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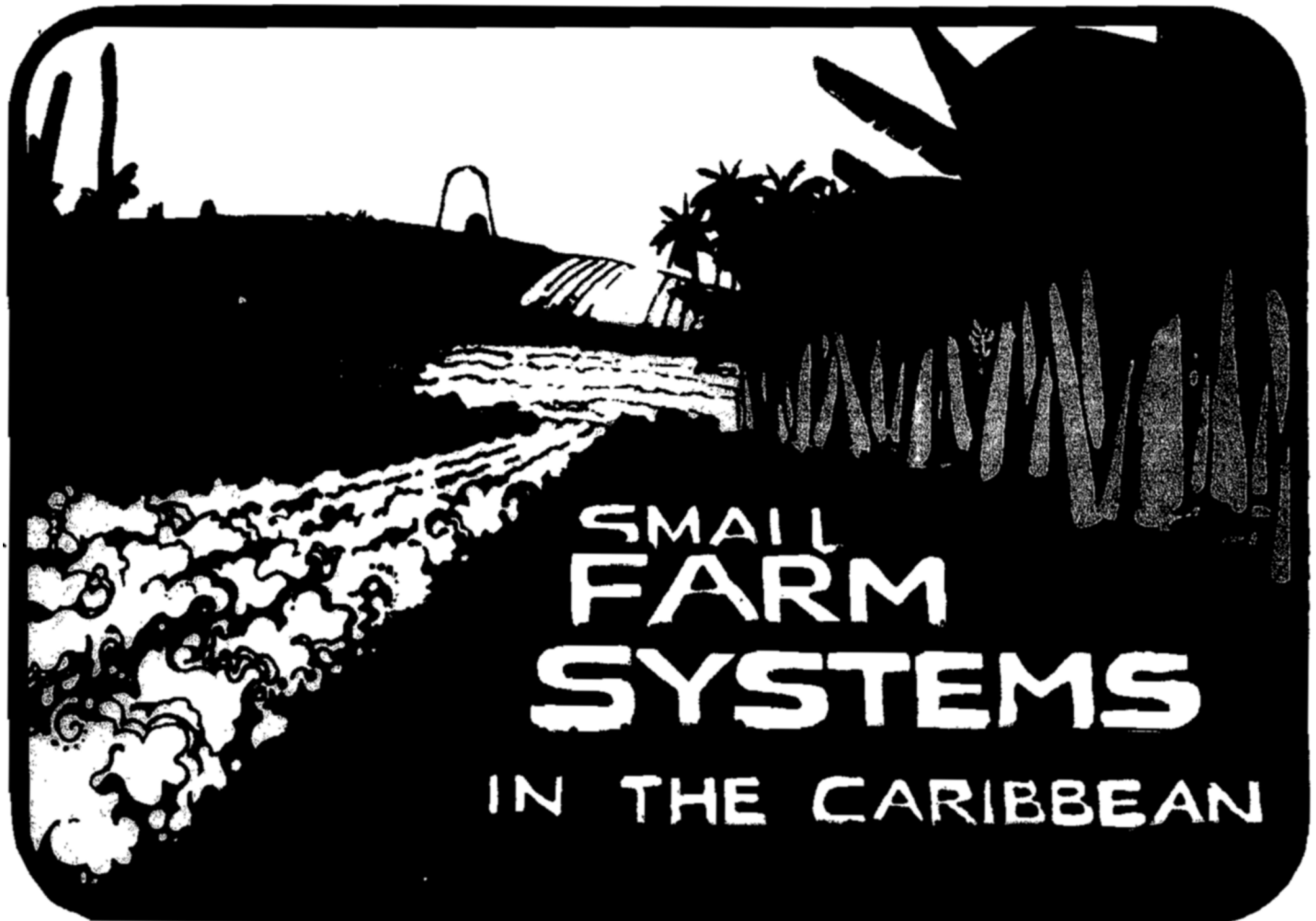
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Biological Basis for the Breeding of Better Food Yams

