Some lessons drawn from twelve years of dynamic management of winter wheat populations (*Triticum aestivum* L.) in France

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Abstract

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Since the 1960's, genetic conservation of major crops has been based mainly on static *ex situ* conservation. Whatever their efficiency, genebanks cannot solve the problem of the 'evolutionary freezing' of stored genetic resources. This paper presents one answer, based on the conservation of artificial genetically heterogeneous populations. Some results are presented on the adaptation of populations and the conservation of genetic variability obtained in a pilot programme of dynamic conservation of genetic resources of wheat. Although this experiment concerns a cultivated species, lessons are drawn that could be of interest for conservation experiments on wild species.

Introduction

Over the last thirty years, large collections of the genetic resources of major cereals (rice, wheat and maize), including wild relatives, have been assembled. Nearly all of these collections are maintained in the form of seed samples, kept in cold storage, in genebanks, e.g. those managed by the International Agricultural Research Centres (IARCs).

The main question now appears to be not so much how to increase these collections as how better to preserve and use them. It is true that gene banks play a crucial role in the conservation of genetic resources but their efficiency is hampered by a number of obstacles:

- cost and methodological problems (identical regeneration of samples) arising from the mere fact of maintaining these huge collections (more than 72 000 accessions of cultivated and wild wheat are conserved in Mexico at CIMMYT, Centro International de Mejoramento de Maíz y Trigo, IPGRI 1993)
- the difficulty of assessing these genetic resources, and the fact that the assessment is imperfect and necessarily piecemeal –which limits their use.
- the isolation of all the varieties in storage from their environment. Whereas genetic resources are protected in cold storage rooms or freezers, parasites evolve and the climate may change. These resources cease to be subjected to the selection pressures which made them adapt to their environment.

The first two obstacles could be removed with appropriate funding, but more money would not suffice to remove the third, which calls for measures which complement gene banks. It is in this spirit that, in France, a pilot programme for the dynamic management of the genetic resources of winter wheat (*Triticum aestivum* L.) was set up. This programme began to operate in 1984 and consists in allowing composite wheat populations to evolve in different environments (Henry & al. 1991).

Although the programme only concerns a cultivated species, it now seems possible to draw information from it for use in experiments in the conservation of other species. We shall briefly describe the methods used in this dynamic management experiment and then go on to list the main findings and their implications.

Experimental protocol

The aim of the dynamic conservation experiment is both to maintain the initial level of genetic variability and to let the populations evolve under the effect of natural selection pressures in order to benefit of their adaptation to the environments. A way to achieve this (Henry & al. 1991) is to organize a metapopulation by splitting an initial population into several local populations and assigning gene flow between them. This allows the combination of mechanisms of natural selection, which act differently in each environment, and gene flowbetween local populations, which can locally renew the genetic variability. Diversity is expected to decrease under selection and genetic drift in each local population, but if the environments are different, the total amount of variability is expected to be maintained.

Three initial populations with a broad genetic basis (named PA, PB and PS) were created by the French National Agronomical Research Institute (INRA). They were based on 16 parental lines in the case of populations PA and PB (Fig. 1) and 50 in the case of the PS population. PA and PB were subject to *T. aestivum*'s natural self-fertilising reproductive system. PS was forced to outbreed by means of the introduction of a recessive male sterility nuclear gene: male-sterile and male-fertile plants grow side-by-side but only the former, pollinated by the latter, are harvested. Dwarf genes were found in all three populations.

In 1984, a batch from each initial population was sent to all 13 points of a multi-site network comprising INRA stations and agricultural high schools and universities throughout France (Fig. 2). Since then each local population has been cultivated each year using seeds harvested at the same place the previous year, without any conscious selection.

