Tetraploid hybrids from interploid 3x/2x crosses in cooking bananas

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ABSTRACT - The genetic improvement program of CIRAD-FLHOR for bananas and plantains is based, in the short term, on obtaining tetraploid hybrids according to a crossing scheme which uses a triploid cultivated variety as female parent and natural or hybrid diploid varieties as male parents. This article reports our preliminary results on evaluation of the fertility of 38 varieties of the type French plantain and 5 varieties of the sub-group Popoulou/Maia Maoli (all cooking types), pollinated repeatedly by the wild species *Musa acuminata burmannicoïdes* (clone Calcutta 4). The quality of seeds from these crosses was studied and chromosome number distributions of progenies checked by chromosome counting. With these crosses, 40-50% of seeds collected contained no embryo. *In vitro*, the quality and percentage of germination (37-100%) varied considerably as a function of seed quality. Moreover, no relation was found between seed quality and the chromosome number in the embryos. Some tetraploid and heptaploid hybrids from Popoulou/Maia Maoli and Plantain were obtained from good seeds with endosperm.

Hybrides tétraploïdes obtenus par croisements de triploïdes et de diploïdes chez la banane à cuire.
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RESUME - Le programme d'amélioration génétique des bananes et plantains, poursuivi au CIRAD-FLHOR, est basé, à court terme, sur l'obtention d'hybrides tétraploïdes à partir d'un schéma de croisement faisant intervenir un cultivar triploïde utilisé comme parent femelle et des variétés diploïdes sauvages ou hybrides prises comme parent mâle. Le document présente les résultats préliminaires obtenus à partir de l'évaluation de la fertilité de 38 variétés du type French plantain et de 5 variétés appartenant au sous-groupe Popoulou / Maia Maoli (toutes étant des bananes à cuire), pollinisées de façon répétée par l'espèce sauvage *Musa acuminata burmannicoïdes* (clone Calcutta 4). La qualité des graines obtenues à partir de ces croisements a été étudiée et la répartition des différents niveaux de ploïdie parmi les descendants a été analysée à partir du comptage des chromosomes. Dans le cas des croisements effectués, 40 à 50 % des graines récoltées ne contiennent pas d'embryon. En conditions *in vitro*, la qualité et le pourcentage de germination (de 37 à 100 %), utilisés comme un critère de la qualité des graines, varient considérablement. Par ailleurs aucune relation entre la qualité des graines et le nombre de chromosomes dans les embryons n'a pu être mise en évidence. Quelques hybrides tétraploïdes et heptaploïdes entre Popoulou / Maia Maoli et Plantain ont été obtenus à partir de bonnes graines avec endosperme.

KEYWORDS: Bananas, *Musa*, hybridization, fertility, chromosome number, tissue culture.

MOTS CLES : *Musa* (bananes à cuire), hybridation, fertilité, nombre chromosomique, culture de tissu.

Introduction

With a production of about 72 million tons per year (FAO, 1992), banana is the most economically important fruit crop in the world. Only 11 percent, mainly dessert bananas are exported. The other 89 percent are produced for local consumption or internal trade within developing countries.

Nearly all edible bananas have originated from two wild diploid species (2n=22), *Musa acuminata* (genome A) and *Musa balbisiana* (genome B). These herbaceous plants produce seedy fruits with little pulp and multiply by sexual reproduction as well as vegetative propagation, with suckers arising from the sympodial underground growth of the corm.

Evolution and domestication processes lead to the emergence of varieties bearing almost sterile flowers, and ovaries develop into parthenocarpic fruits (without any pollination).

Edible bananas are of monospecific (pure *M. acuminata* cultivars) or bispecific origin (*M. acuminata* x *M. balbisiana* cultivars). Moreover, there are different ploidy levels: diploid (AA or AB groups), triploid (AAA, AAB, ABB groups) and

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very rarely tetraploid. Plantain (AAB) is a very important subgroup of cooking bananas of major importance in the diet of millions of people in Africa, Latin America and the Caribbean. Popoulou/Maia Maoli is another cooking banana AAB subgroup, largely distributed in Polynesia, but closely related to Plantain.

