

## Crop wild relative conservation: Wild yams are not that wild



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### ABSTRACT

Extension of land use has been the main way to increase agricultural production to date. Natural habitats have consequently decreased and became increasingly fragmented, putting high pressure on the wild relatives of main crops. In this study, we assessed the diversity of wild relatives and cultivated varieties of yam, *Dioscorea rotundata*, a tuber crop grown in West Africa. Using nuclear markers, we showed that 19% of the wild plants were in fact hybrids between wild and cultivated varieties. Using whole chloroplast sequences, our results suggest that hybridization may be even stronger, with 43% of the wild individuals presenting either chloroplast or nuclear introgression with the cultivated yams. Adaptation of agriculture to current new pathogen outbreaks and ongoing climatic changes will require mining the vast diversity found in crops wild relatives. However, our study suggests that wild yam diversity is already largely tainted by crop-to-wild gene flow. The need to focus on in-situ wild yam conservation is even more crucial, since today, ex-situ genebanks contain nearly no wild yam accessions.

**Data profile:** Microsatellite allele scoring is available as an online appendix; NGS data (.bam file) are available as SRA bioproject PRJNA383673.

### 1. Introduction

Crop wild relatives play a key role in agriculture. They have been widely used in modern breeding to improve important agronomic traits. In their review, Hajjar and Hodgkin (2007) showed that wild relatives have been intensively exploited for pest and disease resistance, to such an extent that nearly all disease resistance genes of tomato are derived from one of its wild relatives. Wild species have also been used although to a lesser extent as a source of abiotic stress resistance (e.g. salt-tolerant sunflower), to increase yield (e.g. hybrid tomato) and improve quality (e.g. higher quality grain in some wheat varieties). Wild-to-crop gene flow has also been exploited by farmers in traditional agriculture, for example in maize, rice, pearl millet or sorghum (Jarvis and Hodgkin, 1999). This is especially true for vegetatively propagated crops, where inter-specific hybrid seeds are used to eliminate diseases, create new varieties, and introduce new diversity in existing varieties (e.g. potato, yam, Jarvis and Hodgkin, 1999, Scarcelli et al., 2006). The importance and usefulness of crop wild relatives is internationally recognized and considerable effort has been invested in their conservation (Meilleur and Hodgkin, 2004; Heywood et al., 2007). However, there is still a significant absence of crop wild relatives in ex-situ collections (Castaneda-Alvarez et al., 2016) even though they are

expected to be particularly threatened by global changes (Ford-Lloyd et al., 2011). Indeed, over the last 400 years, more than half of our natural habitats have been converted into cropland and rangeland (Foley et al., 2011; Ellis et al., 2010), resulting in the destruction or fragmentation of wild plant habitats. Climate change is expected to further reduce areas that are suitable for wild plants (Jarvis et al., 2008). Tropical regions have seen a significant proportion of their wild habitat destroyed (Foley et al., 2011). These regions were also the cradle of domestication for many crops including cereals of worldwide importance (e.g. maize, rice) and root and tuber crops (e.g. cassava, potato and yam) (Harlan, 1992).

If crop wild relatives are threatened by the destruction of wild habitats, the extension of agriculture also creates increased opportunities for gene flow from cultivated to wild populations. Generally, crop-to-wild gene flow is common across species as long as wild and cultivated relatives occur in sympatry. In their review, Ellstrand et al. (1999) showed that most of the important crops (wheat, rice, maize, soybean, barley, cotton, sorghum, millet, beans, rapeseeds, sunflower and sugar cane) were able to hybridize with their wild relatives in at least some parts of their cultivation area. More importantly, in most cases the hybrids were fertile, which opens the possibility of introgression. According to a recent survey, post-zygotic barriers must accumu-

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late over long divergence times (hundreds of thousands to millions of generations) before complete hybrid sterility occurs (Levin, 2012). Thus, unless hybridization is strongly prevented by pre-zygotic barriers, most crops are likely to interbreed successfully with their wild relatives. Both theoretical modeling and genetic studies suggest that hybridization can lead to the extinction of a wild species when invader or domesticated species are introduced (for a review see Haygood et al., 2003 and Todesco et al., 2016). The two main processes involved are genetic swamping (also known as genetic assimilation) and demographic swamping. Genetic swamping arises when hybrids are more fertile than their wild parents. In this case, they may overwhelm the wild population and contribute to the replacement of wild genes by cultivated ones. Demographic swamping occurs when hybrids are less fertile than the wild population. In this case, the wild population may shrink. In their literature survey of living populations, Todesco et al. (2016) showed that the risk of genetic swamping is more frequently reported than the risk of demographic swamping. With their mathematical models, Haygood et al. (2003) also showed that genetic swamping necessarily occurs when crop-to-wild gene flows are recurrent and that demographic swamping can amplify this effect. Examples of genetic swamping due to crop-to-wild gene flow have already been reported. In California, wild radishes are no longer strictly wild but are inter-specific hybrids between the cultivated species *Raphanus sativus* and the wild species *R. raphanistrum* (Hegde et al., 2006). Similarly, high contamination rates of wild rice *Oryza* spp. by cultivated rice *O. sativa* have been observed in China, Taiwan and Thailand (Kiang et al., 1979; Akimoto et al., 1999; Song et al., 2006).

If, as shown by these examples, the risk of contamination of wild relatives is real, it has not yet been studied in many species, mainly under-studied crops. In this study, we investigated the impact of crop-to-wild gene flow between yam and its wild relatives.

