

Studies on the reproductive biology of white yam (*Dioscorea rotundata* Poir.)

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Summary

Investigations were conducted on the identification and distribution of yam natural pollinators, flowering pattern and hybridization of white yam (*Dioscorea rotundata* Poir.) at the International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria, in order to provide informations for producing hybrid seeds needed for yam genetic improvement.

Insects belonging to the Coleoptera (48.0%), Diptera (20.4%), Hymenoptera (20.0%), Hemiptera (5.8%), and Thysanoptera (5.8%) were caught around yam plants and presumed to be pollinators: they entered open-receptive-flowers and their presence on yam plants coincided with the duration of the flowering period.

Studies on the flowering pattern revealed that: (i) Male and female clones differed in their periods of flower initiation as well as the flowering duration; (ii) Seed production and conventional breeding methods are feasible if staggered planting, water and soil fertility could be managed to ensure that flowering periods of males and females nick and also extend flowering.

Artificial pollinations within white yam and between white yam and yellow yam (*D. cayenensis* Lam) using the camel hair brush method were successful, but resulted in a relatively low fruit set (31.8% maximum). This method was more effective than natural pollination (19.2%) and can thus supplement it for the production of hybrid seeds for introducing genetic variation in yam breeding populations.

Introduction

The genus *Dioscorea* L. (Dioscoreaceae) includes over 600 species. The edible starchy tubers produced by *Dioscorea* species (yams) provide the staple carbohydrate food for about 70 million people of over a dozen countries of Tropical Africa.

For centuries, yams have been vegetatively propagated from tubers of local cultivars. Yam improvement has remained the selection of acceptable clones from collections resulting from open

crosses. This continued vegetative propagation and the lack of hybridization have precluded the possibility of new genetic characteristics, resulting in a stagnation of yam improvement (Sadik & Okereke, 1975a, b).

Efforts to improve the white yam, *D. rotundata*, through hybridization have been frustrated by the low rate of flowering, the very low rate of fruit setting and poor seed germination. Following the development of methods of germination and growing large number of yam seeds, Sadik and Okereke

(1975a, b) and Okoli (1975) raised hopes of rapid improvement of yams by the conventional breeding methods of hybridization and selection.

Accordingly, this study on the reproductive biology of white yam was undertaken:

- (i) To identify the insect pollinators of yams and assess their efficiency with regard to yam natural pollination.
- (ii) To study the flowering pattern of yams and look into the problems connected with pollination and subsequent production of hybrid seeds.
- (iii) To investigate the possibilities of massive production of yam hybrid seeds through hand pollination methods.

Materials and methods

During March 1990, twelve separate spatially isolated crossing blocks were established in the experimental field (IITA, Ibadan, Nigeria). Adjacent blocks were located 300 to 500 meters apart at least from each other. The objective of this practice was to separate genetically the selected parents and to obtain varied microclimates that could influence both flowering and the distribution and activity of natural pollinators. The parents used in this experiment were chosen on the basis of proven ability to flower profusely enough and regularly from one year to another, thus possessing characteristics amenable to breeding.

Three male clones: TDr 131, TDr 205, TDc 760 and three female clones: TDr 90, TDr 747 and TDr 750 were used. Tuber sets of about 500 grams were planted in handmade mounds 40–60 cm high spaced at 1★1 m; mound tops were grass-mulched for humidity conservation. Individual plants were also dressed with 500–1000 grams of well decomposed poultry manure after vine emergence. Each block contained five plants of pollen parents juxtaposed with five plants of female genotypes. The female parents were also planted alone to monitor pollen transfer by natural causes. During April 1990, a second planting was made at each site, identical to the preceding one: this second plant-

ing was supposed to extend the flowering period of plants and allow more hand pollinations.

Various aspects of the reproductive biology were observed including the role of entomophilous fauna on the natural pollination of yam, its flowering pattern and the production of hybrid seeds from the selected cross parents.