Despite a great number of morphological forms, the genetic basis of the Plantain group is very narrow and isozyme electrophoresis cannot clearly distinguish between different varieties (HORRY, 1989). From a genetic point of view, plantain cultivated worldwide can be considered as monoclonal, especially with respect to disease resistance. This is also true for export dessert bananas, only one group of which (Cavendish, AAA) is cultivated.

This monoclonal culture system and the increasing threat of parasites (black leaf streak disease, Panama disease, weevils, viruses) are deleterious to banana and plantain production. Moreover, chemical controls are not appropiate for small farmers in developing countries. To address this situation, FLHOR, the Fruit and Horticultural Crops Department of CIRAD, (Centre de coopération internationale en recherche agronomique pour le développement) has undertaken, since 1982, a major genetic improvement program for bananas and plantains (BAKRY *et al.*, 1990). In the short term, this program aims at obtaining hybrids from crosses between a triploid variety, as female parent, and wild *M. acuminata* or improved diploid AA varieties as male parent (PERSLEY and DE LANGHE, 1987, for review).

Some triploid varieties produce non-reduced female gametes (2n=3x=33) which are able to produce seeds once fertilized. This phenomenon has already been observed among varieties of the sub-groups Gros-Michel (AAA), Mysore (AAB) (CHEESMAN, 1932), Pome/Prata (AAB), Plantain (AAB) and Pisang Awak (ABB) (SHEPHERD *et al.*, 1986).

The crossing scheme is based, from a genetic point of view, on complete conservation of the 3x genome, contributing the valuable agronomic and fruit qualities of the female parent, associated with a haploid genome carrying a dominant disease resistance gene with high penetrance provided by the diploid male parent (STOVER and BUDDENHAGEN, 1986). Thus, only tetraploid hybrids (2n=4x=44) are retained from the descendants, since these alone would involve the participation of non-reduced female gametes.

This paper presents results of a study on the fertility of several cooking varieties from the Plantain and Popoulou/Maia Maoli sub-groups. The evaluation of seed quality, and chromosome number of hybrids obtained from crosses with a diploid wild species of banana are also presented.

Material and Methods

The Calcutta 4 *(M. acuminata spp. burmannicoïdes)* clone, highly resistant to black leaf streak disease, was used as male parent in this study. Calcutta 4, which is strongly homozygous, showed 100% pollen viability determined by the Alexander method (1969).

34 French type varieties of the sub-group Plantain and five varieties of the sub-group Popoulou/Maia Maoli were crossed several times with Calcutta 4.

At maturity, the bunches were harvested and placed in a ripening area. Seeds were removed from the ripe fruits and counted. Only seeds with black, hard integuments, similar to those of wild bananas, were taken into account, the others being aborted seeds.

In vitro culture of the embryos

Immediately after picking, the seeds were surface-sterilized by soaking for 10 min in aqueous silver nitrate solution (1% m/v), then placed for 30 s in a sterile aqueous solution of sodium chloride (0.5% m/v) and rinsed three times in sterile, distilled water.

The seeds were then opened (aseptically) and their quality (structure of embryo and albumen) noted and compared to that of the control diploid seed-producing varieties (DARJO and BAKRY, 1990). The embryos were then placed on a solid culture medium, derived from MS (MURASHIGE and SKOOG, 1962): MS mineral salts, 1 mg/l calcium pantothenate, 1 mg/l nicotinic acid, 1 mg/l pyridoxine HCl, 1 mg/l thiamine, 0.001 mg/l biotin, 100 mg/l meso-inositol, 30 g/l saccharose, 2 g/l Gelrite (SICCAP - EMMOP, Marseille, France), 1 mg/l benzylaminopurine (BAP), 0.4 mg/l indoleacetic acid (IAA) and 8 mg/l bromocresol purple. After adjusting the pH to 5.7 with KOH, the medium was autoclaved for 20 min at 118°C, then transferred into 9 cm diameter Petri dishes each containing 30 ml.

