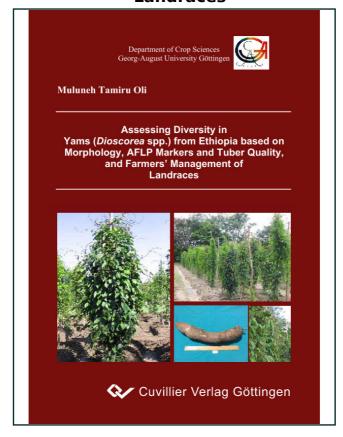


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Assessing Diversity in Yams (Dioscorea spp.) from Ethiopia based on Morphology, AFLP Markers and Tuber Quality, and Farmers' Management of Landraces



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1. General Introduction

1.1. Yam: origin and distribution

Yam belongs to the genus *Dioscorea* in the family Dioscoreaceae. The family is believed to be among the earliest angiosperms and probably originated in Southeast Asia (Coursey 1976). The various *Dioscorea* species apparently followed a divergent evolutionary course in three continents separated by the formation of the Atlantic Ocean and desiccation of the Middle East (Hahn 1995). Accordingly, the major food species originated in three isolated centers: Africa, Southeast Asia and South America (Alexander and Coursey 1969). These centers are also considered areas for independent yam domestication, and represent considerable diversity (Asiedu et al. 1997).

The economically most important yam species include *D. alata*, *D. rotundata* and *D. cayenensis*. *D. alata* originated in Southeast Asia, more specifically in tropical Myanmar and Thailand (Orkwor 1998), and is currently the most diversified and extensively distributed species. The spread of Asiatic yams, mainly that of *D. alata* and *D. esculenta*, took place more than 2000 years ago, reaching Africa around 1000 AD (Coursey 1967). *D. alata* was, then, introduced into tropical America from West Africa around the 16th century by Portuguese and Spanish travelers (Onwueme and Charles 1994).

The species *D. rotundata* and *D. cayenensis* are native to West Africa (Coursey 1976). Of the two, *D. rotundata* is currently the leading species in terms of total area of production worldwide. It is extensively cultivated in West Africa, the West Indies and, to some extent, in East Africa. The introduction of the African species into tropical America is believed to have taken place as early as the 16th century (Coursey 1967). Lamarck gave the first description of *D. cayenensis* in 1792 based on a specimen from French Guiana (and hence the name Cayenne), whereas *D. rotundata* was described in 1813 by Poiret based on a sample from Puerto Rico long before their African origin was established (Hamon et al. 2001). These species, however, had limited eastward movement reaching only as far as East Africa. There is little or no cultivation of the African species in Asia (Onwueme and Charles 1994).

D. bulbifera, characterized mainly by the production of bulbils (aerial tubers), is native to both Asia and Africa, where wild forms still exist (Onwueme and Charles 1994). There are, however, appreciable differences between the two continental forms (Alexander and Coursey 1969; Terauchi et al. 1991). The cush-cush yam (D. trifida) is the only yam of Tropical American origin to have attained significance as a food crop, but its production is currently restricted to the West Indies (Brücher 1989; Onwueme and Charles 1994). Other yam species of minor economic importance in several tropical regions include D. dumetorum, D. opposita, D. japonica, D. hispida and D. transversa (Asiedu et al. 1997).

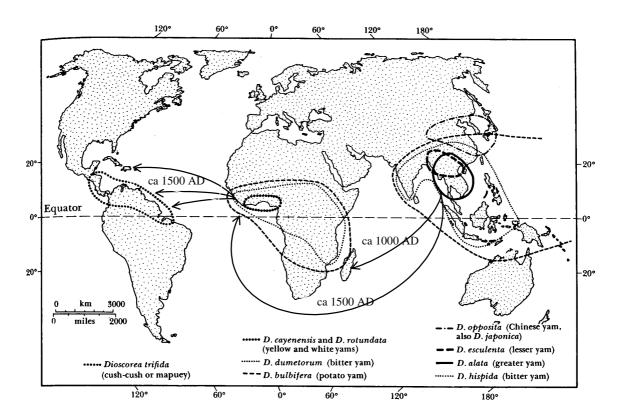


Figure 1.1. Approximate areas of origin and times of distribution of the major cultivated yam species (adopted from Coursey 1967; Harris 1972).