Identification and distribution of natural pollinators

To be acquainted with the problems associated with very low natural fruit set, investigations were made to provide an insight on the nature and distribution of natural agents responsible for pollen transfer from anthers to stigmas. From July to September 1990, insects were regularly collected every two weeks on- and around-yam flowers between 10.00 hrs and 16.00 hrs using a mouth aspirator. Insects collected were later transferred into a killing bottle which is a glass vial 2–3 cm in diameter, containing killing agents such as ethyl acetate or alcohol. They were identified and counted by species; the hairiness of their body was also scored on a 1 to 3 subjective score where: 1 = less hairy; 2 = moderately hairy; and 3 = very hairy.

Those insects presumed to be yam pollinators fulfilled three conditions: (i) They were present on yam plants from July to September; these months coincided with the annual period when yam blooming occurs; (ii) They were collected on- and around-yam flowers between 10.00 hrs and 16.00 hrs; these hours coincided with the day period when sweetly scented yam flowers are open and attract pollinators; (iii) They were smaller in size, so as to be collected preferably with a mouth aspirator, considering the size of the yam flower (1–3 mm in diameter for staminate flowers; 4–8 mm long for pistillate flowers, and open by a 100–200 μ m three-way slit). Those insects which could not fulfill simultaneously the three conditions were simply discarded.

Flowering patterns

To understand pistillate and staminate cultivars whose flowering synchronize and how they produce viable seeds, observations were also made on the population of white yam. In isolated blocks, the

date of flower initiation and cessation were recorded for both sexes. Six characters were selected and studied (Table 2) as regards their influence on the abundance of staminate flowers in the field, and efficiency of pollination, fruit set and seed set.

Artificial pollinations

Hand pollinations involving intraspecific crosses within white yam and interspecific crosses between white and yellow yam (*D. cayenensis*) were made: Female spikes containing mature but not yet opened pistillate flowers were selected daily in each block. They were bagged carefully using thrip-proof cloth-bags, between 7.00 hrs and 10.00 hrs. Hand pollinations usually occurred in the afternoon, under apparently cool atmospheric conditions presumed to be ideal for pollen germination (Akoroda, 1981). Excised anthers from recently opened staminate flowers were transferred to stigmas of opened pistillate flowers using camel brush bristle tips.

To evaluate accurately the crossability between clones, the pollination scheme enabled that each female genotype received pollen from all the male parents each time it was hand pollinated. As control, other pistillate spikes were left unbagged to allow natural pollination by insects.

Fruit set (%) and hybrid seed production were estimated for overall spike for each cross combination under natural and artificial pollinations, as each pistillate flower has six locules and could bear up to six seeds.

Results

Identification and distribution of yam natural pollinators

A total of 701 insects representing 13 species were collected between July and September 1990 from the 12 separate spatially isolated yam crossing blocks. They represent 5 families: Coleoptera: 336 (48.0%), Diptera: 143 (20.4%), Hymenoptera: 140 (20.0%), Hemiptera: 41 (5.8%), and Thysanoptera: 41 (5.8%).

Those insects were very active on- or around-sweetly scented yam flowers during the day while they were opened (10.00–16.00 hrs). Insect populations (Table 1) varied within the flowering period of yam plants. Flowering started in June, reached its peak period in early August and stopped in early September: Insect populations varied in the same pattern.

Table 1. Type and distribution of insects caught on isolated blocks of yam (natural pollinators?)

Name	Order	Family	Hairiness (score 1–3)	Number caught on (date):				
				15/7	1/8	15/8	1/9	Total
1. <i>Apis mellifera</i>	Hymenoptera	Apidae	3	8	13	5	5	31
2. <i>Barombia humeralis</i>	Coleoptera	Chrysomelidae	2	13	21	31	12	77
3. <i>Brachymeria ovata</i>	Hymenoptera	Chalcididae	3	23	18	28	10	79
4. <i>Chauliognathus pennsylvanicus</i>	Coleoptera	Cantharidae	3	13	22	34	6	75
5. <i>Cheilomenes sulfurea</i>	Coleoptera	Coccinellidae	3	13	15	6	5	39
6. <i>Chrysolagria</i> spp.	Coleoptera	Lagriidae	3	17	31	19	0	67
7. <i>Dysdercus superstitionis</i>	Hemiptera	Pyrrhocoridae	1	14	17	10	0	41
8. <i>Lagria villosa</i>	Coleoptera	Lagriidae	3	8	10	15	0	33
9. <i>Larothrips dentipes</i>	Thysanoptera	Thripidae	3	7	14	17	3	41
10. <i>Musca domestica</i>	Diptera	Muscidae	3	4	7	12	3	26
11. <i>Nacerda melanura</i>	Coleoptera	Oedemeridae	3	11	18	12	4	45
12. <i>Polistes variatus</i>	Hymenoptera	Vespidae	2	7	14	9	0	30
13. <i>Stomoxys calcitrans</i>	Diptera	Muscidae	3	28	144	32	13	177
Total			–	166	244	230	61	701

