Vegetative and Sexual Management in Food Yam Improvement

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Yam models are described, giving several required characteristics for clonal cultivation of *Dioscorea alata*, *D. cayenensis*, and *D. trifida*. Intraclonal selection is possible because of tuber internal heterogeneity, clonal population diversity, and time dispersed production and germination of individual plant bulbil. A kind of "somatic drift" is observed.

Several aspects of determinism of tuberization and flowering are cited, and day/night ratio, light intensity, soil mineral balance, internal vegetative phases, and genetic factors are recognized in flowering and in sex-ratio determinism.

Basic management using axillary structure growth-substance treatment for vegetative, tuberization, flowering, and sex control is discussed. In addition, the genetic analysis of characteristics, and different cultivation systems are examined.

Yam improvement has normally been based on the introduction of clonal cultivars selected from traditional populations. Use of the sexual system for food yams has been attempted; however, it is among pharmaceutic yams that the sexual system has been extensively used and studied.

Improvement of the food yam through its sexual system began in 1966 with *D. trifida* in Guadeloupe (Degras 1969), and it is now spreading through an inter-Caribbean selection on behalf of the ISTRC-CFCS yam study group. The largest food yam breeding potential now comes from IITA where, since 1970, Sadik and Okereke (1975) have developed the sexual utilization of *D. cayenensis* ssp. *rotundata*, and tested a large amount of seeds throughout the tropics.

This does not, however, mean that clonal selection should be stopped, rather it still may have an important role to play.

Yam Models in Current Clonal Cultivation

At the present time, all cultivated yams are clonally propagated. The characteristics of *D. alata*, *D. cayenensis*, and *D. trifida* in the French West Indies are as follows: *D alata* — (1) high cooking quality (white flesh), (2) long storage without loss of weight, (3) resistant to anthracnosis and viruses, (4) resistant to water stress, (5) high yield with medium and regular size tubers (other characteristics existing widely in the species are: good dormancy, resistance to *Penicillium oxalicum*, germination in dry conditions, and good yield without staking); *D. cayenensis* ssp. *rotundata* — (1) fair tuber maturity long before foliage decay, (2) good tuber regrowth after commercial harvest, (3) high cooking quality (whitish flesh), (4) year-round tuber development, (5) medium storage duration of commercial harvest, (6) prickless roots, (7) high early yield; *D. trifida* — (1) tubers available year-round because of: (a) fresh production all season, (b) food storage duration, (2) high cooking quality with sweet taste, (3) tuber grouping near soil surface, (4) high yield with 10% seed sized tubers, (5) resistant to viruses, *Penicillium oxalicum*, nematodes, and mealy bugs, (6) spheroidal tuber shape, (7) resistant or tolerant to drought.

Intraclonal Selection

Variation within a clone exists. Heads, middles, and tails from the same tuber differ in earliness of germination, yield, and number of stems or tubers produced. In addition, normal bud regulation is suppressed when the slice size is greater than 5 g (Degras and Mathurin 1975). It is important that differences have been repeated over first and second generations of two *D. trifida* clones obtained from different parts of a tuber of cultivar INRA 25: flowering time differences at the second generation were in accordance with behaviour in the first generation, differences in time to maturity were up to 1 month.

We do not know the level of genetic homogeneity of traditional cultivars, but some may include mutational variations. Off-types are

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Table 1. Agronomic variability from *D. cayenenis* cultivar Krenglé intraclonal tuber selection.

Tuber shape (seed tuber)	Plant size (200 days)	Growth duration[a]	Yield[b]	Tubers harvested[b]	Mean tuber weight[b]
Cylindrical[c]	100	100	100	100	100
Cylindro-conical	110	111	91	103	89
Conical	100	104	88	108	82
Ovoidal	113	104	82	88	94
Spheroidal	103	100	73	102	67

[a]Statistical significance has been found for shape × seed tuber weight interaction in cycle duration.
[b]Significative differences $p = 0.05$.
[c]Cylindrical data are taken as basis = 100 for each trait.

normally easily recognizable when cultivated with cultivars: cultivar individuality is a fact. Nevertheless, in the well known cultivar *D. cayenensis* ssp. *rotundata* "Krenglé," in central Ivory Coast, a number of tuber forms could be separated. When cultivated separately they have distinct performances (Table 1).

Another case of intraclonal variation that may be explored arises from different times to maturation of the bulbils of the plant. In *D. bulbifera* and *D. alata*, the difference may reach 1 month.

