Farmers' practices and the consequences for the genetic conservation of clonally-propagated RT crops. The case of yam

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Abstract

A growing number of evidences suggest that clonally-propagated RT crops are not maintained in strictly asexual reproduction system. Studies on yam, cassava, potato and taro show or suggest that farmers use the sexual reproduction of the cultivated species and sometime of the wild relative species. The consequences of this mixed reproductive system on the evolution and the adaptive potential of the plants are important. Indeed, the maintenance of sexual reproduction allows the creation of new diversity and thus maintains the adaptation potential while the use of asexual multiplication allows the maintenance of the best genotypes. The consequences for conservation, however, strongly depend on farmers' practices and management.

Here, we review results obtained on yam (*Dioscorea* sp.), a clonally-propagated RT crop mainly cultivated in West Africa. Results showed that farmers introduce the products of hybridization between wild and cultivated yams into the cultivated pool. Moreover, varieties consist in only one genotype and some closely-related genotyped differing by some mutations instead of a mix of different genotypes originated from sexual events. The consequences of these results on the conservation and use of wild and cultivated yams are discussed.

Keywords; Farmers' practices, conservation, diversity, clonally-propagated crops, yam.

Introduction

Among root and tuber crops, the main species (cassava, yam, taro, potatoes) are cultivated in traditional tropical agrosystems by clonal propagation. In such crops, opportunities for sexual recombination are greatly reduced, since propagation by farmers does not require seed production. Indeed, many clonally-propagated crops show disruption of flowering and fruiting mechanisms as well as unbalanced chromosomal arrangements (Zohary 2004). Consequently, it is often believed that the evolution of clonally-propagated crops occurs in the absence of sexuality and is thus slowed down because selection can act only on few new genotypes created by mutations (Hurst and Peck 1996; Barton and Charlesworth 1998).

However, this general belief in the lack of sexuality of clonally-propagated crops lacks evidence. On the contrary, flowers and seeds can frequently be found in the field (potatoes, Johns and Keen 1986; cassava, Elias *et al.* 2000, 2001; yam, Sadik and Okere 1975). Moreover, RT crops have been cultivated for thousand of years and present a high genetic diversity incompatible with purely asexual reproduction (Zhang *et al.* 1998; Birmeta *et al.* 2002; Lakhanpaul *et al.* 2003; Sardos *et al.* 2008). It has recently been shown that traditional farmers' practices actively use this residual sexuality (Elias *et al.* 2000, 2001; Scarcelli *et al.* 2006a, b). Depending of the plants, farmers collect seeds (potatoes, Johns and Keen 1986) or select plants spontaneously growing in the wild (yam, Dumont and Vernier 2000; taro, Sardos *et al.* 2008) or in the field (cassava, Elias *et al.* 2000). The new plant is then introduced in an existing variety or is given a new name. The consequences of this mixed reproductive system on the genetic diversity of clonally-propagated crops are not well known but they will depend on the way sexuality is used by farmers and will then be different for each plant.

Here we review recent results about the role of sexuality in yam (*Dioscorea* sp.) genetic diversity and structure. First we will look at the evidences that farmers use the sexuality of wild and cultivated yams, then we will look at

the role of sexuality and mutation in the genetic diversity observed in yam varieties. Finally we will discuss the consequences for the use and conservation of yam genetic resources.

The use of yam sexuality by farmers

The traditional practice of ennoblement

Yam farmers never collect seeds nor use seeds to grow a new plant. However, several sociological studies have documented a practice named 'ennoblement' (ex. Dumont 1998, Baco 2000, Dumont and Vernier 2000, Okry 2000, Houemassou Bossa 2001, Tostain *et al.* 2003, Vernier *et al.* 2003). Farmers collect tubers of wild yams and plant them in their fields. They select tubers for their likeness to cultivated varieties, e.g. in northern Benin, they look for plants with large green stems, with large tubers and white flesh and without spines. According to farmers, some of these plants develop — after 3-6 years of special cultivation practices — a tuber that is morphologically close to those of cultivated varieties. The tubers are then multiplied and cultivated if farmers are satisfied with their morphology. The biological processes underlying the change in tuber morphology and its maintenance over generations are unknown.

Genetic evidences

Using AFLP and microsatellites, Scarcelli *et al.* (2006a, b) gave the first evidence that farmers actually collect wild and hybrid yams (Figure 1a). Hybrid yams result from spontaneous hybridizations of wild (*D. abyssinica* and *D. pra*eh*ensilis*) and cultivated yam (*D. rotundata*). These studies also showed that a part of the plants selected by farmers is not wild or hybrid but has a cultivated genotype. Those plants can have two distinct origins: volunteers, i.e. a fragment of tuber forgotten in a field and that managed to survive when the field became a fallow; or progenies of cultivated varieties, i.e. new recombinant genotypes. It was impossible to discriminate between the two origins.

As a result of this selection of new genotypes by farmers, studies found wild and hybrid genotypes within the cultivated varieties (Figure 1b). This means that through the practice of ennoblement, farmers cultivate new genotypes created by the sexual reproduction of wild and cultivated yam.

