Repères

Tropical Plant Breeding

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CIRAD SPI

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Yam

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Yams are herbaceous twining plants with tubers, very rarely with rhizomes, sometimes producing small aerial tubers called bulbils (Plate XXIV, 1 and 2). They are widely distributed in every continent, and are adapted to very different ecological environments: tropical savanna or forest regions, highlands and temperate regions.

Yams, genus *Dioscorea* of the family Dioscoreaceae, are monocotyledons. The genus *Dioscorea* includes more than 600 species worldwide but the list is probably not yet complete—two species were recently described in Peru (Tellez-Valdes, 1996). In Africa, there are around 20 indigenous or introduced species belonging to seven botanical sections (Miege and Lyonga, 1982; N'kounkon et al., 1993). The section *Enantiophyllum* includes more than half the wild yam species of African origin. Several of them have been domesticated, and these cultivated yams have been assigned to the *D. cayenensis-D. rotundata* complex.

Wild species are either annuals (aerial and underground parts annually reviving), or semi-perennial (aerial part with 12- to 24-month cycle, with perennial underground part), or perennial (aerial and underground parts visible throughout the year). Cultivated species are generally grown as annuals.

Many species are edible or have become so as a result of domestication. Among these, ten species are currently cultivated. Several wild species are included in pharmacopoeia and some are used in the pharmaceutical industry.

World production of yams for food reached 30 Mt in 1994 (FAO, 1995). West Africa provides 94% of this production. Nigeria is the

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Taxonomy

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largest producing country with 22 Mt, followed by Côte d'Ivoire (2.8 Mt), Benin (1.3 Mt) and Ghana (1 Mt).

Yams are an essential staple food in several West African countries (Plate XXIV, 3). Most of the production is used directly by farmers but some is also sold in urban markets. The tubers are most often consumed in the form of a compact puree. But traditional processing of dried roots has recently increased in Nigeria and Benin. Commercial processing of yams was developed in Nigeria and Côte d'Ivoire during the 1980s by international agrofood stakeholders.

In West Africa, most yam production relies on the *D. cayenensis-D. rotundata* complex. Nevertheless, other species may be of considerable economic importance. This applies to *D. alata*, of Asiatic origin, which predominates in the Baoulé region in central Côte d'Ivoire, and *D. dumetorum*, an indigenous African species cultivated on a large scale in western Cameroon.

D. cayenensis-D. rotundata yams have been the focus of much research over the last twenty years. This chapter reviews the knowledge acquired to date on these yams.

EVOLUTIONARY ORGANISATION OF THE *D. CAYENESIS-D. ROTUNDATA* COMPLEX

Taxonomy

In West Africa, yams of South-East Asian origin are cultivated—*D. alata* with an alate stem and *D. esculenta* which forms a bunch of small tubers—as well as African yams—*D.bulbifera*, that produces many bulbils, *D. dumetorum* with trifoliate leaves, and a group of yams that belong to none of these species. There is currently a controversy as to the scientific nomenclature applied to the latter group.

Two distinct species were first described: *D. cayenensis* by Lamarck in 1792, based on a specimen from French Guiana, and *D. rotundata* by Poiret in 1813, based on a specimen from Puerto Rico. The African origin of these yams, established later, raised doubts about their taxonomic independence.

In 1918, Burkill thus questioned the separation of the species *D. cayenensis* and *D. rotundata*. Martin and Rhodes (1978) reached the same conclusion, based on a morphological and agronomic study conducted on 68 cultivars. These formed two main groups linked nonetheless through many intermediate forms. Akoroda and Chheda (1983) also separated *D. cayenensis* from *D. rotundata*, while indicating the probable existence of interspecific hybrids. On the other hand, the classification, by Onyilagha and Lowe (1986), of 22 cultivars on the basis of 76 morphological characters led to two groups that were better individualised and assimilated to the species *D. cayenensis* and *D. rotundata*.

Recent studies have shown that at least four species gave rise to the present cultivated forms, classified as *D. cayenensis* or *D. rotundata* (Hladik et al., 1984; Hamon and Toure, 1991; Terauchi et al., 1992; Dumont et al., 1994). On the whole, these yams therefore form a botanical complex. *D. cayenensis-D. rotundata* nomenclature was recommended in the international conference on root and tuber plants, held in Cameroon in 1978. It takes into account the multispecies origin of these yams while according them common characteristics: these yams, of West African origin, are all cultivated, generally non-bulbiferous and have entire leaves and non-pubescent stems, more or less prickly and non-winged.