These examples show that a form of "somatic drift" of clonal expression of a yam genotype could proceed from conscious successive selection of extreme phenotypic variations. It is obvious that in current cultivation, such variations do not cause marked changes of the clonal population. But we think that through controlled cultivation (planting time and density) and controlled dormancy duration we could expect to alter the phenotypic balance of clonal properties. The selection of the type of planting material from tubers of a clone could at the same time determine the best rate of multiplication and the highest rate of phenotypic variation that could be explored through environment × growing condition interactions (Mathurin and Degras 1974, Degras and Mathurin 1975). In this respect, an experiment is now in progress using *D. trifida* cultivar INRA 25.

Flowering Determinism

Flowering Stage and Vegetative Development Relation

Wild and domestic yams seem to give preference to the vegetative system over the sexual system (Burkill 1960). In many cases the sexual phase is very depressed in annual cultivation. A kind of competition exists between vegetative accumulation and sexual development for the following reasons.

Tuberization and flowering seem to be favoured by short days for a number of species. This has been shown for bulbils and for tuber growth. *D. alata* and *D. trifida* normally flower in the autumn, but Henry (1967) obtained earlier flowering for a number of seedlings under short days.

High light intensity is necessary for flowering and tuberization: Henry (1967) observed a lower level of flowering of *D. trifida* seedlings when shaded. For most species, staking, which permits more light to enter the canopy, gives higher tuber yields. The difference is striking for a number of dry-forest climax species like *D. cayenensis*, whereas it is less important for rain-forest climax species like *D. alata* and *D. trifida*.

The physiological response to fertilization suggests a common process for initiation of tuberization and flowering. We observed that given balances of NPK in *D. cayenensis* increased the tuber yield and the percentage of plants that flower. In *D. alata*, stem fasciations, which may be considered in some cultivars from central Ivory Coast as a substitute for flowering, occurred when tuber yields were greatest.

Generally speaking, flowering seems to be triggered by a certain level of development of the vegetative organs. This could account for the low level of flowering observed in the first growing cycle of *D. trifida* seedlings when compared to the second cycle. This level is not merely a matter of biomass: plants with heavy vegetative organs do not necessarily flower. It seems that the relation is both qualitative and quantitative.

Aspects of the control of the vegetative and flowering stages are also seen in the balance between bulbil and inflorescence development in some species. Along one plant of *D. bulbifera* (Martin 1974) there are a succession of foliar axils, first with bulbils alone, then with both bulbils and inflorescences, then with inflorescences alone. Among populations of primitive cultivars of *D. alata* some clones bear only bulbils and others only inflorescences. Bulbil setting begins somewhat before the flowering time.

Genetic factors also control flowering formation. Apart from the wide differences known between cultivars in a *D. cayenensis* for instance, it is known that sexual reproduction and selection can increase the percentage of flowering (Sadik and Okereke 1975).

So, ecological factors like day/night ratio, light intensity, soil mineral balance, internal vegetative phases, and genetic makeup control yam flowering.

Sex-Ratio Determinism

Though dioecism is the general case in yams, a number of cases have been observed where some level of monoecism and even of hermaphroditism is obvious. In central Ivory Coast the occurrence of monoecious plants in *D. cayenensis* is affected by mineral fertilization and season, and its occurrence is higher in sexual progenies than in clonal material. Sadik and Okereke (1975) have recently confirmed these findings.

In a number of species a prevalence of male flowers is reported. In some wild species, the female form is unknown, for example in Madagascan flora (Burkill et al. 1950) or in Mexican flora (Matuda 1954). Martin (1966) who studied the behaviour of steroid species, suggested that the variations of sex-ratio in progenies proceed from the different heterosomic status of the male parents, which in tetraploid species could be XXXY, XXYY, or XYYY. The latter is lethal or only gives males.

In *D. trifida*, Henry (1967) observed a high prevalence of males in common clonal propagation, a lower prevalence in the first seedling growth cycle, and a still lower prevalence in clonal multiplication of these seedlings. Degras et al. (1973) observed an increase of female plants when flowering was increased. In *D. trifida* seedlings a 3/1 male/female ratio, which in the case of predominant tetraploidy, could result from a XXYY male. In *D. cayenensis* spp. *rotundata*, Sadik and Okereke (1975) observed no female inflorescence in the first seedling cycle, but in the following growth cycle, female plants appeared in a higher proportion than in traditionally vegetatively reproduced populations.

Another aspect of *Dioscorea* flowering seems constant: the time of female flowering with respect to that of males. This may be associated with the tendency toward higher tuber yields from female plants.

To obtain high levels of yam crossing the following are recommended: (1) a high level of vegetative growth, which is necessary for full female expression; (2) several plantations of both parents for simultaneous flowering; and (3) common staking of male and female inflorescences so that flowers are close (pollen is sticky and wind dispersal poor).

New research could lead to a better management of yam flowering. The very specific nature of the nodal and axillary yam structure is obvious from the special vascular organization (glomeruli) ascribed to this genus (Ayensu 1972). These glomeruli are capable of developing into flowers, bulbils, or chiots. A systematic screening of growth substance, and the nutritional and physical effects on the yam nodal axillary system, as applied to the axillary complex of *Euphorbiaceae* (Champault 1973), may be successful in increasing flowering.

