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CIRAD

The Agricultural Research Centre for International Development, CIRAD, is a French agricultural research centre working for development in developing countries and the French overseas regions. Most of its research is conducted in partnership.
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International Plant Genetic Resources Institute, IPGRI, is an international research institute with a mandate to advance the conservation and use of genetic diversity for the well-being of present and future generations. It is a Centre of the Consultative Group on International Agricultural Research (CGIAR). Founded in 1974
IPGRI has a staff of about 300, in 22 offices around the world. Its budget in 2004 was US$35 million.

Tribute

This book is dedicated to the memory of I.H. Burkill († 1965), D.G. Coursey († 1983) and J. Miège († 1993), our illustrious predecessors in the world of Dioscoreaceae. Their observational and intuitional talents generated the basic knowledge required to study African yams, thus paving the way to a fascinating and disconcerting plant kingdom that never ceases to stimulate scientific curiosity.

One major concern of these three botanists was to gain insight into the origin of *Dioscorea rotundata* yams. The wild parents were identified presumptively but the technical sequences leading to their cropping remained unexplained. The results of several recent studies now provide sufficiently solid arguments for the re-examination of these questions. Various interpretations and hypotheses put forward in this book are still open to debate and require further research.

This in-depth study was undertaken by French-speaking scientists, but the bibliographical references highlight the substantial contribution of the English scientific literature. The generally high quality input of African researchers on both sides of the linguistic divide has also been considerable.

Contents

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Foreword

The domestication of wild yams is still common practice in West Africa. This phenomenon offers one of the few remaining opportunities to gain insight into how farmers use their empirical knowledge to tap the genetic resources of wild plants and create products suitable for agriculture. Strangely enough, until recently, yam agronomists and breeders have not focused much attention on, or have completely ignored, this agricultural biodiversity generating and organizing process.

The present book aims to fill the gap by pooling existing knowledge on the subject. The prospects for scientific progress in this original field are considerable, at a time when scientists are becoming aware of the potential for technical progress and adaptation to environmental change based on farmers' knowledge and practices relating to genetic resource management.

It deliberately deals only with domestication leading to *Dioscorea rotundata* yams, which by far represent the most widely cultivated type in West Africa and throughout the world. However, the taxonomy and botanical identity of this yam and its wild parents must be clarified before domestication is discussed. A large initial section of this book is therefore devoted to the biodiversity of *D. rotundata* yams and the wild forms from which they derive.

The opening chapter defines and characterizes *D. rotundata* yams in terms of their phyletic relations with the *D. cayenensis* species and also on the basis of botanical, agronomic, technical and genetic criteria.

The following chapter focuses on *D. abyssinica* and *D. praehensilis*, i.e. wild yams used by 'domesticator' farmers to create *D. rotundata* yams. It highlights their relations with different ecosystems and their diversity, differences and similarities.

The final chapter of this first section presents and discusses different phenomena that could modify the variability of these wild yams and make them suitable for domestication.

Domestication is examined in detail only after addressing these different topics. Chapter 5 analyzes the significance and practical importance of the domestication process, while Chapter 6 discusses techniques used by farmers to obtain *D. rotundata* yams from yams collected in the wild.

The book concludes with various hypotheses to explain the phenotype transformations that take place as a result of domestication practices and their maintenance by vegetative propagation. Further studies are needed to assess these hypotheses, which are potential research topics for geneticists. Some are already being verified by combined teams of researchers from the North and South using the most recent molecular marker techniques.

Introduction

According to a study by IFPRI (Washington International Food Policy Research Institute; Scott *et al*., 2000), sub-Saharan Africa accounts for nearly 96% of the world's yam production, while production in Africa increased by 183% between 1983 and 1996. Virtually all of this African output is confined to West Africa, with *Dioscorea rotundata* representing nearly 90% of all yams cropped in this region. The only exception is Côte d'Ivoire, where *D. alata* accounts for over 70% of all yam produced (Doumbia, 1998), even though 75% of the domestic trade involves *D. rotundata* yams (Touré *et al*., 2003).

Yams were adapted to monocropping by societies belonging to what Miège (1952) called the 'civilization of the yam'. This adaptation occurred in savannah areas that had probably replaced a more wooded environment, as suggested by the presence of residual areas of mesophyll forest. Aubréville (in Schnell, 1971) put forward the idea that initially forested regions were converted to savannah as a result of human activities.