The cultures (10 embryos/petri dish) were placed in the dark at 27°C until the embryos had germinated. The seedlings were then transferred individually into tubes containing the medium mentioned above but without growth regulators (15 ml medium/tube) and placed for 16h/24h under artificial light (Mazda "daylight" fluorescent tubes, 100 $\mu mol\ m^{-2}\ s^{-1}$).

30 to 40 days later, the rooted plants were transferred to the nursery on an artificial substrate (Giffy-7, Giffy Products Ltd., Norway), at a temperature of 25-26°C during the night and 30-35°C during the day, under natural light of 40-150 $\mu mol\ m^{-2}\ s^{-1}$ and 75-100% a relative humidity. Thirty days later, the plants were finally transferred to 3 litre pots in a mixture of river sand and peat, enriched with 10 g/plant of complete fertilizer (N-P-K and microelements).

Cytological studies

Chromosome counting was carried out following the method defined by Shepherd (pers. comm.). The root tips were taken from the plants in the nursery between 6:30 a.m. and 8:00 a.m. and placed in 0.03% w/v hydroxyquinoline solution, open to the air at 20-25°C for 6 - 8 h. The tips were then immersed for at least 3 h into a macerating/fixing mixture (AcOH:EtOH:water, 4:1:5). Finally, the root tips were crushed between the microscope slide and cover-slip in a drop of stain (orcein 2% in a solvent of lactic acid: phenol:glycerol:water, 1:1:1:1). Counting was carried out at 1000 (10 × 100) magnification.

Results and Discussion

Apparent female fertility (AFF)

AFF is defined as the number of seeds obtained from each pollinated bunch, irrespective of their quality.

Among the varieties of the sub-group Plantain, 22 out of 34 tested produced seeds (table 1). The Ekona, Kar Ngou and Kelong Mekintu varieties displayed the greatest fertility among the clones tested, with a minimum of 16 seeds per bunch.

Among the varieties of the sub-group Popoulou/Maia Maoli, (table 2), the cultivars Poingo and Maia Maoli were the most fertile; whereas the variety Popoulou (CIV) proved to be the least fertile.

The apparent female fertility of Popoulou/Maia Maoli plants was on average superior to that of Plantain.

Seed quality

The appearance of the seeds cultured *in vitro* was similar to that of the seeds of wild bananas (black, hard integument). However, dissection showed that 51% of the Plantain seeds (41% for Popoulou/Maia Maoli) did not contain an embryo. The endosperm was not always present.

The seeds containing an embryo were divided into 3 classes (figure 1 and photos 1, 2, 3, 4).

The Class 1 seeds contained little or no endosperm; the embryo was more or less well-formed. The Class 2 seeds had a well developed, starchy endosperm, entirely filling the internal cavity; the embryo was deformed, the haustorium was sometimes absent or giant-sized; embryo development was sometimes incomplete, i.e. stopping at the globular stage (early) or of cylindrical form (later). The Class 3 seeds were perfectly formed, neither embryo nor endosperm presenting

Table 1. Apparent female fertility (AFF) of the sub-group Plantain.