1.2. Taxonomy and important features of *Dioscorea*

The family Dioscoreaceae is generally classified under the monocotyledons. However, some features in yams such as the presence of a second non-emergent cotyledon and reticulate-veining of the leaves are typical of certain dicotyledonous plants (Purseglove 1972). This has led to the suggestion that the genus *Dioscorea* might have been

derived from plant forms that occurred before the differentiation of monocots and dicots (Degras 1993). Currently, the major *Dioscorea* species are widely distributed in the tropics and sub-tropics although a few species of minor economic importance are found in the warmer regions of the temperate zone (Coursey 1967). About 600 species have been described under the genus *Dioscorea*, making it the largest genus of the family Dioscoreaceae (Alexander and Coursey 1969). However, only few assume importance as crop plants. The genus is subdivided into sections, under which the various species are classified.

The section Enantiophyllum is the largest in terms of number of species, and includes the most important species of *D. alata*, *D. rotundata* and *D cayenensis*. Other members of this section are *D. opposita*, *D. japonica* and *D. transversa* (Asiedu et al. 1997). Vines that twine to the right, i.e. in clockwise direction when viewed from the ground upwards, characterize members of section Enantiophyllum. On the other hand, vines twining to the left distinguish species in sections Lasiophyton (*D. dumetorum* and *D. hispida*), Opsophyton (*D. bulbifera*), Combilium (*D. esculenta*) and Macrogynodium (*D. trifida*) (Onwueme and Charles 1994) (Table 1.1).

Despite the significant progress made over the last couple of decades in understanding the origin, domestication, phylogeny and diversity of the common food yams, their taxonomy remains complicated. For instance, some authors treat the major African species (*D. rotundata* and *D. cayenensis*) as separate (Burkill 1960; Akoroda and Chheda 1983), while others consider them as belonging to the same species (Martin and Rhodes 1978) or a species complex (Ayensu and Coursey 1972). Phylogenic studies based on RFLP¹ markers in chloroplast and nuclear ribosomal DNA¹ indicated common ancestry of the two species, with some evidence suggesting *D. rotundata* as the maternal parent of *D. cayenensis* (Terauchi et al. 1992). More recent findings based on isozyme and molecular markers, however, seem to support the separate identity of the two species (Ramser et al. 1997; Dansi et al. 2000a; Mignouna et al. 2005).

It appears that the process of yam domestication was marked with significant evolutionary changes. Under cultivation, yam is commonly propagated vegetatively by

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¹All abbreviations and acronyms are listed on page -VIII- following list of figures.

the use of either small whole tubers (seed yams) or pieces of large tubers (setts). Sexual reproduction is extremely irregular in cultivated species, the flowering behavior ranging from no flowering to monoecious or dioecious plants, depending on the species and cultivar (Bai and Ekanayake 1998). Even in flowering species or cultivars, seed production is a rare event due to a high degree of flower and ovule abortion (Onwueme 1984).

Yams² also exhibit considerable inter and intraspecific variations in ploidy level, which ranges from 2× to 16× based on basic chromosome numbers of either nine or ten (Table 1.1.). For example, three ploidy levels (4×, 6×, 8×) were determined in accessions of *D. rotundata-D. cayenensis* complex from Cameroon (Dansi et al. 2001). Egesi et al. (2002) reported tetraploid and hexaploid plants in accessions of *D. alata* from West Africa. Degras (1993) and Hahn (1995) give detailed review of the chromosomal behavior in yams. In general, intensive vegetative multiplication, reduced fertility and the co-existence of several ploidy levels means that the potential of each clone as well as the relationship between known landraces or cultivars needs to be determined to utilize the available genetic resources in crop improvement programs.

1.3. Production status and importance of yams

Yam is a staple food for millions of people in many regions of the tropics including Africa, Asia, the Pacific and Tropical America. It is the fourth most important tuber crop in the world next to potato, cassava and sweet potato (Levand and Shriver 1998, quoted by Mignouna and Dansi 2003). Mean annual production for the period from 1990 to 2005 was estimated at 34 million metric tons, Africa accounting for about 95% of the total output (Table 1.2). Compared to the year 1990, while yield per area nearly remained constant, total production increased by about 88% in 2005. This was mainly brought about by the increase in the total area harvested, which more than doubled over the same period (FAO 2005).

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²Throughout this thesis, the term 'yam' is used to distinguish the crop from the other root and tubers, and 'yams' in reference to the various species under genus *Dioscorea*.

Table 1.1. The main sections under the genus *Dioscorea* and corresponding cultivated species including their common names, origin and ploidy levels.