First Data from Genetic Analyses

Martin (1966) attempted an interpretation of sex-ratio heredity in yam, and we have limited data on *D. trifida* (Degras 1969, Degras et al. 1973). We now have more complete data for a number of crosses in this species.

Anthocyan in Tuber Flesh

Table 2 gives the distribution of anthocyan in progeny. Interpretation is difficult because of: the limited seed germination; the death of a number of plants in the field; and the possible interaction of anthocyan expression with degree of maturity of harvested seedlings. Nevertheless we observed: (1) a dominance of purple over white; (2) a transgression beyond the purple; and (3) an occurrence of intermediate levels; suggesting a number of modifying factors.

Length of Nontuberous Parts of Stolon

The length distribution of the stolons, for 40 progeny of *D. trifida* (C.C.V. × INRA), was

Table 2. Distribution of anthocyan in tubers of 40 progeny of *D. trifida* (C.C.V. × INRA).

Flesh colours	Skin colours			
	Deep purple	Purple	Light purple	White
Deep purple	3.3	1.6	—	—
Purple	—	22.9	18.0[a]	—
Light purple	—	3.3	18.0	—
Very light purple	—	1.6	3.3	—
White	—	1.6	6.6	19.6[b]

[a]C.C. Violette type.
[b]INRA 40 type.

as follows: less than 10 cm 32.2%; 10–15 cm 26.2%; 15–20 cm 20.8%; and more than 20 cm 20.8%. Long stolons appear dominant over short ones. Here also a transgression beyond parent limits is observed. It seems that for most characteristics, in accordance with the general high level of polyploidy in cultivated yams, multiple level factor determinism is the rule.

The analysis of yam genetics will benefit from the utilization of autofertile monoic or hermaphroditic plants. If androgenesis could be applied to yam pollen to give haploid clones, this would open new opportunities of genetic analysis. Recently attempts have been successful (Arnolin 1976, personal communication).

Sexual Progeny Selection

The success of selection from free and controlled pollinated crossings of *D. cayenensis* in West Africa, and *D. trifida* in the West Indies, shows that theoretical knowledge of the genetic mechanisms are not needed to make advances.

The first conscious agronomic utilization of hybridization in *D. cayenensis* occurred in 1955 at Bouaké (Ivory Coast) where Franck harvested 3020 seeds from cultivar "Assaoua" and obtained 48 seedlings. Only 13 clones were retained. We studied them from 1956–58, and selected from them Assaoua B9 (Van de Venne 1973, personal communication).

Among many selection criteria we noticed, at the first clonal cycle, the value of flowering, sex expression, and phyllotaxy. Nonflowering plants produced 668 g, monoic 770 g, and female 1135 g (mean tuber weight). Leaf and branch balance on successive nodes gave a yield of 1000 g (worst balanced system) to 3000 g (best balanced systems). A relation between sex type and yield has also been found by Sadik and Okereke (1975).

Seed germination and many aspects of the two first progeny growing cycles of *D. trifida* were studied by Henry (1967). Since 1965 in Guadeloupe, about 5000 seedlings from 20 crosses have been observed and tested, and improved cultivars have been obtained. Among them INRA 25 and INRA 5-20 associate a number of the required characteristics. Resistance to diseases (*Penicillium* rot, viruses) and pests (mealy bugs, nematodes) are still lacking in our hybrids. Special genetic searches are projected in the Guyanas.

New Horizons

Now that the feasibility of genetic improvement of yams is well established, we can examine some new cultivation systems.

First, more intensive cropping will proceed from the following genetic modifications: (1) greater efficiency in translocation of assimilates to the tuber, including limitation of stem development, shortening of the prebulking tuber phase, and faster tuber maturation; (2) lower interplant competition, permitting higher plantation density; (3) more rapid drying of the tops at maturity to aid mechanical harvesting; (4) underground structure superficially compacted for better mechanical harvesting; and (5) higher nutritive value of tuber. Known variability permits a reasonable expectation of obtaining clones with most of these traits.

Other quite new genetic modifications can be envisaged if sexual seeds become the basic material for plantations. Preliminary requirements are: highly prolific female parents; good seed germination; and knowledge of the combining ability of the parents.

Two levels of these crop modifications can be projected: (1) the tubers from the seedling may be used as propagating material for commercial production; and (2) the seedling cycle must give good tuber yields and hence breeding selection will change from clonal to seedling performance. In both cases a relative genetic homogeneity is wanted in the progeny. Both parents, or at least one of them, should be built through successive brother × sister crossings in order to reach some level of homozigosity for main characteristics.

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