Variety	AFF	AFF (range)	number of hybrids	Number of chromosomes of the hybrids						
				22	23/32	33	34/43	44	45/76	77
Apantu (1)*	0	–	–	–	–	–	–	–	–	–
Bend Mossenjo (3)	0	–	–	–	–	–	–	–	–	–
Banane Serpent (4)	0	–	–	–	–	–	–	–	–	–
Congo 2 (3)	0	–	–	–	–	–	–	–	–	–
Domenico Harton Enano (1)	0	–	–	–	–	–	–	–	–	–
Elat (2)	0	–	–	–	–	–	–	–	–	–
French Rouge (2)	0	–	–	–	–	–	–	–	–	–
Mnalouki (6)	0	–	–	–	–	–	–	–	–	–
N'selouka (8)	0	–	–	–	–	–	–	–	–	–
Okele (2)	0	–	–	–	–	–	–	–	–	–
Owang (1)	0	–	–	–	–	–	–	–	–	–
Red Yade (2)	0	–	–	–	–	–	–	–	–	–
Diby 2 (1)	1	–	–	–	–	–	–	–	–	–
Terrinha (1)	1	–	–	–	–	–	–	–	–	–
Nzumoigne (4)	1.25	0–5	–	–	–	–	–	–	–	–
Mbi Egome 1 (5)	1.4	0–3	–	–	–	–	–	–	–	–
Zue Ekon (1)	2	–	1	–	–	1	–	–	–	–
Obubit Ntanga (1)	2	–	–	–	–	–	–	–	–	–
18 Rouge French (1)	2	–	–	–	–	–	–	–	–	–
PX1/Amou (2)	2	1–3	–	–	–	–	–	–	–	–
French Moyen Vert (2)	2	1–3	1	–	1	–	–	–	–	–
Banane Blanche (4)	2.25	0–5	4	–	3	1	–	–	–	–
French Sombre (2)	3	0–6	1	–	1	–	–	–	–	–
PX3 (6)	3	1–5	–	–	–	–	–	–	–	–
Mbindi (4)	3.75	0–8	3	1	1	–	–	1	–	–
Njombe 1 (1)	4	–	–	–	–	–	–	–	–	–
Rose d'Ekona (2)	4	0–8	2	2	–	–	–	–	–	–
Lifongo Liko (1)	5	–	–	–	–	–	–	–	–	–
Mbang Okon (2)	5	0–10	–	–	–	–	–	–	–	–
French Clair (2)	6.5	6–7	2	–	2	–	–	–	–	–
Kwa (2)	7.5	3–12	5	2	2	1	–	–	–	–
Ekona (1)	16	–	–	–	–	–	–	–	–	–
Kelong Mekintu (2)	30	17–43	12	2	10	–	–	–	–	–
Kar Ngou (1)	47	–	1	–	1	–	–	–	–	–

* Number of pollinated bunches

Table 2. Apparent female fertility (AFF) of the sub group Popoulou/Maia Maoli.

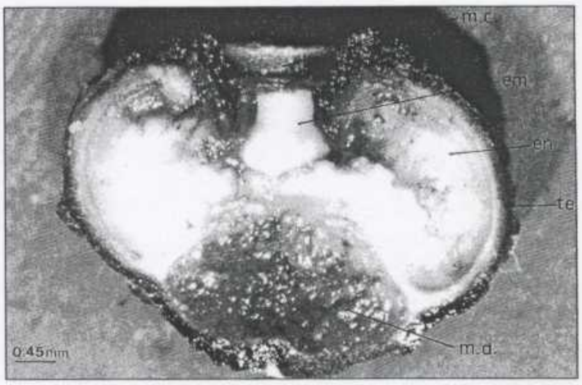
Variety	AFF	AFF (range)	number of hybrids	Number of chromosomes of the hybrids						
				22	23/32	33	34/43	44	45/76	77
Popoulou (CIV) (4)*	3.5	0–7	6	–	1	–	–	4	–	1
Iho-U-Maohi (1)	13	–	–	–	–	–	–	–	–	–
Popoulou (CMR) (7)	38	0–111	13	3	9	–	–	–	1	–
Poingo (14)	68.8	1–221	46	11	23	–	4	5	–	3
Maia Maoli (10)	94.3	19–184	66	22	44	–	–	–	–	–

* Number of pollinated bunches

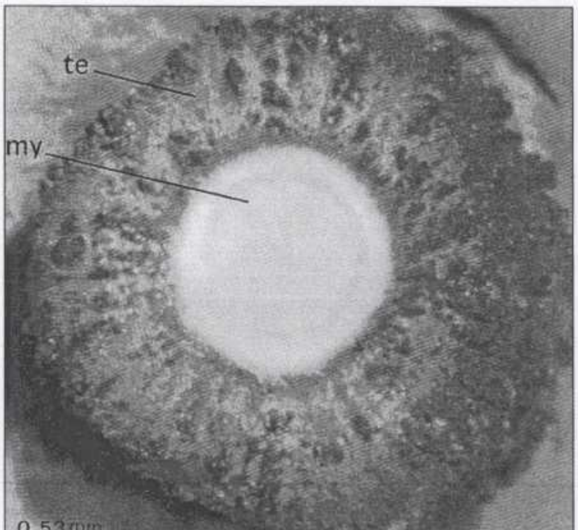
any abnormality, and were identical in every way to those observed in wild bananas (photos 1, 2, 3 and 4).

