & Godt (1990) summarized the information obtained from isozymatic data in 449 plant species representing 165 genera. For the purposes of this paper, perhaps the main conclusions of this review are that: 1) at the species level the geographic range is the best predictor of levels of genetic variation (genetic diversity increases as the geographical range of distribution expands), 2) at the population level two traits, geographic range and breeding system, are the best predictors of genetic variation, and 3) predominantly clonal species can maintain as much genetic variability within populations as sexually reproducing species. Life form is important in the distribution of variation within populations – genetic diversity (H_e) is significantly higher in long-lived woody species than in annual and short-lived herbaceous perennials. Diversity among populations (G_{st}) is higher in annual species and in short-lived perennials. Among the five life form categories (annual, short-lived perennial, either herbaceous or woody, and long-lived perennial, herbaceous or woody) woody perennials have G_{st} values that are 3 to 4 times lower than annual or herbaceous species. Seed dispersal is also relatively important in the distribution of variability within populations. Those species with short distance dispersal mechanisms (gravity or explosive dispersal) maintain lower allozyme variation than species with long distance dispersals (wind or animals).

Structuring in plant populations

Spatial and temporal structuring in plant populations reduces the effective size of populations. Structuring arises when pollination is limited, at least partially, to neighbouring plants or to plants coinciding in flowering time, therefore increasing inbreeding in open-pollinating species and reducing the probability of cross-pollination in predominantly self-pollinating species. Furthermore genetic structuring is increased by the spatial structuring of family or kin groups that arises when seeds are dispersed a short distance from the parent plants and in some species with multiseeded fruits. In these species many neighbouring plant are related by a common lineage. The situation is still more complicated in long-lived perennials, with mother plants living together with progenies that originated in different years, and in which low density can result in yearly progenies from crosses among the same neighbouring plants; or in which a gradual germination from the seed bank mixes together different generations of a lineage. Furthermore, the breeding system interacts with spatial processes, such as pollination and propagule dispersal, to shape the spatial pattern of genetic variability (Clegg & al. 1992), and in turn ecological and demographic factors, such as population density, can significantly influence levels of inbreeding in species with mixed-mating systems, that is species in which seeds are partially produced by self-pollination and partially by cross-pollination (Karron & al. 1995, Vaquero & al. 1989). Again, a better knowledge of demographic data on longevity, seed bank recruitment, seed dispersal, successional stages, and so on, will produce a better understanding of plant population genetics and resource conservation.

Breeding system

Two topics should be mentioned because of their importance in plant life strategies and evolutionary potential. These are the method of reproduction, or breeding system, and polyploidy.

When dealing with plant species, it is necessary to consider these two important evolutionary characteristics: the diverse methods of reproduction (sexual, outcrossing or selfing, apomictic, vegetative) and polyploidy. Polyploid species are often more widely adapted and successful in colonizing and forming dense stands than their diploid relatives.

The reproductive system exerts a major influence on the recombinationpotential of a species and therefore on its genetic structure. Effective recombination requires two premises: sexual reproduction and heterozygosity. Clonal modes of reproduction, and some apomictic ones may therefore generate higher-order genetic structures in populations by keeping genotypes unchanged, although clonal species may maintain a higher level of variability within populations. Inbreeding reduces the population frequency of heterozygotes, which entails a great reduction of effective recombination and a sharp increase in allelic disequilibria in self-pollinating species. The allelic disequilibria in turn imply that selection at any given locus is likely to affect much of the genome, generating non-random multilocus structures with multiple epistatic interactions. As a final consequence, the genetic structure of populations of inbreeders is characterized by one, or more generally, by several multilocus associations which increase adaptation to a local environment. There are some good examples of the relationships between multilocus structure and adaptation in annual grass species such as oats, barley, wheats, etc. (for references see Pérez de la Vega & García 1997, this volume). Locally adapted genotypes also occur in clonal plants, although they are more likely to evolve in species with a repeated seedling recruitment (RSR) strategy than in species with a initial seedling recruitment (ISR) one. In ISR species the genets which eventually become established are generally those derived from a cohort that colonized a new area early on, while in RSR species genets are recruited continuously and populations are formed by a mixture of genets cohorts. In RSR species high fecundity and high seed dispersal ability are expected to be of selective importance while in IRS ones to be a successful genet is more a question of chance – a question of recruitment at a good site at the right time (Eriksson 1993).

Table 1. Examples of homoallelic and heteroallelic genotypes in tetraploid and hexaploid inbreeding plant species.

Genotype		Chromosomes		
		Homoeologous		
	Homologous	Homologous	Homologous	Equivalent to the diploid genotype:
Homoallelic	11	11	--	11
	22	22	--	22
	11	11	11	11
Heteroallelic	11	22	--	12
	22	11	--	12
	11	22	11	12*
	22	11	22	12*
	11	22	33	123*

* These genotypes do not have real equivalent in diploid species since allelic combinations and ratios 112, 122, and 123 are not possible.

The combination of polyploidy with self pollination or asexual reproduction leads to new genetic potentials. Plants in these polyploid species may be homoallelic (the same allele present in homologous and homoeologous chromosomes) or heteroallelic (different alleles at each pair), which makes heteroallelic plants equivalent to heterozygotes (Table 1), but with the difference that the heteroallelic stage is not affected by recombination or segregation. The success of polyploids has often been attributed to heterosis associated with the ability to breed true for a highly heterozygous or heteroallelic state. It is worth noting, however, that homoallelic genotypes are often the best adapted (García & al. 1991).

Both, the reproductive system and polyploidy have played crucial roles in plant domestication since most of the early plant species to be domesticated were self-pollinating species (Zohary & Hopf 1993). Furthermore, the shift from an open-pollinating breeding system to a facultative self-pollinating one and/or to vegetative propagation have occurred and succeeded during domestication of several plant species; sometimes this change was accompanied by polyploidy (Zohary 1997, this volume).

I should like to conclude with a last reflection on genetics and demography. Brown & Schoen (1992) wondered if considerations of demography should replace those of population genetics in conservation planning. They pointed out that 'plant population genetic structure is so rich and varied among species that it cannot be ignored in any long-term conservation planning. Indeed for many plant species, particularly inbreeders, it may well be the dominant consideration'. In my opinion population genetic structure and demography are so interrelated that conservation of plant biodiversity has to rely on both, that is to say, on genetic demography.

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