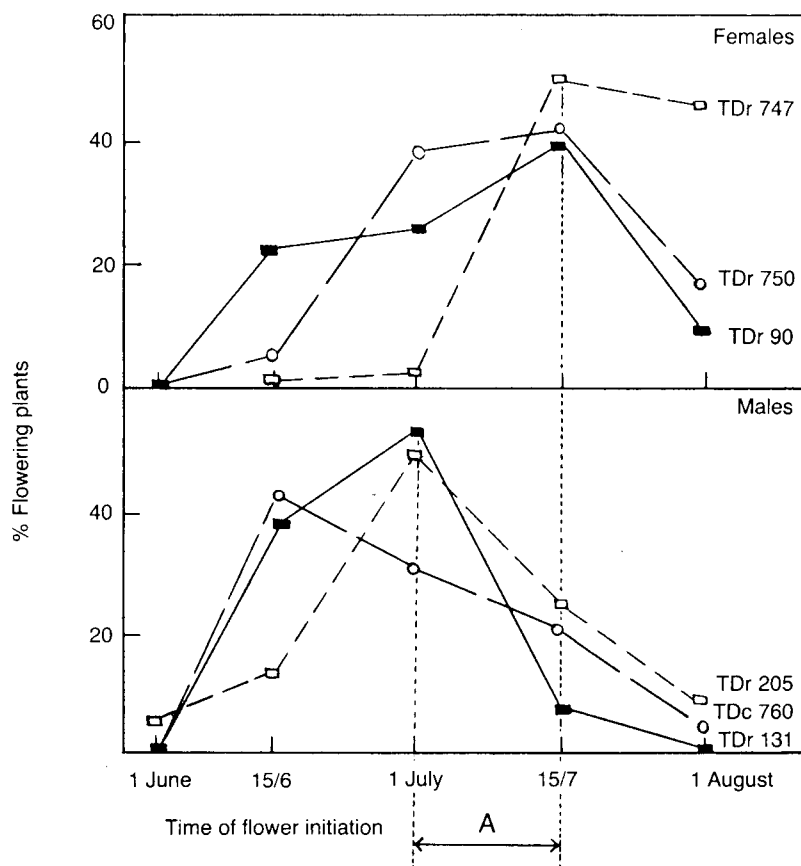


Fig. 1. Flowering distribution in white yam. A: Note that the difference between the two peaks is 15 days.

Flowering patterns in white yam

The populations differed in days to flowering as well as in flowering duration. Distribution of flowering time in the six clones (Fig. 1) shows that staminate plants flowered earlier than pistillate ones.

In male clones, TDr 131 and TDr 760 with 39% and 46%, respectively, of plants that flowered in early June were the earliest, as compared to TDr 205 with 19% only of flowered plants within the same period. After flower initiation, the number of flowering plants in most clones followed a normal distribution with its peak located in August. During this study, three monoecious stands were observed among plants presumed to be completely female (TDr 747 and TDr 90). In these stands, completely male spikes appeared earlier than did

completely female spikes. Those with male, inter-

Table 2. Vegetative characteristics influencing flowering abundance of yam male clones in the field

Character	Yam male clones		
	TDr 131	TDr 205	TDr 760
1. Plant establishment (%)	100 a	85 b	80 c
2. Plant leafiness (1-5 scale)	3.2 a	2.6 a	2.3 b
3. Flowering plants (%)	93 a	80 a	65 b
4. Flowering branches (%)	19.5 NS	12.8 NS	14.8 NS
5. Flowering intensity (1-4 scale)	2.8 a	1.8 b	1.4 b
6. Flowering duration (weeks)	9.3 a	7.5 b	9.1 a

mediary forms and female flowers appeared at an intermediary date.