Genetic Diversity

Biology and Reproduction

D. cayenensis-D. rotundata yams are hemicryptophytes with an annual cycle. Their biological cycle alternates between the vegetative and dormant phase. This begins with the disappearance of the aerial organs at the end of the rainy season, followed by a tuber dormancy phase that lasts from several weeks to four months.

Vegetative propagation predominates in traditional cultivation. The plant is derived from a fragment of tuber—termed a short sucker or yam seed—that has been planted in the soil. There are two stages in the vegetative period. Initially, the plant is entirely dependent on the energy reserves stored in the sucker. The stem elongates and produces cataphylls (rudimentary leaves) while the root system begins to grow. Thereafter the roots become functional, the aerial part develops and the plant becomes autonomous. The onset of tuberisation coincides with slowing down of vegetative growth (Trouslot, 1982). Vegetative development and tuberisation dynamics are governed by the sunshine level (Okezie et al., 1993). A long sunny period prompts leaf mass growth and delays tuberisation—this effect is reversed by short sunny periods. Early plantation, well before summer begins, is therefore essential to obtain good yields. It maximises photosynthesis, a crucial factor for increasing tuber weight.

Many *D. cayenensis-D.rotundata* cultivars have retained their sexuality. These yams are usually dioecious and therefore necessarily cross-pollinated. Cases of monoecism have been reported but the sexual behaviour of these plants is not yet known.

The inflorescences are spikes that emerge from the leaf axils. Generally 1 or 2 such spikes arise in female plants and 2 to 8 in male plants.

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The density of male flowers per spike is three to four times that noted on female plants (3 to 8 per cm versus 1 or 2). Flowering is acropetal (Plate XXIV, 2). Pollination is entomophilous and ensured by thrips (Pitkin, 1973).

Floral biology studies undertaken in Côte d'Ivoire confirmed observations obtained in Nigeria (Akoroda, 1983) and Guadeloupe (Bulle-Legrand, 1983). Studies carried out on the varietal groups described by Hamon et al. (1986) helped to characterise the flowering pattern of both sexes in several varieties (Zoundjihekpon et al., 1997).

On male plants, the first flower buds appear between 3 and 13 weeks after sprouting, depending on the varietal group. The first flowers generally open 4 to 7 weeks later and almost all will have opened within 15 to 20 days. Floral opening is maximum during the early part of the day, between 10 and 14 h, peaking at noon. Male flowers open and close every day for three to four consecutive days.

On female plants, the first flower buds appear between 5 and 16 weeks after sprouting, i.e., 2 to 3 weeks later than in male plants. The first flowers open 3 to 6 weeks later and almost all will have opened in 3 to 5 days. Floral opening is maximum during the early part of the day, between 9 and 13 h, peaking on the 4th day. This peak coincides with the maximum pollen availability and pollinating insect activity in Côte d'Ivoire, according to observations on okra (Hamon and Koechlin, 1991). Once opened, a female flower does not close.

Although male inflorescences appear earlier than female ones, intervarietal synchronisation is therefore fairly good for most of the plant material studied if the maximum floral opening per plant is taken into account.

Morphological Diversity

The cultivated *D. cayenenis-D. rotundata* forms are highly diversified. Their variability is expressed mainly in the aerial vegetative apparatus: plant structure, colour and appearance of the stem, size, leaf shape and colour. In the vegetative underground apparatus, this diversity is observed in the shape, size and colour of the tuber flesh as well as the maturation period, which determines whether there can be one or two harvests per annual cycle.

A study of morphological diversity in *D. cayenensis-D. rotundata* was undertaken in Côte d'Ivoire during the 1980s. From 800 samples, mostly collected in this country, 20 varietal groups more or less morphologically homogeneous were formed, so that intragroup morphological variability was always less than the intergroup variability (Hamon et al., 1986; Hamon, 1988).

These morphological varietal groups have been divided into two classes (Hamon and Tio-Touré, 1990b). The first class comprises 2 groups characterised by a long vegetative cycle (over ten months), intense yellow or violet pigmentation of the tuber flesh and inability to provide two harvests per year. The second class contains the other 18 groups, having a short vegetative cycle (less than ten months), a colourless or slightly pigmented flesh and capable of providing two harvests in each crop cycle.