Theoretically, only Class 3 seeds are capable of germinating after traditional direct sowing. This class represented only 5% of seeds with embryo produced by Plantain, but 53% of those from Popoulou/Maia Maoli. It was noted that, for Plantain, the majority of seeds belonged to Class 2. In general, seeds from Popoulou/Maia Maoli were better-formed and appeared to be of higher quality than those of Plantain.

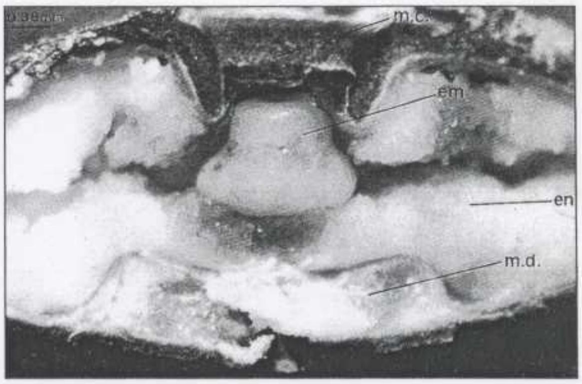
In vitro embryo germination



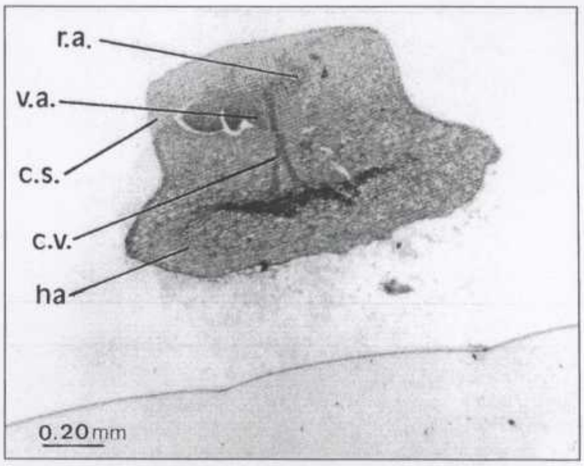
2



1



3



4

Photo 1. Regular seed of Musa balbisiana *with hard and black tegument.*

Photo 2. Open regular seed of Musa balbisiana.

Photo 3. Open regular seed of Musa acuminata.

Photo 4. Cross section of Musa balbisiana *embryo.*

Structure of banana seeds.

Legend: c.s.: cotyledonary sheath; c.v.: conductor vessels; em: embryo; en: endosperm; ha: haustorium; my:mycropyle; m.c.:mycropylar collar; m.d.: mucilaginous disc; r.a.: root apex; te: tegument; v.a.: vegetative apex.

Germination of the well-formed embryos (Class 3) started readily within 15-20 days; the germinated seedlings consisted of a 3-5 mm high coleoptile supported by a fleshy plate, from which the rootlets emerged after approximately 45 days in culture. The transfer of these seedlings into a medium without growth regulator allowed the roots and the leaves to develop.

Germination of abnormal embryos or those from seeds without endosperm (Classes 1 and 2) was more difficult: the embryo sometimes developed directly into a vegetative shoot similar to Class 3 seeds. Most often, heterogeneous calli formed from haustorium tissues. These were found to be composed of quite soft, light-brown zones giving rise at the periphery, to more compact tissues, of ever lighter colour, organized into meristematic nodules. These nodules regenerated into vegetative shoots after transfer of the calli into a medium containing BAP and adenine hemisulfate as the only growth regulators.