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The food yams can now be considered to be no more difficult to improve than many other plants. Their system of building up and accumulating useful reserves, their system of ecological adaptation as well as their system of genetic variations offers a sufficient range of diversity to be within the reach of selection pressures. Their sexual behaviour is progress-

ively reset among the important species where it was deficient. Evolutionary evidence and the sapogenine species experience give wide prospects for attempts of intraspecific introgression. Last but not least, through *in vitro* technology, new horizons are rising for the modern venture of food yam improvement.

Efforts to improve edible yams (*Dioscorea* sp.p.) are not very ancient. This fact, added to the low number and the wide dispersal of concerned research workers, account for the doubtful feelings often expressed against this improvement. However, it appears not more hazardous than, among others, the banana or the sugarcane ones. The weak international interest in yam exchange is a major difference with these crops and, in turn, accounts widely for their relegation aside of agronomic priorities, while biological hindrances are generally put forth. Our thesis is that basic knowledge exists now, which warrants actual achievements to pluridisciplinary programs aiming at yam improvement through breeding.

Biological processes in yams which are at the breeder's disposal can be outlined from three levels: systems of reserve biosynthesis and assimilates accumulation, systems of ecological adaptation, and systems of genetic variation. Considering the genus *Dioscorea* as a whole, the diversity of biological paths brought to our knowledge offers an uppermost but interesting challenge to the breeding prospects.

Systems of Biosynthesis and Storage of Assimilates Photosynthetic Apparatus

Even over a small country, the photosynthetic apparatus of the yams can establish itself quite at variation among species and cultivars. The cataphylles phase duration, the phyllotaxy and the vine architecture, the lamina individual area, are concerned.

Burkhill (1960) mentioned the wide phyllotaxic spectrum of the genus, going from alternate to seven-verticillate leaves.

How such situations could be practically significant can be seen through the low sensitivity to no-staking of the more or less deeply lamina indented species (*D. dumetorum*, *D. trifida*), according to the deeper penetration of light in their canopy.

Highly different efficiencies of transportation and sink setting of assimilates are to be expected from the different weight ratios of aerial part to tuber, this not only among species but also cultivars. However, care must be taken when the plantation time is changed: its shift from March to June has reversed the rank of ratios of two *D. alata* cultivars (Degras et al., 1977).

Characters of the Products Stored in Tubers

There is no need to detail this basic point that a hundred *Dioscorea* species which store starch (85-99% of tuber d.m.) are edible with a useful content of protein and vitamins, even if for a

limited number a detoxification could be required. It is worth mentioning that:

1. The tuber can be eaten crude in some species like *D. fandra* of Malgasy (Madagascar);
2. In the tuber's enzyme activities noticeable variations have been found between and within species (Diopoh, and Kamenan, 1981, etc.);
3. In starch viscosity a large variation is known (Coursey, 1980) as well as in flavour at cooking (Osinowo, 1977); and
4. Starch digestibility may be as high (*D. dumetorum*) as the Cassava one (Szyllit et al., 1980), while unknown substances seem to carry some digestibility problems in *D. alata* cultivars (Martin, 1980).

Morphology and Physiology of the Tuber Growth

Though a fair number of cultivars need a good soil depth for their tuber, it is not uncommon to access easily to the starch sink. Letting aside the aerial production of *D. bulbifera* (and at a lower level of some *D. alata*), rather superficial underground productions are known with *D. alata* (i.e. 'Lupias' or 'Belep' types of New Caledonia), *D. cayensis* (cv. 'Krengle' of Ivory Coast), or *D. trifida* (cv. 'Moengo 5' of Guyana) etc.

Quite different balances between the size of individual tubers and their number by plant can be managed through cultivar variation, enforced by plantation date, vegetative seed size, chemical treatment, plantation densities, staking, fertilization and so on.