Scientists studying yam domestication were soon struck by the cultural importance of this crop. This topic has been discussed by several authors, including Coursey (1976), Seignobos (1992), Assogba (1993) and Allomasso (2001), who traced this trend back to the remote past of West African societies.

Societies belonging to the civilization of the yam are settled and well structured. *D. rotundata* can ensure a community's food needs throughout the year when all of its resources are tapped. Several West African ethnic groups have taken full advantage of these resources. For many reasons, others use only early-maturing cultivars, e.g. to bridge the gap between cereal harvests, because local climatic conditions are unfavorable for late-maturing cultivars, or because these late yams are scarce, low-yielding and thus unable to compete with *D. alata* yams (Côte d'Ivoire).

In 1939, Burkill was convinced that *D. rotundata* was the result of the domestication by African farmers of yams they found growing wild. However, this hypothesis was not scientifically confirmed until the end of the 20th century, when very powerful tools (enzymatic and molecular markers, flow cytometry) were used to reveal genetic relationships between *D. rotundata* and wild yams. Further insight was also acquired on traditional yam domestication methods. Firstly, on the basis of the findings of a survey

of 150 farms in two regions of northern Benin (Dumont and Vernier, 1997a) and more piecemeal information obtained in other African countries. Relevant information was subsequently obtained in five in-depth studies conducted in Benin (Baco, 2000; Okry, 2000; Adoukonou, 2001; Allomasso, 2001; Mignouna and Dansi, 2002). Surveys in Nigeria (Vernier *et al*., 2003) also indicated that yam domestication techniques used in several regions of the country were similar to those implemented in Benin. Lastly, Hildebrand (2003), in a study undertaken in southwestern Ethiopia, reported on a local form of domestication involving several wild yams with numerous similarities to the practices used in West Africa.

We felt that the time was now ripe to pool all available knowledge on the domestication of African yams from a substantial number of publications, unpublished and even unprocessed experimental results and, most importantly, field observations. Much of this information concerns Benin and Côte d'Ivoire but some was also collected in Guinea, Togo, Burkina Faso, Nigeria and Cameroon. The present review therefore covers most of West Africa in varying degrees, while extending into Central and East Africa on a number of occasions.

We venture beyond the scientifically proven results in our discussion and advance many hypotheses, some of which are based on very recent theories that have considerably broadened the scope of yam genetics. The future will judge the merits of the viewpoints proposed.

The technical terms are defined in a glossary at the end of the book.

The *Dioscorea rotundata* Poir. yam

Botanical aspects

There has long been considerable confusion regarding the yams *Dioscorea rotundata* Poir. and *D. cayenensis* Lam. In English-speaking West Africa, particularly Nigeria, they are known as 'white yam' and 'yellow yam', respectively, and pooled under the term 'Guinea yam'. Farmers in French-speaking Africa, on the other hand, do not make a clear distinction between *D. rotundata* and *D. cayenensis*, whereas a generic name is used for all other cultivated yams (*D. alata, D. bulbifera, D. dumetorum, D. esculenta*)—although the latter are not regarded as 'true yams' by many ethnic groups (figure 1). The diagnoses of Lamarck (1792) and Poiret (1813) proved to be too inaccurate to separate *D. cayenensis* and *D. rotundata* (in Miège and Lyonga, 1982). Finally, Miège still regarded *D. rotundata* as a subspecies of *D. cayenensis* in the 1968 edition of his *Flora of West Tropical Africa*. This botanical status, first assigned to *D. rotundata* by Grisebach in 1854, was endorsed by Prain and Burkill in 1919 and Chevalier in 1936 (in Coursey, 1976). Because of this confused situation, the concept of a *D. cayenensis-D. rotundata* species complex was proposed at the 1978 Seminar on Yams in Cameroon, funded by the IFS (International Foundation for Science, Stockholm, Sweden). This concept was then defended by Hamon (1987) as a way of "pooling all West African cultivated yams that are not bulbiferous and have entire leaves under the same name".

D. cayenensis and *D. rotundata* are yams domesticated from wild Dioscoreaceae of the Enantiophyllum Uline section that have speciated in Africa. They differ with respect to various botanical and genetic traits but have never been definitively separated. It is thus essential to present *D. cayenensis* before investigating *D. rotundata*.

