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Secondary polyploids, heterosis, and evolutionary crop breeding for further improvement of the plantain and banana (*Musa* spp. L) genome

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Abstract Several primary tetraploids with desirable attributes have been selected by *Musa* breeding programs. Diploid parental stocks have become available for further genetic improvement of the *Musa* genome. Hence, new genome manipulations should be tested before they become routine in breeding programs. Through comparison of the performance of triploid landraces, their primary tetraploid hybrids and secondary polyploid derivatives, plus diploid ancestors, it was found that the production of secondary triploids (TM3x) is more rewarding than developing secondary tetraploids. TM3x achieved significant high polyploid-parent heterosis for yield either by maximizing heterozygosity through crosses between unrelated parents, or by selection of linkats in hybrids derived from crosses between euploid full-sibs. There were significant differences in bunch weight between full-sib secondary polyploids, which suggested that specific combining ability should be re-defined considering not only a specific cross combination but also the individual performance within each cross. This paper proposes a crop-breeding strategy which takes into consideration the process of domestication of banana and plantain. Current data suggest that this type of evolutionary breeding approach may be feasible in *Musa*.

Key words Heterotic groups · Maximum heterozygosity · Ploidy manipulations · Progressive heterosis · Specific combining ability

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Introduction

Banana and plantain (*Musa* spp. L.) are important as cash or subsistence crops in Africa, America and Asia (Robinson 1996). They are derived from intraspecific or interspecific crosses between *M. acuminata* Colla and *M. balbisiana* Colla (Simmonds 1995a). The total yield potential has not been realized in *Musa* because breeding has lagged until recently (Simmonds 1993). Indeed, all bananas and plantains cultivated today are farmers' selections of somatic mutants from old landraces, and may have a very narrow genetic base. High yields have been achieved in commercial plantations as a result of enhanced crop husbandry (Simmonds 1993). Nevertheless, the potential for increasing yields through genetic improvement is higher in *Musa* than for any other crop (Poleman 1975).

Disease and pest pressure on banana and plantain has impelled the genetic improvement of this crop (Ortiz et al. 1995 a). Resistant tetraploid hybrids have been released to mitigate yield losses due to the fungal diseases black sigatoka and fusarium wilt (Rowe and Rosales 1993; Vuylsteke et al. 1993b, 1995). Improved germ plasm was obtained by crossing improved, cultivated, or wild paternal diploid parents with maternal triploid landraces (Rowe and Rosales 1993; Vuylsteke et al. 1997). Concomitantly, *Musa* breeders have been able to gain considerable insight into the *Musa* genome (Ortiz 1995 a). Further improvement of plantain and banana will ensue from this new knowledge, which will also increase the efficiency of *Musa* breeding.

Diploid stocks have been developed by several *Musa* breeding programs elsewhere (Rowe and Rosales 1993; Vuylsteke and Ortiz 1995). Their breeding values should be assessed through progeny testing before their subsequent utilization in *Musa* breeding schemes. Moreover, the availability of tetraploid and diploid germ plasm provides a means for the assessment of the best breeding strategy to produce high-yielding genotypes through appropriate ploidy manipulations.

This report compares the performance of secondary polyploids (triploids and tetraploids) with their available parents and grandparents. The results are discussed in the context of an evolutionary breeding approach for further improvement of the *Musa* germ plasm.

Materials and methods

Plant materials

Seven plantain-derived secondary triploid hybrids (TM3x), three plantain-derived secondary tetraploid hybrids (TM4x), seven primary tetraploid plantain hybrids (TMPx) which are parents of TM3x and TM4x, two selected diploid parents of TM3x (TMP2x 1549-7 and SH-3362), one grandparent wild banana (Calcutta 4), two grandparent plantain landraces (Bobby Tannap and Obino l' Ewai), three cooking banana landraces (Bluggoe, Cardaba and Fougamou), four cooking banana primary tetraploids (TMBx), and one tertiary cooking banana tetraploid (FHIA-3, an offpring derived from Cardaba) were assessed in a yield trial from 1994 to 1996 in a humid forest site in southeastern Nigeria.