The germination level (the ratio of the number of embryos that produced at least one seedling to the number of embryos placed in culture) was closely linked to the seed quality (figure 2): it was highest with Class 3 seeds and lowest with Class 1 seeds. It should be noted that this value was never lower than 37% (seeds of Plantain, Class 1), which is quite satisfactory for seeds of such moderate quality. For a given class of seed, no significant difference was demonstrated between seeds originating from Plantain or Popoulou/Maia Maoli plants.

Ploidy of seedlings

The ploidy level of the hybrids can vary from 2x to 7x but most of these hybrids were diploid or aneuploid with 23 to 32 chromosomes (figure 3).

Tetraploid and heptaploid plants can be easily identified in the nursery (drooping plant, thicker leaves): they rarely escape observation and may be rapidly selected. On the other hand, aneuploid plants (mainly 23/32 chromosomes), or indeed diploids, can also display phenotypes similar to tetraploids with leaves somewhat corrugated with wavy margins and so can be misidentified. The only way in which all the hybrids can be positively identified for their chromosome number is by chromosome counting before planting in the field.

Among Plantain plants (table 1), only the Mbindi cultivar gave a tetraploid embryo (1 embryo 4x from 3 seeds with embryo). Among Popoulou/Maia Maoli plants (table 2), no

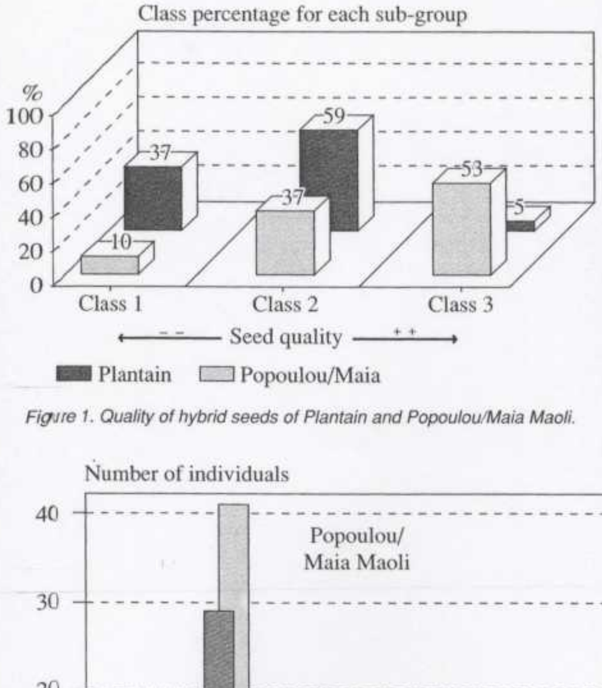


Figure 1. Quality of hybrid seeds of Plantain and Popoulou/Maia Maoli.

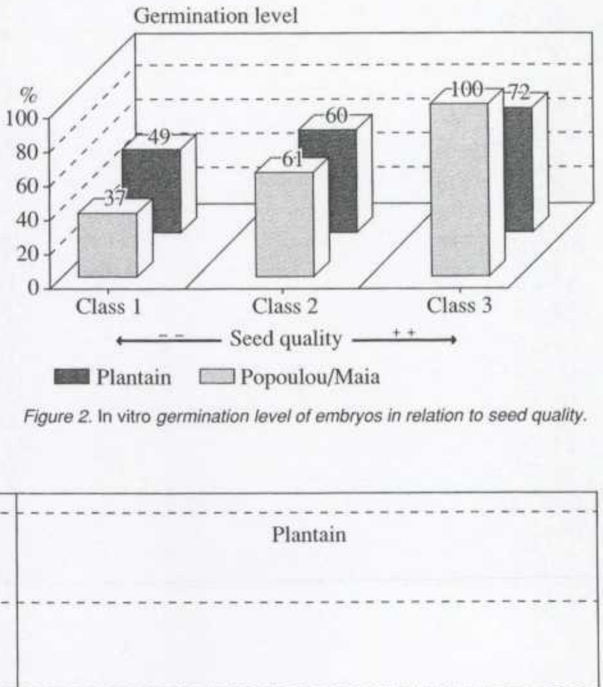


Figure 2. In vitro germination level of embryos in relation to seed quality.