The genetic struture of cultivated yam

Previous results and limitations

The genetic structure of cultivated yam has never been fully understood, mostly because of technical limitations. Several studies used morphological and genetic markers to analyse the genetic diversity within yam varieties (ex. Hamon *et al.* 1986, Dansi *et al.* 1999, 2000a, 2000b). Results varied among varieties and studies but most of them showed intra-variety diversity. These results, however, were not obtained on varieties, but on 'cultivar groups' – each group corresponding to a mix of varieties with similar morphology. Those cultivar groups were created in order to organize the huge morphological diversity but they cluster together distinct varieties. As a result, an analysis on cultivar group may overestimate the genetic diversity because the analysis was not done on the actual intra-variety diversity. Moreover, the genetic markers available at that time were not appropriate because they were not polymorphic enough (isozymes) or because they were not reproducible enough (RAPDs).

New data on the role of mutation and sexual reproduction

In an attempt to clarify the genetic structure of cultivated yams, Scarcelli *et al.* (submitted) used microsatellite to analyze the genetic diversity of few varieties. This study was done in only one village in Benin and only one ethnic group in order to be sure that the name given to a variety by different farmers corresponds to the same plant. However, because of the limited scale of the study, results may no be extrapolated to different regions.

Results revealed intra-variety diversity. An analysis of the relationship between the genotypes found in each variety showed that the intra-variety diversity is the result of mutations while each variety is a result of sexual reproduction. In this part of Benin, a variety can thus be considered as a product of sexual reproduction that has evolved by mutations. This result suggests that product of sexual reproduction introduced by the ennoblement practice are mostly given a new name rather than introduced in an existing variety. This result also suggests that farmers' management are able to avoid mixing between varieties.

Implications for genetic conservation and improvement

The concept of variety

Varieties are usually considered as an entry point to the genetic diversity and its conservation. In Guyana, cassava seeds spontaneously germinate when a new field is opened. Farmers select plants and introduce them in the morphologically closest variety or create a new variety if the phenotype is distinct enough (Elias *et al.* 2000, 20001). This suggests that within-variety diversity should be high, in term of mutants as well as product of sexual reproduction, and is in accordance with the founding of Jarvis *et al.* (2008). In this system, focusing on varieties only will not be enough as intra-variety diversity may be lost by drift. This conclusion however may be different for other RT crops. Results presented here suggest that focusing on varieties is a good way to preserve yam diversity.

Taking farmers into account

As it was shown or suggested by different studies, several RT crops have a mixed reproductive system (Johns and Keen 1986, Sardos *et al.* 2008, Elias *et al.* 2000 and 2001, Scarcelli *et al.* 2006a, b). This use of sexuality in asexually propagated crops has some evolutionary consequences. Indeed, farmers combine the advantages of both sexuality and asexuality. By testing and selecting new combinations created by sexuality, farmers maintain the potential for future adaptation, and, at the same time, they preserve their best genotypes from recombination by using asexual reproduction. This suggests that traditional practices associated to the use of sexuality should be preserved in order to preserve the adaptive potential of clonally-propagated RT crops.

In the specific case of yam, results suggest that the use of wild yam diversity through the ennoblement practice should be maintained in order to maintain the genetic diversity of cultivated yams. Thus, the *on-farm* conservation of cultivated yams should address both the *in-situ* conservation of wild yam diversity and the conservation of traditional knowledge and farmers' practices.

What can be learnt for genetic improvement?

Yam improvement is not an easy task, particularly because of the difficulty to master flowering and crossing. Until today, few improved varieties have been produced and even fewer have been widely accepted by farmers. Wild yams have been mostly neglected in these programs and their potential has never been tested. The recent studies showed that farmers use this potential by selecting and cultivating F1 hybrids between wild and cultivated yams. They suggest that improvement programs can beneficiate from studying the agronomical properties of spontaneous hybrids, as well as from introducing those hybrids in the selection schemes.



Figure 1. Principal component analysis (PCA) of the genetic diversity of wild and cultivated yams. \blacksquare = wild yam *D. abyssinica*; \blacktriangle = wild yam *D. praehensilis*; \bigcirc = cultivated yam *D. rotundata*. Genotypes were assessed at 11 microsatellite loci. (A) Plotting of spontaneous yams (+) selected and tested by farmers through ennoblement. A part of the spontaneous yams clusters with *D. abyssinica*, *D. praehensilis* or *D. rotundata*. The other spontaneous yams are intermediate between the wild and the cultivated species. (B) Plotting of cultivated yams (\bigcirc) showing a wild or an intermediate genotype. The assignation of each sample to one of the three species has been tested by assignment tests (Scarcelli *et al* 2006b). Moreover, hybrid origins of intermediate genotypes have been tested by assignment tests and the existence of spontaneous hybridizations has been tested by paternity tests (Scarcelli *et al*. 2006b).

Adapted from Scarcelli et al. 2008.



Figure 2. NJ-Tree representing the relationships between genotypes found in different yam varieties. Genotypes were assessed at 13 microsatellite loci. Bootstrap values are given in percentage. Each genotype is represented by a circle. The colour(s) of the circle indicate the presence of the genotype in one or more varieties. Fourteen different genotypes were found. In most of the cases, a genotype is associated with only one of the six varieties. For a given variety, different genotypes could be observed, however these genotypes cluster together in the NJ-tree. According to allele frequencies and mutation rate, the slight differences between genotype inside each cluster were interpreted as the product of few mutations appearing during the clonal propagation phase while the different clusters were interpreted as products of sexual reproduction (Scarcelli et al. submitted). As the 6 clusters correspond to the 6 varieties, it can be considered that these yam varieties correspond to different products of sexual reproduction that have evolve by mutation.

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