The TM3x and TM4x hybrids were selected in an early evaluation trial because their bunch weight significantly exceeded ($P < 0.05$) that of their breeding population and they showed partial black sigatoka resistance (Ortiz and Vuylsteke 1994 a). TM3x and TM4x were derived from crosses between non-related germ plasm or euploid full-sibs (Ortiz and Vuylsteke 1994a). All primary tetraploids, (except 1187-8), and the diploid hybrid parents are partially resistant to black sigatoka (Vuylsteke et al. 1993b; Vuylsteke and Ortiz 1995), while the maternal plantain grandparents are susceptible to this fungal disease (Ortiz and Vuylsteke 1994b). Bobby Tannap and Obino l' Ewai are the most successful female-fertile parents of most of the TMPx hybrids released by IITA (Vuylsteke et al. 1993b). Calcutta 4, the paternal grandparent, shows an extremely resistant (or hypersensitive) host response to black sigatoka (Ortiz and Vuylsteke 1994b). Three of the TMBx hybrids were somaclonal variants of TMBx 612-74, which were selected in Cameroon and Nigeria after their micropropagation in Belgium and Nigeria. In vitro propagules of the 30 genotypes were micropropagated through shoot-tip culture (Vuylsteke 1989), and transplanted to the field following 8 weeks hardening in a nursery.

Experimental design of field trial and data analyses

The experiment was planted at the High Rainfall Station of the International Institute of Tropical Agriculture (IITA) in Onne, Nigeria. This site is in a secondary center of plantain diversification and has been described elsewhere (Ortiz 1995b). The experimental layout was a rectangular simple-lattice design with two replications of four plants each, as recommended by Ortiz and Vuylsteke (1995 a), with 3 m between rows and 2 m between plants within rows, i.e., 6 m^2 $plant^{-1}$. All plots were surrounded by a black sigatoka-susceptible landrace to provide a uniform field inoculum pressure in this trial. Crop-management practices for sole-crop experiments were as described by Ortiz (1995b). Data were collected on growth and yield characteristics (see Table 1).

Yield potential (YLD, t ha^{-1} $year^{-1}$) was calculated as:

$$YLD = [(608.455 \times BW)/(DF + DFF)],$$

where BW was the bunch weight (kg $plant^{-1}$), and DF and DFF were the days to flowering and for fruit filling, respectively. High polyploid-parent heterosis ($H_{POLYPLOID}$, %) for bunch weight was determined as:

$$H_{POLYPLOID} = 100 * [BW_{HYBRID\ OFFSPRING} - BW_{PARENTS}]/[BW_{PARENTS}].$$

In a similar way, high polyploid-parent heterosis was calculated for yield potential.

In addition, available data were collected from an experiment replicated in six West African environments (PBIP 1996) to compare the performance of FHIA-3 with respect to that of selected plantain-derived tetraploid hybrids (TMPx) and Cardaba. These environments were Azaguie (Cote d'Ivoire), Kade (Ghana), Ibadan (Nigeria), Onne-sole crop, Onne-alley crop, and Umuahia (Nigeria). Statistical analyses of on- station and multilocational trials were carried using MSTAT-C (1989).

Results

There were significant differences ($P < 0.05$) among clones for growth characteristics, host response to black sigatoka, and bunch weight and its components (Table 1). Bunch weights of some of the secondary triploids, such as TM3x 15108-6 (14.4 kg), TM3x 15108-2 (12.7), TM3x 15108-1 (11.6) and TM3x 14604-35 (14.0), outyielded their primary tetraploid parents, their triploid plantain landrace and diploid wild banana grandparents (Figs. 1. and 2).

TMPx 4479-1 showed 25% high polyploid-parent heterosis for bunch weight (Table 2), while this heterosis ranged from 29% (for TM3x 15108-1) to 60% (for TM3x 15108-6) in its secondary triploid offspring (Table 2). In the other cross between full sibs, high polyploid-parent heterosis for bunch weight was 57% on the selected TM3x 14604-35 (Table 2). We have not calculated the high polyploid-parent heterosis for TM3x 14604-35 with respect to its first cycle because the grandmother plantain landrace was affected twice by wind damage during the fruit-filling period. High polyploid-parent heterosis for yield potential followed a similar trend.

Only one secondary tetraploid (TM4x 15090-102) significantly ($P < 0.05$) out-yielded its polyploid maternal parent and grandparent (Fig. 1), while its full sib had similar ($P > 0.05$) bunch weights to both polyploid ancestors. Another previously selected secondary tetraploid, TM4x 15955-3, had significantly lower ($P < 0.05$) bunch weight than its highest-yielding primary tetraploid parent TMPx 4698-1 (Fig. 2). The black sigatoka-susceptible primary tetraploid 1187-8 and the triploid plantain landrace Bobby Tannap produced very poor bunches (Table 1) as a result of the reduced leaf area available for photosynthesis (< 6 fully functional standing leaves at flowering).