Observations made on the three male clones used in this experiment, namely TDr 131, TDr 205, and TDc 760 revealed (Table 2) that they all differed significantly in their ability to establish in the field. Also, TDr 131 and TDr 205 did not differ significantly when plant leafiness and the proportion of flowering plants were considered, as compared to TDc 760 whose performances for those two characters were low (2.3 and 65%, respectively).

No significant difference was noted on the proportion of flowering branches between the three clones. Furthermore, the highest flowering intensity and duration (2.8 and 9.3 weeks, respectively) which characterized TDr 131, in addition to its high rates of establishment and flowering ability (100% and 93%, respectively), clearly showed that this clone is amenable to selection and for use as a pollen parent.

Artificial pollinations

Crosses within white yam cultivars, and between white and yellow yam (*D. cayenensis*) were made

by hand pollination; some flowers were left to natural pollination in the isolated plots. Fruit set (%) and potential seed production (Table 3) showed that fruit formation, development, and retention on pistillate plants produced from tuber cuttings were low. Also, the fruit set (%) from hand pollinations was relatively higher than from natural (insect) pollination.

When the female clone TDr 90 received pollen from the three selected male parents, and from unknown sources (control) through insect pollination, the fruit set significantly differed among pollen sources: crosses with pollen from TDr 131 was the highest (31.81%), and the TDr 90 × TDc 760 interspecific cross had the lowest fruit set (6.57%).

On the other hand, when the pistillate clone TDr 747 was crossed with pollen from the same selected parents, the fruit set was highest but not significantly different when pollen from the two parents TDr 131 and TDr 205 was used. Their fruit sets (27.33% and 24.70%, respectively) were significantly higher than natural (insect) pollination with 19.23%. Here again, the interspecific cross TDr 747 × TDc 760 had a significantly lower fruit set (7.69%).

With the pistillate clone TDr 750, only its combination with the staminate parent TDr 131 resulted in a significantly higher rate of fruit set (28.73%).

Table 3. Fruit set and potential seed production from natural and hand pollinations within white yam and between white and yellow yam (*D. cayenensis* Lam.)

Female parent	Male parent	Flowers pollinated	Fruit set		Potential seed production (no)
			(number)	(%)	
TDr 90	TDr 131	88	28	31.81 a	168
	TDr 205	52	10	19.23 b	60
	TDc 760	76	5	6.57 d	30
	Natural	262	34	12.98 c	204
TDr 747	TDr 131	150	41	27.33 a	246
	TDr 205	85	21	24.70 a	126
	TDc 760	104	8	7.69 c	48
	Natural	447	86	19.23 b	516
TDr 750	TDr 131	46	13	28.73 a	78
	TDr 205	37	7	18.92 b	42
	TDc 760	44	2	4.54 c	12
	Natural	323	55	17.02 b	330
Total		1714	310	18.08	1860

The other combination TDr 750 ★ TDr 205 was not significantly different when compared with the natural pollination (18.92% and 17.02%, respectively). The interspecific cross TDr 750 ★ TDc 760 resulted in a much lower rate of fruit set (4.57%).

Interspecific crosses between white yam and yellow yam gave very low fruit sets of below 10%, suggesting genetic incompatibility between those two yam species.

Discussion

The proportion of flowers that naturally set fruits varied greatly in the field. This variation could be attributed to the relative location of a given isolated block, which is affected by the presence of natural pollinators responsible of flower pollination and fertilization. Natural pollinators collected from open scented flowers were varied in size, form, and mobility. So their efficiency as pollinators would also vary.

Taking into account their small size, thrips (*Laurothrips dentipes*, Thysanoptera, Thripidae) would have the possibility of penetrating in both staminate and pistillate flowers, thus playing a role in yam pollination as earlier reported (Pitkin, 1973; Sadik & Okereke, 1975b; Akoroda, 1981, 1985). Other pollinators included insects belonging to the Coleoptera, Diptera, Hemiptera and Hymenoptera. To achieve effective pollination, plants must produce food for insects to make visits worthwhile, while stimulating further visits to other flowers and plants. Flowers must be easily recognized and accessible by insects. Unfortunately, flowering in yam is characterized by a lack of synchronization and flower size is too small (1–3 mm in diameter for staminate flowers; 4–8 mm long and 1.5–2.5 mm in diameter just before opening for pistillate flowers, and open by a 100–200 µm three-way slit). Therefore a yam flower would give inadequate food and is not easily accessible. Insects may favour more accessible flowers with more food: this may partly explain the poor fruit set of open-pollinated flowers in the field.