Section	Characteristics	Species	Common Name	Origin	Ploidy
Enantiophyllum	Vines twining to the right	D. alata L.	Water yam; Greater yam; Winged yam	SE Asia	2n = 20, 30, 40, 50, 60, 70, 80
		D. rotundata Poir.	White Guinea yam; White yam	W Africa	2n = 40, 80
		D. cayenensis Lam.	Yellow Guinea yam;Yellow yam	W Africa	2n = 36, 54, 60, 63, 66, 80, 120, 140
		D. opposita Thunb.	Cinnamon yam	China	2n = 40
		D. japonica Thunb.	Chinese yam	Japan	2n = 40
		D. transversa R. Br.		SE Asia	
Lasiophyton	Vines twining to the left	D. dumetorum (Kunth.) Pax	Bitter yam; Trifoliate yam; Cluster yam	Africa	2n = 36, 40, 45, 54
		D. hispida Dennst.	Asiatic bitter yam	SE Asia India	2n = 40, 60
Opsophyton		D. bulbifera L.	Aerial yam; potato yam	Africa Tropical- Asia	2n = 30, 40, 50, 60, 70, 80, 100
Combilium		D. esculenta (Lour.) Burkill	Lesser yam; Asiatic yam	Indochina Oceania	2n = 30, 40, 60, 90, 100
Macrogynodium		D. trifida L. f.	Cush-cush yam	Tropical- America	2n = 54, 72, 81

Source: Coursey 1967; Alexander and Coursey 1969; Purseglove 1972; Rehm and Espig 1991; Degras 1993; Onwueme and Charles 1994; Asiedu et al. 1997.

Table 1.2. Mean annual production of yam for the period from 1990 to 2005 (Source: FAO 2005).

	Area harvested ('000' ha)	Yield (Kg/ha)	Total production ('000' MT)
World	3,572	9,694	34,355
Africa	3,418	9,708	32,874
Africa (West)	3,149	10,088	31,388
Ethiopia ⁺	68	4,065	277

⁺Figures are mean values for the years between 1992 and 2005

The so-called 'yam belt' of West Africa, which comprises Cameroon, Nigeria, Benin, Togo, Ghana and Côte d'Ivoire (Hahn 1995), is the principal area of yam production. Within this 'belt', yam is closely related to socio-cultural life of the inhabitants. For example, for some societies in West Africa, yam is the totem of maleness and also used as a status of wealth based on number, size and diversity of yams offered during feasts, parties and marriage (Hahn et al. 1987). Raynor et al. (1992) described different yam tributes signifying the various events associated with yam harvesting and consumption in Micronesia.

Yam is among the mandated crops of the International Institute of Tropical Agriculture (IITA), which has devoted considerable resources in collecting yam germplasm for purposes of maintenance, crop improvement and distribution on request (Ng 1991). Of about 11,500 accessions of yam collected worldwide, IITA maintains close to 3000 accessions mainly from West Africa (FAO 1996). Yam germplasm from other parts of Africa is hardly represented in the collection. This is the main reason why the status and diversity of yams in other African countries outside the 'yam belt' is not known, leading to the perception that yam is only a West African Crop.

1.4. Yams in Ethiopia: an overview

Very few reports deal with aspects of yam production and its diversity in Ethiopia. Most of the references on these subjects are often scant and fragmentary. This is the result of research neglect that yam and other traditional crops have been subjected to in the past. Consequently, yams are hardly known to many of the researchers, policy makers and development agents in the country.

Ethiopia is generally considered as 'an isolated center of yam cultivation' outside the 'yam belt' of West Africa (Norman et al. 1995). Among the first accounts of yams in Ethiopia is the one given by Westphal (1975) who described the various *Dioscorea* species grown in complex farming systems with cereals and other root and tuber crops in Southern, Southwestern and Western parts of the country. Edwards (1991) reported that *Dioscorea* species are widely distributed in Ethiopia, and are one of those crops with wild relatives in the country.

It is widely believed that *D. abyssinica* Hochst. ex Kunth is native to Ethiopia (Coursey 1967; Rehm and Espig 1991), and is currently distributed in the savanna regions of Africa. Nonetheless, little is known about its exact place of origin, production and distribution. In their description of the cultivated and wild yams of Ethiopia, Miége and Demissew (1997) indicated the presence of *D. praehensilis* Benth., which is widely considered as native of West Africa. *D. abyssinica* and *D. praehensilis* are believed to be among the wild species that are ancestors of the cultivated African species (Hahn 1995). These and similar reports contributed a lot in creating awareness and interest about yams in Ethiopia. Nevertheless, the role of yams in the farming systems and local livelihood, their diversity and taxonomic status remain far from clear.

Etissa (1998) reported results from field characterization and evaluation of yam accessions assembled during a collection mission jointly undertaken by Melko Research Center and the then Plant Genetic Resource Center of Ethiopia (PGRC/E) about twenty years before. Although four species could be identified in the collection, several accessions remained unidentified. Gemeda (2000) gave a brief account of the role of yam and other tuber crops in the local livelihood of inhabitants in West Ethiopia. He reported that yam is more productive than the other tuber crops in the area, apparently due to its relative tolerance to drought and termite damage, with an estimated yield of about 20 tons per hectare.