Parental line	**Genealogy**	**Cytoplasm**
C45-6-3	Artois/2-6-11//2-6-11/A18	*aest.*
C3275-1-2	FAO(61)69/US(67)136	*aest*
DC^2-30	*A. ventricosa/T.dicoccum* // Nainari 60/3/2 Capelle	*vent*
Mironovskaïa 808	Sélection Artemovka (CEI)	*aest*
Clément	Hope/Timstein/3xHeinesVII/Riebesel57-41 /2xHeinesVII/4/Cleo (Netherland)	*aest*
C61-5-6-2	US(60)43/Prieur	*aest*
Top	TF354/Capelle	*aest*
V1 7-5-PV-5-3	(VPM x Capelle)	*vent*
Rivoli	Reso/Champlein	*aest*
C1-6-5	Martonvasari/2-6-11 (Courtot sib-line)	*aest*
Kavkaz	Lutescens314 H147/Bezotayal (CEI)	*aest*
TJB636	?	*aest*
D48	Martin/K3/Hohenheimer/3/Oro/4/Etoile de Choisy/5/Capelle	*aest*
Oxley	Penjamo 62/4 x Gabos 56//TPP/Nainari 60 /4/Lerma Rojo//Norin 10/Brevor/4/3 x Andes (Australia)	*aest*
Loros29	Loros/3/Capitole/VPM/Moisson	*aest*
Weihenstephan 1007/53	Heines Bart/Rye 4X//? x T. aestivum (Germany)	*aest*

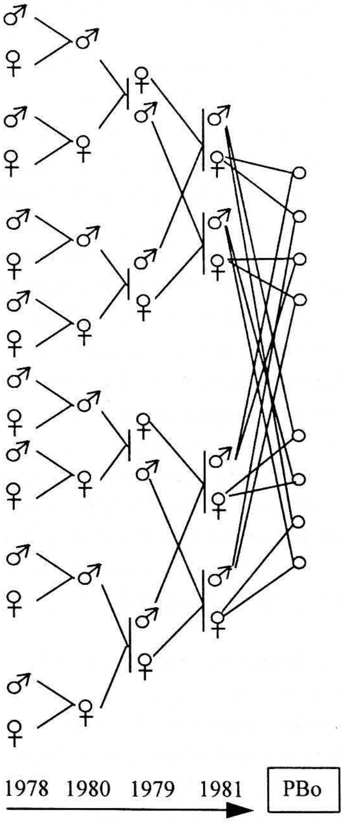

Fig. 1. Crossing and multiplication design of the population PB.

The studies conducted as part of this programme for the dynamic management of genetic resources have so far been designed to highlight the differentiation between the local populations and the initial population. Local populations have been compared during controlled trials, after 6 cycles of cultivation.

Results

After 6 years of cultivation, numerous changes have been observed; their origin is mainly to be sought in the following three selection pressures: (i) pedological and climatic factors, (ii) competition within populations, (iii) pathogenic agents. There are numerous arguments against the hypothesis of genetic drift effects alone. We shall give some examples of these changes; more detailed findings are published in the quoted reference works:

(1) A North-South precocity gradient established itself for the self-fertilising (selfing) populations PA and PB (David & al. 1992). The populations bred in the South became

genetically more precocious than their Northern counterparts. In our opinion this was due to an adaptation to climatic constraints, such as the risk of water shortages in the south.

(2) The size of plants increased in all self-fertilising (selfing) populations (Pontis 1992, David & al. 1992). This increase in size may be interpreted as the result of competition for light within a given local population. This competition results in ever faster evolution since the presence in the polymorphic state of dwarf genes (Pontis 1992) leads to considerable genetic size variations.

(3) Fertile pollen production increased in the male-fertile plants of the PS cross-fertilising (outbreeding) populations in comparison with those in the initial population (David & Pham 1993). Once again we think that this increase results from competition between male-fertile plants for the pollination of male-sterile plants, since the reproductive value of the former depends exclusively on fertilising the latter and, hence, on the quantity of fertile pollen produced.

(4) The most recent results (Le Boulc'h & al. 1994, Le Boulc'h 1994) show that, depending on the breeding site and probably the local pathogenic pressures, there has been an evolution in the populations' mildew resistance. In PS cross-fertilising (outbreeding) populations, new combinations of genes for resistance seem to lie behind increased resistance in the field.