Enzymatic Diversity

The enzymatic polymorphism of the *D. cayenensis-D. rotundata* complex was studied to classify its genetic organisation (Hamon and Tio-Touré, 1990a). Five enzymatic systems were analysed by electrophoresis on starch gel using about 450 samples from among the 800 representatives showing diversity with respect to morphological traits and vernacular nomenclature. These were isocitrate dehydrogenase (IDH), malate dehydrogenase (MDH), 6-phosphogluconate dehydrogenase (PGD), shikimate dehydrogenase (SDH) and phosphoglucose isomerase (PGI).

The diversity revealed varies considerably depending on the varietal group. Some appear to be genetically monomorphic and therefore constitute a single genotype on the basis of these markers. Others are highly polymorphic because they contain 16 genotypes of the total 62 identified during the study. In three of the enzyme systems (IDH, SDH, PGD), some zymograms are characterised by the presence of slow mobile electrophoretic bands.

The enzymatic classification also indicates on organisation with two principal classes that respectively include 15 and 5 varietal groups. The first class presents the lowest level of genetic diversity. The second is genetically heterogeneous and differs somewhat due to the presence of slow mobile electrophoretic bands.

A comparison between the morphological and enzymatic classifications indicates that the morphological class with a long vegetative cycle is included in the class with slow mobile electrophoretic bands (Table 24.1). It also shows that the highest morphological variability is observed in the class with the lowest enzymatic diversity.

The *D. cayenensis-D.rotundata* complex in Cameroon is also organised in two main classes (Dumont et al., 1994). Interestingly, the morphological and enzymatic characteristics that prompted this two-class separation are similar to those also documented in Côted'Ivoire.

Ploidy Levels

Cultivated yams of the *D. cayenensis-D. rotundata* complex are polyploid, with a basic chromosome number of 10. Three ploidy levels have been shown by chromosome counts (Baquar, 1980; Zoundjihekpon et al., 1990), which were later confirmed by flow cytometry determination of the

Table 24.1: Main characteri
represented in Côted'Ivoire

Varietal group	Morp. class*
Afoubessou	
Cocoassié	
Frou	
Gnan	
Kponan	
Krandoufou	
Kreglé	
Kroukroupa	
Lokpa	
Nandokaka	
Spoéré	
Soussou	
Vinvan	
Waraga	
Zrézrou	
Baniakpa	
Kpôpôkpôkpô	
Sammancou	
Kangba	
Yaobadou	

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Related Wild Species

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Table 24.1: Main characteristics of yams of the *D. cayenensis-D. rotundata* complex as represented in Côted'Ivoire (from Hamon et al., 1986 and Hamon, 1988)

Varietal group	Morphological class*	Enzymatic class**	DNA content (pg)	Ploidy level
Afoubessou				
Cocoassié				
Frou				
Gnan				
Kponan				
Krandoufou				
Kренglé				
Kroukroupa			1.24	4x
Lokpa		1		
Nandokaka	A			
Spoéré				
Soussou				
Vinvan				
Waraga				
Zrézrou				
Baniakpa				
Kpôpôkpôkpô			1.77	6x
Sammancou		2		
Kangba	B			
Yaobadou			2.59	8x

*A: Aerial vegetative cycle less than 10 months, tuber flesh never highly pigmented, able to produce one or two harvests per crop cycle.
*B: Aerial vegetative cycle more than 10 months, tuber flesh most often highly pigmented, unable to produce two harvests per crop cycle.
**1: Absence of slow electrophoretic components for IDH, PGD and SKDH.
**2: Presence of slow electrophoretic components for IDH, PGD or SKDH.

DNA content (Hamon et al., 1992a). Only the 15 varietal groups of the least diversified enzymatic class are tetraploids (2n = 4x = 40). The most heterogeneous enzymatic class comprises four hexaploid varietal groups (2n = 6x = 60) and an octoploid varietal group (2n = 8x = 80).