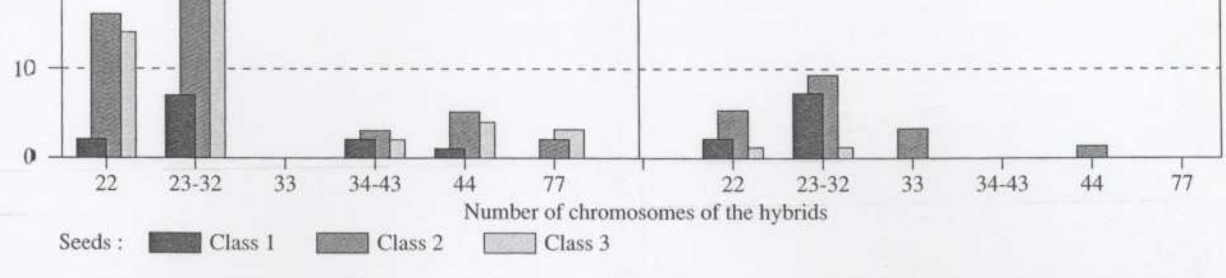


Figure 3. Relation between seed quality and chromosome number of the hybrids.

4x embryo was obtained from Maia Maoli cultivars (66 hybrids studied); the Poingo cultivar produced five 4x embryos from 46 seeds with embryo whilst the Popoulou (CIV) cultivar produced four 4x embryos from 6 seeds with embryo.

The tetraploids probably arose from a female 2n gamete (2n=3x=33) by nucleus restitution, the male parent supplying only haploid pollen (n=x=11), as has already been mentioned for other banana clones (SHEPHERD *et al.*, 1986). The heptaploids observed (table 2) probably arose from hexaploid embryonic sacs (4n=6x=66) which owed their origin to a double restitution which is also common in the genus Musa (SIMMONDS, 1960). To our knowledge, this is the first time that restitution (single or double) of the female nucleus has been demonstrated in Popoulou/Maia Maoli plants. However, this phenomenon has already been observed in Plantain plants with the Terrinha clone (SHEPHERD *et al.*, 1986).

It should be emphasized that no restitution was observed in the Plantain plants producing large numbers of seeds; in the same way, this phenomenon was rare or non-existent among the most "fertile" of the Popoulou/Maia Maoli plants. In fact, our preliminary results suggest that restitution is more frequent in varieties with a low apparent female fertility as is the case for example in Mbindi and Popoulou (CIV) plants. Cytogenetic studies on the meiosis of the triploid parents might provide useful information to understand these results more fully.

A relation was sought between the quality of seeds and their level of ploidy: for the sample observed, no correlation was found (figure 3); in particular, perfectly normal seeds very often contain aneuploid embryos or euploid embryos; moreover, 3 out of the 5 heptaploid embryos of Popoulou/Maia Maoli came from perfectly normal seeds, which implies that a tridecaploid endosperm (66 + 66 + 11 = 143 chromosomes) may develop like a triploid endosperm of a seed from a wild banana plant.

Evaluation of hybrids

Tetraploid hybrids produced droopy leaves, which is common for this ploidy level (VAKILI, 1967), and consequently were rather susceptible to foliage breakage by wind. They did not show any inhibition of suckering similar to the male parent and were faster ratooning.

The tetraploids were parthenocarpic and their bunch weights were lower than those of the triploid female parents due to a reduction of fruit length for Plantains and reduced diameters for the Popoulou/Maia Maoli fruits. These unfavourable features were carried by the wild male parent. The tetraploids were cooking bananas but with a soft flesh which never equalled the high quality of the triploids.

The hybrids have been transfered to the Regional Center for Bananas and Plantains (CRBP) in Cameroon to be evaluated for their resistance to black leaf streak disease which is not present in Guadeloupe.