The well known inter-species variation for harvesting time rests upon a large intra-species one. A recent datum: among a population of about 400 hybrids pertaining to three progenies of *D. cayensis-rotundata* obtained from sexual seeds of IITA in Guadeloupe, maturity extended last year from seven to eleven months after planting.

The general inverse correlation between duration of vegetative growth and duration of dormancy over the annual cycle, does not impede some independent combination, as have resulted from selection pressure in *D. trifida* progenies (Arnolin, unpublished data).

A differential sensitivity of cultivars of *D. alata*, under cool (18° C) storage of their tuber, is expressed by the extension of the onset of germination of 79 cvs from seven to thirteen months after harvest.

Systems of Ecological Adaptation

A limited number of significant data will be quoted only among the possible ones.

Some species are rich in cultivars with a tendency to a perennial aerial system. Among *D. cayenensis-rotundata*, "Yellow yam" cultivars, if not or if partially harvested, hold many of their first leaves over two years in high rainfall areas. Among *D. esculenta* and *D. trifida*, the leaves of two successive growing seasons are often overlapping. However, the annual disorganization of the aerial system is widely prevailing.

In the northern hemisphere, when plantation is progressively delayed from July to December, the leafy growth part of the cycle and the yield are reduced first, then are gone quite haywire in most cases. But cultivars of *D. cayenensis* and *D. trifida* can be less affected (Arnolin, 1982, 1983).

Cultivars geographical adaptation appears favoured by archaic traits and vigour, considering the dispersal of the *D. alata* primitive group (Marrin, 1974; Degras, 1976) or the experimental behaviour of selected *D. trifida* hybrids compared to traditional Guyanese cultivars (Degras, 1980). The correlation observed by Toure and Ahoussou (1978) between cultivars performances in the centre and the south of Ivory Coast also supports this idea. The recent world dispersal of some cultivars of *D. alata* from the germplasm collected by F. Martin in the seventies, though highly linked to their low susceptibility to anthracnose, is not entirely at discrepancy with it (Degras et al., 1983).

Much has to be described of the different levels of susceptibility to diseases and pests of the yams among and within species. While they seem clear for anthracnose, they could appear inconspicuous for nematodes: the classification of the same cultivars of *D. rotundata* by Adesiyian (1977) and Bridge (1978) is so different that the adequacy of methodologies has to be questioned. Nevertheless, species rank in susceptibility may be safely evaluated regarding definite nematodes in definite areas (Hickling, 1974; Nwauz and Fawole, 1981). The situation could be the same for virosis susceptibility: in the Caribbean area, decreasing levels of tolerance to the virus complex are seen from *D. esculenta* to *D. trifida* through *D. alata* and *D. cayenensis* (Mohamed and Mantell, 1976; Marchoux, 1980). Another field of species variation has recently been discovered in Guadeloupe (Kermarrec, Febvay and Guerrier, person. comm.): the decreasing level from *D. cayenensis* to *D. alata* or *D. bulbifera* through *D. trifida*, of their leaves cut by the Attines ants.

The Systems of Genetic Variation

These systems are mainly those which resulted in the different kinds of variation we have briefly reviewed. But, as everywhere, the biotechnology era can not only amplify their effects but give rise to new paths of variation.

Dioecy (with a higher frequency and/or earliness of males perhaps) is characteristic of the genus. Monoics, however, are not unknown (Miege, 1952; Degras, 1957; Burkill, 1960; Sadik, 1975; Toure and Ahoussou, 1978; Abraham and Nair, 1979), but their fertility remains questionable (Martin and Cabanillas, 1966; IITA, 1977).