Genetic Origin of the *D. cayenensis-D. rotundata* Complex

Related Wild Species

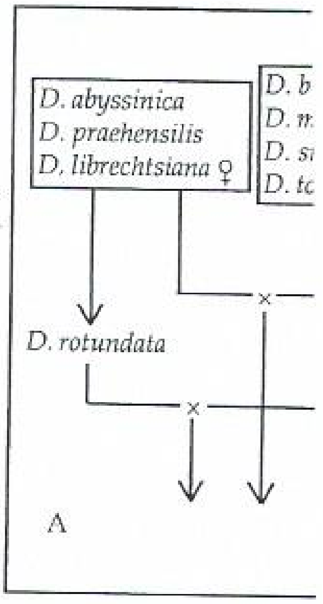
Five wild species—*D. burkilliana*, *D. minutiflora*, *D. abyssinica*, *D. praehensilis* and *D. mangenotiana* (Hamon et al., 1995)—were studied for enzymatic polymorphism, similar to the analysis conducted on cultivated yams. These yams have various biotypes and different biological characters (Table 24.2). The annual species *D. abyssinica* and *D. praehensilis* appear to be genetically close. Two species, *D. burkilliana* and *D. minutiflora*, have very slow mobile electrophoretic components for the three enzyme systems IDH, SDH and PGD. Finally, semi-perennial *D. mangenotiana* has enzymatic characters intermediate between those of annual and perennial yams.

Chromosome counts carried out for several wild species revealed different ploidy levels that extend from 2n = 4x to 2n = 12x (Miege, 1952, 1958; Martin and Ortiz, 1963; Lauzer et al., 1992; Zoundjihekpon, 1994; Table 24.2). The changeover from a wild to a cultivated state is not necessarily accompanied by polyploidisation.

Table 24.2: Characteristics of the wild species studied by Hamon (1988)

Species	Cycle	Habitat	Number of chromosomes (references)
D. abyssinica	Annual	Savanna woodlands; open forests	40 (Miege, 1952; Martin and Ortiz, 1963; Lauzer et al., 1992)
D. praehensilis	Annual	Mesophytic forest	40 (Miege, 1952)
D. mangenotiana	Semi-perennial	Mesophytic and tropical rain forest	80 (Miege, 1952) 40 (Lauzer et al., 1992) 60 (Zoundjihekpon, 1994)
D. burkilliana	Perennial	Mesophytic and tropical rain forest	40 (Miege, 1958)
D. minutiflora	Perennial	Mesophytic and tropical rain forest	120 (Miege, 1958)

A study of relationships between cultivated and wild yams indicated a polyspecific origin for the *D. cayenensis-D. rotundata* complex (Hamon, 1988; Hamon et al., 1992b; Fig. 24.1). The tetraploid forms originated from the annual species *D. abyssinica* and/or *D. praehensilis*. Hexaploid and octoploid forms are partially or totally related to wild perennial or semi-perennial species. The varietal group Sammancou (described in Hamon et al., 1986) resulted from domestication of *D. mangenotiana*, while the varietal group Yaobadou (described in Hamon et al., 1986) has the characteristics of an interspecific cross between *D. praehensilis* and *D. burkilliana*. This polyspecific origin was also demonstrated by RFLP analysis of chloroplast DNAs and nuclear ribosomal DNA (Terauchi et al., 1992). Nevertheless, these authors maintain a distinction between these two species, *D. cayenensis* and *D. rotundata*, although they consider that seven wild species, from which three are common to the study conducted by Hamon et al. (1992b), are related to the cultivated complex (Fig. 24.1).



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DOMESTICATION OF YAM

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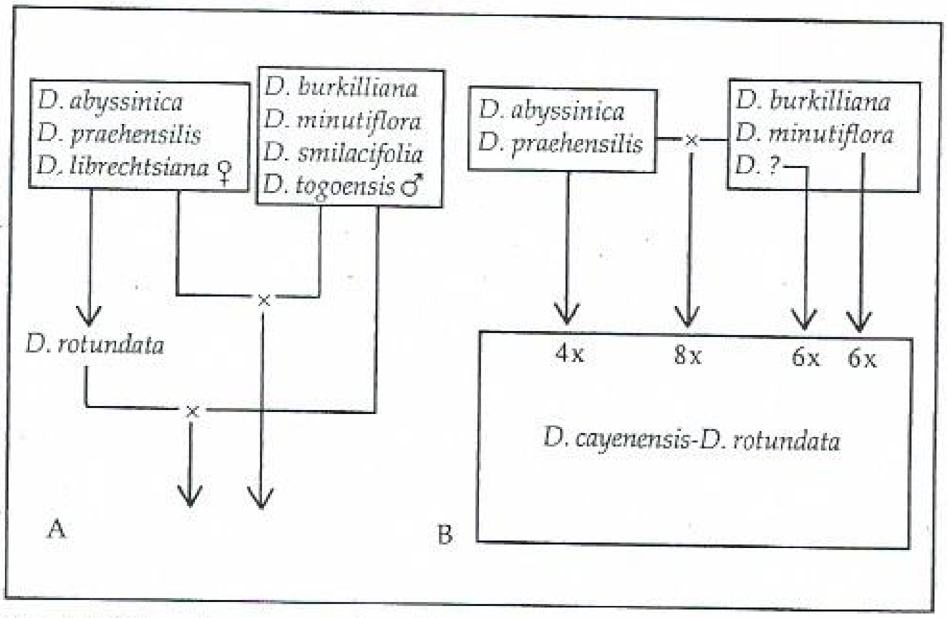

Fig. 24.1: Schematic representation of the polyspecific origin of the *D. cayenensis-D. rotundata* complex, established on the basis of studies by Terauchi (A) and Hamon (B).