The total annual production of yam in Ethiopia was estimated at about 277,000 metric tons from an area of about 68,000 ha, corresponding to a yield of about 4 tons per hectare (Table 1.2). Although widely referred to, the figures included in the FAO statistics represent a gross underestimation of the production and productivity of yams in Ethiopia compared to those given in some reports (Gemeda 2000). However, this is part of the lack of information on yam, which is also often reflected in national and regional statistics. The recent study by Hildebrand et al. (2002) has been a significant contribution towards exploring the status and potential of yams in Ethiopia. The study describes the traditional knowledge and diversity of yams in Sheko (a remote area in the Southwestern edge of Ethiopia), with emphasis on the role and potentials of the crop in local livelihood and priorities for conservation.

1.5. Genetic diversity and its importance

Genetic diversity refers to the amount of genetic variability among individuals of a variety, population or species (Brown 1983), and provides the basis for adaptation to changing environmental conditions and for developing new varieties. This variation can be expressed in differences in morphological characters, physiological properties, biochemical characteristics, or in DNA sequence (Ramanatha and Hodgkin 2002). Consequently, characterization and evaluation of germplasm involves measuring one or a combination of these characters or properties.

Over the last couple of decades, increased studies into aspects of genetic diversity have improved our understanding of the extent and distribution of the diversity present in crops and their wild relatives. In most parts, these studies were triggered by concerns over the loss of valuable genetic resources (Frankel 1974; Harlan 1975) following the introduction of modern crop varieties into centers of crop domestication and diversity (Harlan 1970). This has greatly facilitated the implementation of conservation strategies, both *ex situ* and *in situ*, for the major staple crops (Brush 2000; Scarascia-Mugnozza and Perrino 2002). Nevertheless, many food species can be considered as 'minor', 'underutilized' or 'neglected' (Padulosi et al. 2002) and their status and potential remain mostly unknown (FAO 1996). On the other hand, these crops have national or regional significance as staples, in food supply during certain periods, or for nutritionally balanced diet (Hammer et al. 2001).

It is widely recognized that traditional agro-ecosystems maintain considerable diversity of plants (Bellon and Brush 1994; Brush 2000; Kehlenbeck and Maass 2004) and sustain dynamic evolutionary processes that created this diversity. They also preserve human knowledge that shaped diversity for generations (Bellon 1991). Important elements of crop evolution, thus, are genetic diversity, farmers' knowledge and selection, and exchange of crop varieties (Brush 2000). Individual farmers value diversity in their crops due to heterogeneous environmental and production conditions, risk factors, market demands and requirements as related to the utilization of different products (Bellon 1996). This is often reflected in their decision to grow and maintain diverse crop species and cultivars of the same species. Such human preference and

management have influenced diversity at species and infraspecific levels (Jain 2000) leading to the creation of landraces or traditional varieties.

The concept of a landrace is complex (Zeven 1998). Landraces are often considered as integrated and adapted populations and, more importantly, genetically variable (Harlan 1975). They are also crop populations in balance with their environment, stable over a long period of time and, yet, have a potential for adaptive changes (Frankel and Bennett 1970). Despite the difficulty in defining the term, it is well documented that the diversity present in landraces is very important both in terms of providing the food used by millions throughout the world and as raw materials for breeding modern cultivars (Wood and Lenné 1997).

In general, farmers' decisions and management activities play a central role in determining the availability, composition, distribution and relative abundance of crop species or cultivars in a given agro-ecosystem. This event, referred to as "planned diversity" (Matson et al. 1997), is important both in terms of crop production and in shaping the total biodiversity of an area. It is, therefore, imperative that attempts to study crop diversity in traditional agriculture take into account the role traditional farmers play in creating and managing diversity: an aspect that has been overlooked by many of the endeavors in the field (Thurston et al. 1999; Jain 2000).

1.6. Rationale of the study

Although Ethiopia is the center of origin and diversity of a considerable number of crop species (Vavilov and Chester 1951; Harlan 1969; Zohary 1970; Engels et al. 1991), most research works, and subsequent improvement and conservation programs have so far focused mainly on cereals. However, different root and tuber crops, such as enset (*Ensete ventricosum* (Welw.) Cheesman), Oromo potato or 'oromo dinich' (*Plectranthus edulis* (Vatke.) Agnew), and anchote (*Coccinia abyssinica* (Lam.) Cogn.) were domesticated in Ethiopia. Others such as yam, although believed to have been domesticated elsewhere, developed immense variation in the country (IBCR 2000).

Most of the root and tuber crops did not get a fair share of attention by researchers and policy makers. The curriculum of agricultural colleges and universities also failed to