Yam, *Dioscorea rotundata*, is a native African species mainly cultivated for its tuber across West Africa, especially in the Yam Belt (Nigeria, Benin, Togo, Ghana and Ivory Coast). Its two close wild relatives are *D. abyssinica*, a savannah species, and *D. praehensilis*, a forest species (Terauchi et al., 1992; Ramser et al., 1997). The three species are diploids (Scarcelli et al., 2005). Previous studies based on nuclear markers showed that the three species are genetically distinct (Ramser et al., 1997; Scarcelli et al., 2006). It was suggested that yam domestication occurred at the forest/savannah ecotone, presumably in Nigeria, along the river Niger valley (Coursey, 1976; Hahn, 1995). In the Yam Belt, cultivated lands represent 69% of the total surface, among which yam cultivation accounts for 6% (FAOSTAT, 2014). Yam

is cultivated in the distribution range of its wild relatives (Fig. 1a). Yam fields are small (< 2 ha) and shifted to new places every year after clearing savannah or old fallow, creating sympatry between wild and cultivated plants (Baco, 2000; Dumont et al., 2005). The three species are dioecious and hybridize spontaneously (Zoundjehkpon et al., 1994; Scarcelli et al., 2006). Yam is a vegetatively propagated crop, i.e. no seeds are used by farmers and only tubers are used to plant a field. Therefore, wild-to-crop gene flow is limited and involves selection by farmers and recruitment of wild or hybrid tubers growing outside the field (Vernier et al., 2003; Scarcelli et al., 2006; Chair et al., 2010). Yam cultivation is associated with slash and burn agriculture. Land is cleared after a few years of cultivation and then natural vegetation is allowed to recolonize the land. Consequently, hybrid seeds grow in secondary forests or savannahs. Two types of crop-to-wild gene flow is thus possible: (i) pollination of a wild female by a cultivated male and (ii) recruitment of seeds obtained by the pollination of a cultivated female by a wild male. The diversity of *D. abyssinica* and *D. praehensilis* has been investigated mostly through their relationships with *D. rotundata* (e.g. Mignouna et al., 2003; Scarcelli et al., 2006). Efforts have mainly been aimed at understanding the genetic diversity and structure of cultivated yams at the national level (e.g. Tamiru et al., 2007; Obidiegwu et al., 2009). Even though gene flow has been detected between wild and cultivated yams (Scarcelli et al., 2006), no comprehensive studies have been conducted to understand the impact of gene flow on wild yam diversity. To assess this process, we used both biparental markers (nuclear microsatellites) and uni-parental markers (chloroplast single nucleotide polymorphisms, SNPs) to analyze the genetic diversity and the relationships between cultivated yam and its wild relatives.

## 2. Materials and methods

### 2.1. Plant materials, genotyping and sequencing

In this study, we analyzed 35 cultivated individuals (*D. rotundata*), 34 wild individuals of *D. abyssinica* and 31 wild individuals of *D. praehensilis*. All the individuals were sampled in Benin, West Africa (Fig. 1b and Online Appendix A1), in remote areas where, at that time, yam was mainly cultivated for self-consumption. Part of the individuals was previously genotyped (Scarcelli et al., 2006; Mariac et al., 2014; Scarcelli et al., 2016). Total DNA was extracted from dried leaves as previously described (Scarcelli et al., 2006). Nuclear diversity was revealed using 12 nuclear microsatellites (Da1D08, Da1F08, Da3G04,

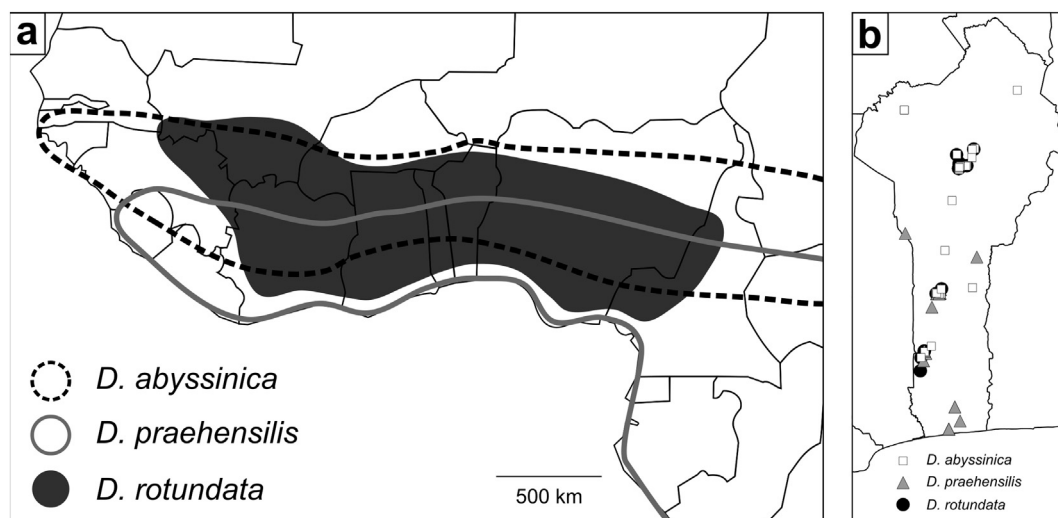


Fig. 1. Yam distribution in West Africa (a) and sampling in Benin (b). Wild yam *D. abyssinica* grows in northern savannahs while wild yam *D. praehensilis* grows in southern forests. *D. rotundata* is mainly cultivated from Ivory Coast to Nigeria, in sympatry with wild yams.

(a) Adapted from Dumont et al. (2005) and Hamon et al. (1995).

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