Domestication of Yams

Yam domestication involves vegetative propagation under cultivation conditions adapted for wild material. This is still done in the vast region of West and Central Africa (Hladik et al., 1984; Hamon, 1988; Dumont et al., 1994). In this region, wild forms that have been cultivated very recently are grown together with older cultivated forms. The selection criteria for wild material have yet to be established.

Morphological modifications that occur when the wild species *D. praehensilis* is cultivated, and whose biotope is a mesophytic forest, were monitored during eight successive cultivations (Chikwendu and Okezie, 1986). The amount of fibre in the tuber declined markedly as the starch content increased. There was a drop in the number of thorns on the stem and along the roots which line the crown of the tuber. The vegetative apparatus reduced in size and the shape of the leaf differed from its initial characteristics. The number of cataphylls borne on the main stem decreased spectacularly. According to Dumont (1977), this reduced number of cataphylls could be due to slower germination that occurs under natural conditions; it might also be highly dependent on the planting date.

As yam is only propagated vegetatively by farmers, it would appear that although gene flow occurs within cultivated forms, there is not sufficient genetic recombination to be tapped in each cultivated generation. Zoundjihekpon et al. (1994) used enzymatic markers to control the conformity of progeny between tetraploid cultivated forms obtained by sexual reproduction and demonstrated that these gene flows also occur between cultivated and related wild forms.

According to Dumont (1982) and Hamon et al. (1992b), genetic recombinations that occur naturally among wild and cultivated forms, as well as within each, regularly renew the reservoir of variability which farmers still exploit for domesticating yams. In its area of origin, the *D. cayenensis-D. rotundata* complex and related wild species constitute constantly evolving genetic material.

VARIETAL IMPROVEMENT

Types of Varieties

Yam varieties are relatively homogeneous clones or groups of clones. The choice of varieties to be cropped is partially determined by the need to extend tuber production by focusing on the harvest periods and storage potential as well as qualitative criteria for local culinary preparations. Productivity is a major concern when the crop is to be marketed.

Breeding Objectives

Breeding objectives are twofold: to enable modernisation of cultivation by reducing the extent of manual labour, and to produce tubers that meet marketing and consumer requirements. The main criteria are listed in Table 24.3.

Breeding Methods

Varietal Choices

Depending on the objectives, the farmer makes a choice from among the many conventional varieties of the *D. cayenensis-D. rotundata* complex or other cultivated species. The African farmer has been doing this for the last 50 years. Nonetheless, the varietal diversity in West Africa has yet to be fully tapped.

When a variety is found to be heterogeneous—that is, when it comprises clones that differ with respect to type of tuber produced—an intravarietal selection may be carried out to homogenise cultivation and production.

Table 24.3: Criteria to be take
D. cayenensis-D. rotundata co

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Table 24.3: Criteria to be taken into account in yam breeding programmes involving the *D. cayenensis-D. rotundata* complex

Moderniisation of cultivation	staking not required
	Specific production of small tubers of homogeneous weight, intended only for sowing
	Production of ovoid tubers, large and small, enabling mechanical harvesting
Tuber quality	Suitability for preservation Resistance or tolerance to various biotic agents (nematodes, mealybugs, fungi, dry rot) ensuring very healthy tubers Suitability for culinary preparations or commercial processing
	Good organoleptic qualities
	Good general appearance (smooth skin with no cracks or rootlets)

Selection by Sexual Reproduction

In the cultivated yam *D. cayenensis-D. rotundata*, carrying out selection by the sexual method implies that clonal selection is not obtained through conventional vegetative propagation, but rather from progeny of seeds obtained by open or controlled pollination. This selection method is still not widely used since there was no effective control of progeny conformity before the work of Zoundjihekpon et al. (1994). Nevertheless, the possibilities of the sexual breeding of yams had been explored in Nigeria and Côte d'Ivoire back in the 1950s (Degras, 1986).