On the other hand, irregular flowering in yam retards progress in genetic improvement. Lack of

synchronization in the flowering of both sexes also constrain improvement work as also reported by other authors (IITA, 1974; Okoli, 1981; Akoroda, 1981, 1983).

Also, the poor seed production from open field crosses generally noted in the field may result in reduced availability of pollen for insect pollinators. The six characters studied in Table 2 are indicators of vegetative vigour, which is positively correlated to the reproductive ability of the plant (Akoroda, 1981).

The higher plant establishment in TDr 131 can be attributed to the fact that the planting material used in establishing that clone in the field was mainly constituted of whole tubers, rather than cut pieces prone to rotting in the soil (TDr 205 and TDc 760). The results of this investigation suggest that in establishing a yam plot for breeding purposes heavier sets preferably constituted of whole tubers must be used.

In addition, greater plant leafiness tends to increase the proportion of flowering plants and flowering intensity in yam breeding populations. Selecting yam clones possessing good vegetative development characteristics, coupled to appropriate agronomic practices (application of organic fertilizers at plant emergence) can improve staminate and pistillate flowers profuseness in the field, efficiency of pollination, and subsequent fruit and seed set.

Differences also exist in the duration of the flowering period: these differences could be attributed to the water and temperature regimes during the flowering period. To overcome the difficulties related to the differences in the period of flower initiation, (i) large number of plants from selected genotypes should be established in order to obtain sufficient flowering plants for an effective hybridization program; (ii) Staminate clones should be planted at 2 week-intervals for two months, so that pollen is always available in the field whenever pistillate flowers are receptive. This cropping pattern known as staggered planting, had also been advised by Okoli (1981) and Akoroda (1985) for massive production of hybrid seeds in white yam.

Artificial pollination within white yam and between white yam and yellow yam (*D. cayenensis* Lam.) is possible using the camel hair brush meth-

od as earlier reported by Akoroda (1981, 1985). The low percentage of fruit set observed in both cases could be attributed to the genetic incompatibility of yam cultivars used in this experiment. This genetic incompatibility most evident in interspecific than intraspecific crosses could result from higher frequency of meiotic irregularities during fruit formation because of differences in chromosome numbers in the two parents (*D. rotundata*: $2n = 40, 60$; *D. cayenensis*: $2n = 36, 54, 60-63, 66, 80, 140$) which led to a high rate of fruit abortion. Such postulations had also been made by Martin (1966) in interspecific crosses between *D. floribunda* and *D. composita*. But Akoroda (1985), on the other hand, obtained a spectacularly high fruit set and seed fertility in a cross between *D. rotundata* and *D. praehensilis* (46.3%) and attributed this success to the matching chromosome numbers of these species ($2n = 40$).

Conclusion

The results obtained from this study do indicate that:

(i) Yams are naturally pollinated by a variety of insects, among which Coleoptera (48.0%), Diptera (20.4%), Hymenoptera (20.0%), Hemiptera (5.8%) and Thysanoptera (5.8%). Natural pollinators are active on yam flowers at periods of the day during which they are open. Because those flowers are sweetly scented they attract diurnal insects in search of food which simultaneously pollinate yam.

(ii) Studies on the flowering pattern of white yam revealed that the genotypes differed in days to flower as well as duration of flowering. In spite of these differences in the flowering behaviour, seed production and therefore conventional plant breeding methods are feasible in white yam if staggered planting, water and soil fertility could be managed to synchronize and extend the flowering periods.

(iii) Hand pollinations within white yam and between white and yellow yam (*D. cayenensis* Lam.) were carried out and the results obtained showed

that: Intraspecific crosses (Hand pollinations) greater than Natural pollinations by insects (Control) greater than Interspecific crosses (Hand pollinations) in terms of fruit set. Hand pollinations can therefore supplement natural pollinations for large scale production of hybrids seeds needed for the genetic variability desired for an efficient yam breeding program.

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