Despite or because of these changes, the diversity of situations to be found across the network has, except in the case of genes which are ill-adapted to inter-individual competition (dwarf genes), maintained overall variability, as detected by means of biochemical markers and features submitted to natural selection alike, since differentiation between populations compensates for the loss of variability in certain local populations (David 1992, Pontis 1992).

Discussion

What lessons can be drawn from twelve years of dynamic management of wheat populations? Do they have consequences for the conservation of wild relatives ? Our purpose is not to say that wild species should be conserved through artificial populations. The manipulation, in numerous ways, of crop species is probably more recognized than is the case with wild species, as the former are in any case seen as the fruit of human activity. For wild species, 'classical' *in situ* conservation, that addresses diversity at the ecological, specific and infraspecific level, is less disturbing for many people, being in agreement with their perception of the natural environment. However, many examples could be cited, where wild relative species are not 'conserved' but used and sometimes managed by humans. In Mexico, a special area was created to protect populations of a wild relative of maize, *Zea diploperennis*. It was shown, however, that this species needs a human-made environment to survive (Benz & al. 1991).

Therefore it seems to us that one of the forms of management of wild species populations might lend itself to experimentation on wheat. This is particularly true in the case of species that are related to cultivated species which are endangered *in situ* because

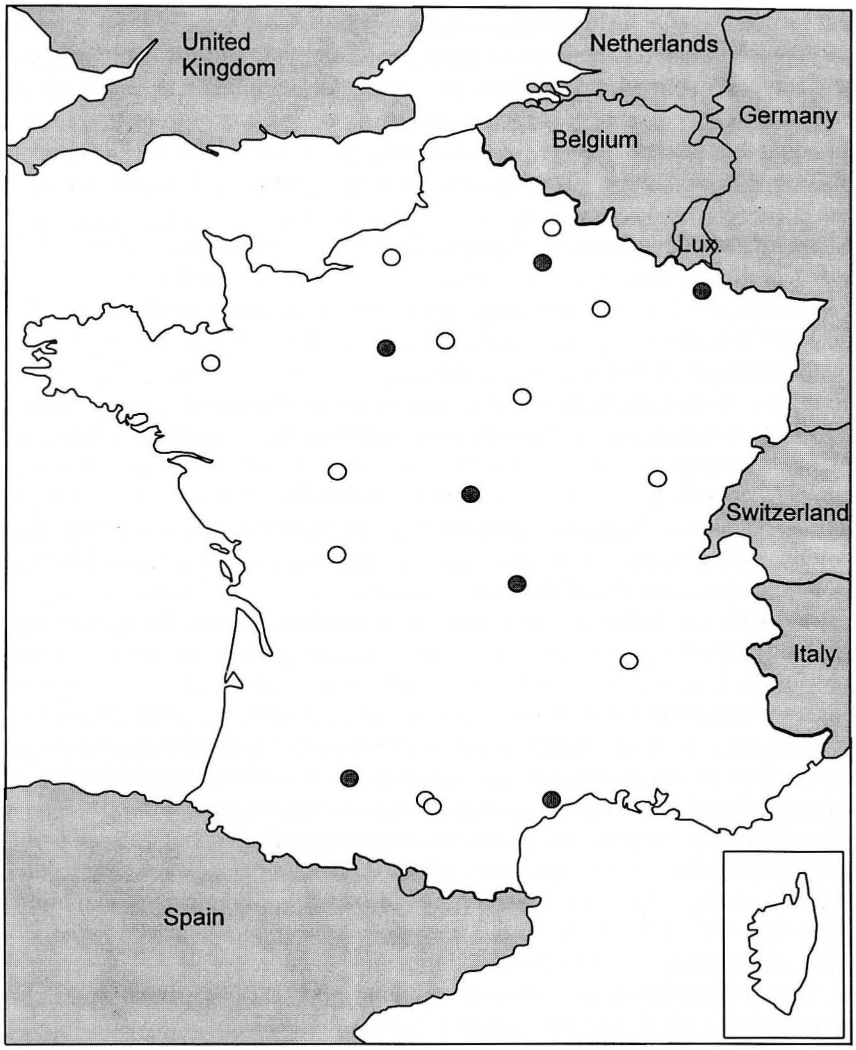

Fig. 2. Geographic distribution of cultivation sites of the pilot experiment of dynamic management of genetic diversity in winter wheat.