However, more than dioecy, the deficiencies of the flowering and seed setting phases are commonly called to mind as the limiting factors in *Dioscorea cayenensis-rotundata* and at lower levels in *D. trifida*. But these cases are far from prevalent among the hundred edible yam species. Moreover, it is only the poor status of the research in yam breeding which lets still aside the fertile circles of wild parent species of any major cultivated ones: since the interesting hypothesis of Prain and Burkill (1939) the likely contribution of *D. persimilis* and *D. hamiltonii* to *D. alata* speciation, no experimental study has tried to utilise them both as a possible source of *D. alata* sexuality renewal. The approach of the relation between the *D. cayenensis-rotundata* complex and its

supposed circle of wild parents is only beginning (Hamon and Toure, 1982).

We consider that, regarding their breeding system, these yams must be each used as sympatric species where panmixy has played a part during their initial sexual history. Sterility should be secondary to the higher ecological adaptation of vegetative reproduction system in humid tropical zones, the easy accumulation of sexually unbalanced genomic and genic combinations and the human selection pressure towards juvenile stage for better food quality. We must have in mind the successful crossings (Martin and Cabanillas, 1966) between diosgenin species pertaining to two botanical sections, quite different either in the systematic of Uline-Knuth (1924) or the Matuda (1954) one. The preferential chymiotropism of the pollinic tube of a *D. trifida* cultivar towards a *D. alata* cultivar pistil could be an experiment of significant value (Bulle-Legrand, 1983).

That the so-called "sterility" is no more an absolute barrier in *D. alata* genetical variation is shown by the breach observed in the Javanese material and now explored by IITA. Meanwhile, works are going on in the perennial cultivation, photoperiods (Miginiac, 1980) or growth substances applications (Bulle-Legrand, 1982). Cool storage (18° C) has recently brought new information on *D. trifida* flowering behaviour (Arnolin, personal communication).

The relatively high flowering and fertility level of some parental combinations in *D. trifida*, followed by a moderate level of variation of their progenies for the main characters, will permit to release "composite" cultivars of clones to the farmers in Guadeloupe. These composites will benefit for one or more clonal generation from the natural virus clean state brought by the sexual reproduction.

The most serious handicap in sexual breeding of yams will remain the absence or the weakness of correlation between seedlings and clonal generations: in *D. trifida* as well as in *D. cayenensis-rotundata* (Degras, 1980; Wilson, 1980) many character variations, among which yield is one, are significant at the second clonal generation only. However, this delay is not greater than the time spent in most grain crops. And it can be used for a vegetative multiplication of a representative sample of each progeny, enabling thus more valuable tests at the optimum generation.

The first contribution of the vegetative system of reproduction to the enlargement of genetical variations through a better efficiency of sexual selection. It can be done by horticultural techniques (stem cuttings in greenhouse) or *in vitro* techniques (nodal micropropagation), under diseases or pest selection pressures.

But we have to expect more and more direct paths of improvement from *in vitro* techniques. The development of micropropagation to improve the exchange and the conservation of germplasm and to ensure an easier diffusion of selected cultivars are yet at work. The cleaning of good cultivars from virus by tip (meristem) culture is currently done in Barbados for *D. alata* and is undertaken by *in vitro* rhizomotherapy in Guadeloupe for *D. trifida*. No consistent permanent variation has yet been registered from yam micropropagation (Arnolin, pers. comm.). So, application of gamma irradiation to vitroplants seems well indicated (Marie, INRA-Montpellier). But true tissue cultures of diosgenin species have shown organs mixoploidy and the feasibility of cellular selection (Karanova, Shamina, 1978).

The next steps should be to renew the tentative of haplomeethod, first by androgenesis (Arnolin, 1976), and to develop the protoplasts and somatic hybridization techniques. Several laboratories are seemingly at work in these directions.

To conclude, when comparing the few lines hallowed by Coursey in his basic monograph to the breeding of the yams with the present stage of continuously released selected cultivars, of

crossing schemes and of effervescent exploratory designs with biotechnological support, it appears that the breeding of yams has definitely entered the field of consideration of university teaching and of major allocations of resources for agricultural development of tropical countries.

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