D. cayenensis stricto sensu (Poiret definition) is found in West and Central Africa. In West Africa it coexists with *D. rotundata* but is not widely cropped, whereas virtually all yams cropped in Central Africa (mainly forested areas) are *D. cayenensis* and *D. alata*, but *D. rotundata* is generally not grown. *D. cayenensis* has numerous vernacular names because of its extremely wide geographical distribution range: Yaobadou for

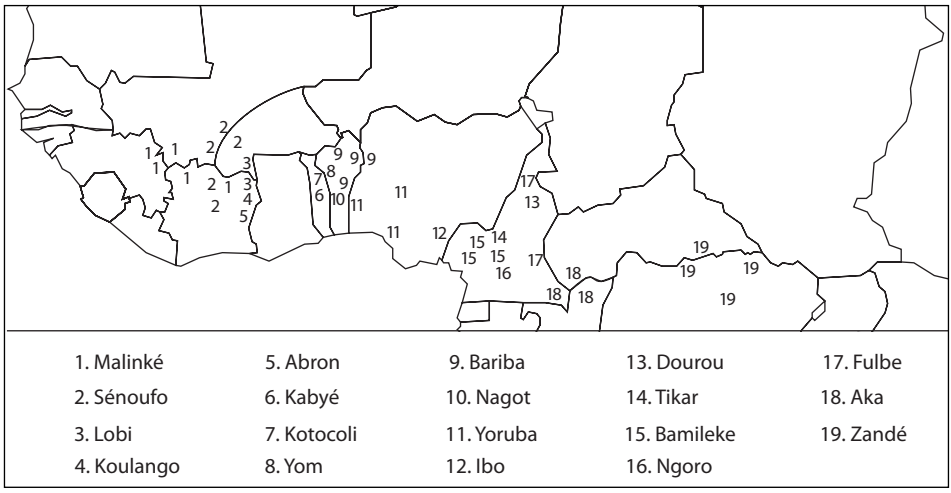

Figure 1. Geographical distribution of the ethnic groups mentioned in this book.

the Baoulé of Côte d'Ivoire (Hamon, 1987), Banoussé, Alakissa (Ikéni) and Kanlin for the Bariba, Nago and Adja peoples of Benin (Dansi *et al*., 1999a), Ji oku and Ishu kpukpa for the Ibo and the Yoruba of Nigeria (Orkwor, personal communication), Mbip and Ekoto for the Dourou and the Bamileke of Cameroon (Dumont *et al*., 1994; Mignouna *et al*., 2002a) and Ako for the Teke-speaking peoples of Central Africa (N'Kounkou, 1993). This list is obviously far from exhaustive.

Several scientific studies and various observations have now been focused on the phyletic relations between *D. cayenensis* and other African yams of the Enantiophyllum section, including *D. rotundata*, but the situation remains unclear. It can be summarized as follows.

Terauchi *et al*. (1992), Ramser *et al*. (1997) and Chaïr *et al*. (2005) reported that *D. cayenensis* and *D. rotundata* bear the same chloroplast DNA (which would make them the same species), differing from that borne by *D. burkilliana*. Moreover, Terauchi *et al*. (1992) presented *D. cayenensis* as an interspecific hybrid on the basis of its nuclear ribosomal DNA characteristics. The female parent might be *D. rotundata*, *D. praehensilis* Benth, *D. liebrechtsiana* De Wild or *D. abyssinica* Hochst ex Kunth, which are all characterized by annual replacement of the vegetative organs and tuber. The male partner would be *D. burkilliana*, *D. minutiflora* Engl. or *D. smilacifolia* De Wild, which have a perennial base plate.

Some results of enzymatic or molecular marker analysis of total DNA point in the same direction as the ideas depicted above, while others diverge. Mignouna *et al*. (2002a) and Mignouna and Dansi (2002) distinguished between *D. cayenensis* and *D. rotundata* but did not divide them into separate species. Hamon (1987) suggested that *D. cayenensis* might be the product of interspecific hybridization but stressed the likely involvement of *D. burkilliana*. Other authors claimed that *D. cayenensis* is phyletically very close to or a domesticated form of *D. burkilliana* (Akoroda and Chheda, 1983; Onyilagha and Lowe, 1985;