Since 1984 and from identical samples of initial mixtures, populations are evolving under natural selection pressures. One to six populations are present in each site according to mixture (1 to 3 : PA, PB and PS) and according to cultivation mode (intensive or extensive). The intensive cultivation mode corresponds to usual commercial conditions of the site (i.e. high inputs of fertilizers, fungicides) while the extensive cultivation mode only receives 1/3 of the nitrogen amount of the intensive type and no fungicide. Until now, local populations have been recreateded each year with seeds of the previous harvest coming from their site and have been cultivated under the same procedures. With the implementation of new sites in 1996 (solid circlesl), gene flow will be established between populations according different procedures while some populations in primary sites (empty circles) remain isolated.

of a threat to their ecological niches. It might be possible, in the case of some species, to bring together the desired genetic diversity in pools, and then to distribute and maintain it in specific types of environment. This is actually an extended approach of artificial recolonization. The advantages of such experiments include: (a) they allow genetic recombination between accessions of varied origins and (b) they facilitate continuous visual assessment. Both these advantages can be appreciable if crop improvement is also a concern.

The first lesson of our experiment of management of artificial populations of wheat is indeed that such experiments can be done. The reliability of the breeding network was crucial on this score. It is of prime importance that the network should be a lasting one, since, just as a cold storage room is built to last for decades, this type of action, whose low costs should be an asset, is intended to be a long-term one.

It seems to us to be very positive that genetic resources should have been brought down from their ivory towers (gene banks and national institutions) and be handled in agriculture colleges by those who are probably their future users. In 1996, other agricultural schools will join the network, providing us with the opportunity of new experiments (Fig. 2). Vaughan & Chang (1992) also proposed to involve schools in genetic resources conservation of rice. In the case of wild species, botanical conservatories could double up as network sites as could educational establishments.

The speed with which differentiation took place is another remarkable point since it was observed after only six generations. This shows that population conservation may have other objectives than just maintaining the initial situation and that all selection sources, including those mentioned above, will have to be taken into account. In particular the geographic factor was extremely important in differentiating populations in terms of cycle duration. This is of importance for the experiments of artificial recolonization of wild species that are necessary when the habitat of a species has disappeared.

The fact that wheat populations grow taller is a nuisance in the case of this crop. For the first time this year, after eight years of breeding, the tallest plants were eliminated before flowering. Selection by man may therefore prove necessary if an aspect of evolution seems to be undesirable diversity. This would, for example, be the case if populations of wild species lost characters relating to dispersal in time or space.

Since some (albeit few) experiments to preserve populations of wild species are now being proposed, the wheat pilot programme indicates that managing populations is feasible and stresses that natural selection pressures can rapidly make the genetic diversity evolve. These results argue for the necessity for a balanced network of multiplication sites covering all the ecogeographic conditions of the species' distribution areas. They also point out that 'panglossian ' vision of natural situation must be carefully interpreted: natural situation (even without human perturbation) does not mean optimal situation for the preservation of the species or its genetic diversity. This also means that conservation cannot be a passive process: on the contrary it is an active management process.

Other phenomenous have also to be considered, such as the inbreeding depression increase in small populations resulting from bottleneck events (Hauser & al. 1994, van Noordwijk 1994). A solution to the reduction of viability induced by the loss of local polymorphism for outbreeding species could be to manage gene flows between populations. Such experiments are now starting in France: LIFE Program for managing populations of *Brassica insularis, Rouya polygona* and *Centaurea corymbosa.*

Theoretical considerations about migration and gene flow are numerous but experimental results are few. As the theoretical model underlying the wheat experiment is a model of a metapopulation where genetic interchange takes place between local subpopulations, gene flow will be implemented in 1996, through seed or pollen exchanges between populations. We hope that this will allow a better assessment of the risks of a real dynamic management of populations. Actually if gene flow can permit the maintainance of versatile abilities, favour new evolution and also make up for the loss of a local population, it could also have negative effects on the level of genetic diversity and further reinforce the extinction risk.

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