Since 1971, IITA (International Institute of Tropical Agriculture) in Nigeria has also been carrying out selection by the sexual method on progeny resulting from open pollinations and theoretically controlled pollinations. The selection criteria are productivity, cultivation without stakes, resistance to mosaic disease and nematodes, tuber shape and volume, suitability for preservation and culinary quality. At the beginning of the 1990s, clonal selection, adopted for these progeny, helped in identifying 45 clones whose characteristics, especially productivity, were equivalent to those of parental varieties (from 13.5 to 18.7 t ha^{-1} for one group of clones and 4.9 to 13.1 t ha^{-1} for the other group).

In India, the variety known as Sree Dhanya, which produces 20 t ha^{-1} and has a bushy aerial architecture was created from half-sib progeny obtained by IITA (Abraham et al., 1989). In addition, clonal selection conducted on progeny obtained by open pollination of Iwo and Umudika cultivars from Nigeria resulted in Sree Subhra and Sree Priya, which are even more productive (Thankamma et al., 1993).

Information acquired in recent years on the genetic organisation of yams and the floral biology of the *D. cayenensis-D. rotundata* complex has resulted in better control of the crosses and widened the prospects for varietal development through sexual reproduction.

In addition to crosses between genetically compatible cultivated varieties, crosses could be made with related wild forms: there is no reproductive barrier between cultivated yams and their wild parents (Zoundjihekpon et al., 1994). These combinations would ensure high fertility in the progeny and transfer of useful characteristics of the wild forms, especially resistance to various pathogens and vegetative vigour.

Contributions of Biotechnology

In vitro Culture

During the 1970s, *in vitro* culture techniques raised great hopes. *In vitro* microcuttings of stems were used for the cultivated Asian *D. alata* yam. This technique was adopted for rapid multiplication of genotypes and production of small uniform-sized tubers, mainly for plantations (Ahoussou et al., 1979). Although this method has technical advantages, it has never been applied in Africa for practical and economic reasons.

Concerning yams of the *D. cayenensis-D. rotundata* complex, *in vitro* culture is currently under way mainly to preserve genetic resources and to sanitise genetic materials (Malaurie et al., 1993, 1995). Meristem cryoconservation and regeneration conditions are now well developed and should facilitate preservation of these resources for a longer period.

Somatic Fusion

Somatic fusion was considered during the 1980s for gene transfer without adopting the sexual method, assumed too difficult at that time (uncontrolled floral biology, time-lag between flowering of male and female plants supposedly rendering sexual reproduction ineffective and small flowers difficult to handle). Today it is possible to regenerate plants from protoplasts of the Oriental Lisbon cultivar of *D. alata* (Kandamasamy, 1996). On the other hand, formation of microcalluses or colonies has been observed in several *D. alata* and *D. cayenensis-D. rotundata* cultivars (Tor et al., 1997).

Molecular Markers

RFLP molecular markers have been used in yam to determine phylogenetic relationships between cultivated and wild yams of West Africa (Terauchi et al., 1992). The polymorphism revealed by microsatellite markers has helped in analysing genetic diversity within natural populations of a Japanese yam, *D. tokoro* (Terauchi and Konuma, 1994). RAPD markers have recently enabled a study of genetic variability in *D. bulbifera*, found in Africa, Asia and Polynesia (Ramser et al., 1996) and identification of varieties cultivated in Jamaica (Asemota et al., 1996).

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DISSEMINATION OF VARIETIES

Various rapid propagation methods have enabled the dissemination of selected clones. The *miniset* method has been well developed in Nigeria by NRCRI (National Root Crops Research Institute) and IITA. It makes use of minifragments of tubers weighing 25 to 50 g to produce plants that provide small tubers suitable for planting. The second method is *in vitro* production of microcuttings and microtubers. Microplants obtained from nodal portions of stems are either transferred directly to the field after a hardening period or used to obtain microtubers. The latter give rise to plants which, after a crop cycle in the field provide seed tubers.

Dissemination of selected varieties is an effective way to improve yam production. However, care should be taken to ensure that this does not cause sudden genetic erosion in the zone of introduction. The Florido clone of *D. alata*, introduced in Côte d'Ivoire from Puerto Rico at the end of the 1970s, led to a major shift away from the local varieties. Similar attitudes have been observed in other West African countries where exchanges of plant material are highly promoted by communications developments. The decay of yam genetic resources is now taking place and this situation could become irreversible if measures to ensure conservation of conventional varieties are not implemented soon.

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