Conclusion

The present results appear to show that, if indeed the phenomenon of gamete restitution exists in varieties of the subgroups Plantain and Popoulou/Maia Maoli, it remains rare. This is contrary to observations made on Gros Michel varieties where most seeds obtained are tetra or heptaploid (CHEESMAN, 1932; SHEPHERD *et al.*, 1986). An early selection of tetraploid hybrids, prior to planting, is therefore necessary. Observing seed quality provides no information on the ploidy level of zygotes. To our knowledge, the only truly accurate method which can be practised at a sufficiently early stage, on the plant in the nursery, is chromosome counting.

This work has shown that tetraploids may arise equally well from well-formed seeds as from abnormal seeds (defects of endosperm and/or embryo). Recourse to *in vitro* culture of the embryos therefore depends on the number and quality of seeds obtained: it is necessary for crosses producing few seeds, such as Mbindi x Calcutta 4, which gave at most only 8 seeds. It is less justified for crosses producing many seeds, such as Maia Maoli x Calcutta 4, where 53% of the seeds were well-formed. In this case, the seeds can be sown directly in the nursery.

Lastly, our results indicate that the potential number of tetraploid hybrids per hybridised bunch is not proportional to the number of seeds obtained. The "apparent" female fertility would not be a deciding factor in the choice of the best female parents; it is possible that the production of tetraploid hybrids is linked to a low fertility. This hypothesis remains to be verified by an indepth study of the meiotic behaviour of the female triploid parents.

This has served as a preliminary study for development of a more ambitious program at the CRBP in Cameroon, where hybridizations will be performed on a much larger scale for the production of improved tetraploids. The identification of cooking bananas showing fertility and producing 3x female gametes is well advanced. In the future, efforts should be focussed on improvement of the diploid male parent, which must meet a certain number of requirements. As well as carrying the desired disease resistances and possessing good agronomic characteristics, the male parent must be highly homozygous and fertile in order to reduce the number of hybridizations and hybrid evaluations (chromosome counting, number of individuals to evaluate in the field). The use of pure lines as male parent would reduce the genetic gamete variability of both parents to zero, the 3x restituted female gametes having the same constitution. Thus, the potential of a cross would be evaluated through observation of a single, or very few tetraploid individuals in the progeny.

The program aimed at the production of tetraploid cooking bananas will be conducted according to this principle at the CRBP.

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RESUMEN - El programa de mejoramiento genético de los bananos y plátanos, llevado a cabo por el CIRAD-FLHOR, se basa para los próximos años, sobre la obtención de híbridos tetraploides a partir de un esquema de cruze haciendo intervenir un cultivar triploïde utilizado como ascendiente hembra y variedades diploïdes salvajes o híbridas como ascendiente macho. El documento presenta los resultados preliminares obtenidos a partir de la evaluación de la fertilidad de 38 variedades del tipo French plátano y de 5variedades pertenecientes al sub-grupo Popoulou/Maia Maoli (siendo todas plátanos), polinizadas repetidamente por la especie salvaje Musa acuminata burmannicoïdes (clono Calcutta 4). La calidad de las semillas obtenidas a partir de estos cruzes fue estudiada y la repartición de los diferentes niveles de ploïdia entre los descendientes también lo fue contando los cromosomas. En el caso de los cruzes hechos, 40 a 50% de las semillas cosechadas no contienen embrión. En condiciones in vitro, la calidad y el porcentaje de germinación (de 37 a 100%), utilizados como criterio de la calidad de las semillas, varían considerablemente. Por otro lado no se pudo poner en evidencia ninguna relación entre la calidad de las semillas y el número de cromosomas en los embriones. Algunos híbridos tetraploïdes y heptaploïdes entre Popoulou/Maia Maoli y Plátano fueron obtenidos a partir de buenas semillas con endosperma.

PALABRAS CLAVES : Banano, *Musa*, hibridación, fertilidad, número de cromosomas, cultivo de tejidos.