The highest-yielding black sigatoka-resistant cooking banana was FHIA-3, a tertiary tetraploid hybrid developed by Fundacion Hondurena de Investigacion Agricola (FHIA). This hybrid significantly ($P < 0.05$) out-yielded its maternal great grandmother, the triploid cooking banana cultivar Cardaba, at Onne

Table 1 Growth and yield characteristics of *Musa* groups grown in as sole crops at Onne (1994–1996). Mean ± standard error. Number of clones (n) in brackets. DF = days to flowering, TNL = total number of leaves, PH = plant height, NSLf = number of standing leaves at flowering, YLSf = black sigatoka youngest leaf spotted at flowering, HTSh = height of tallest sucker at harvest, DFF = days for fruit filling, BW = bunch-weight plant^{-1}, H = hands bunch^{-1}, F = fruits bunch^{-1}, FL = fruit length, FG = fruit girth, CV = coefficient of variation

Clone	DF (days)	TNL (no.)	PH (cm)	NSLf (no.)	YLSf (no.)	HTSh (cm)	DFF (days)	BW (kg)	H (no.)	F (no.)	FL (cm)	FG (cm)
TM3x	304	25	242	12	9	158	116	11.3	7	103	19	12
[n = 7]	± 13	± 1	± 9	± 1	± 1	± 35	± 5	± 1.3	± 0.5	± 9	± 1	± 0.5
TM4x	281	25	231	11	10	263	137	7.6	7	112	16	11
[n = 3]	± 21	± 0.2	± 18	± 1	± 1	± 24	± 21	± 0.8	± 0.4	± 1	± 1	± 1
TMPx	328	25	253	11	8	194	115	8.5	6	79	18	13
[n = 6]	± 15	± 1	± 13	± 0.3	± 0.3	± 21	± 3	± 0.4	± 0.4	± 6	± 1	± 0.2
1187-8	387	21	179	9	7	158	117	2.2	6	65	12	10
TMP2x	204	26	186	13	8	234	109	1.2	7	85	7	4
SH-3362	529	29	240	9	7	226	114	7.8	11	141	14	9
Plantains	374	25	294	8	6	72	80	5.2	6	62	19	12
[n = 2]	± 22	± 1	± 4	± 0	± 0.5	± 2	± 8	± 2.0	± 0.5	± 3	± 2	± 1
Calcutta 4	208	22	174	12	[a]	247	126	0.5	6	81	6	4
Bananas	345	29	305	11	8	278	126	10.0	7	88	15	14
[n = 3]	± 18	± 2	± 3	± 1	± 1	± 15	± 6	± 2.3	± 1	± 25	± 2	± 2
TMBx	317	25	257	14	11	221	147	7.4	6	70	15	13
[n = 4]	± 29	± 1	± 21	± 1	± 1	± 20	± 10	± 1.3	± 1	± 15	± 2	± 1
FHIA-3	319	26	266	11	9	80	102	16.9	8	125	17	14
CV (%)	10	12	8	13	19	18	11	23	11	17	11	10

[a] This clone shows extreme black sigatoka resistance, i.e. a hypersensitive host response

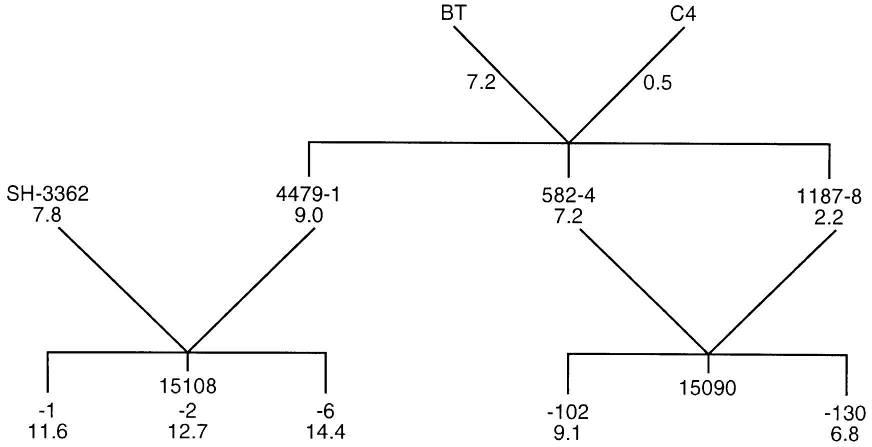


Fig. 1 Ploidy manipulations to maximize bunch weight in Bobby Tannap (BT) × Calcutta 4 (C4)-derived polyploid hybrids. Bunch weights (kg plant^{-1}) of the parents and offspring are indicated below their respective name or code. $\mathrm{LSD}_{0.05} = 2.0$

(Table 1) and throughout West African multilocational trials (Fig. 3). In addition, FHIA-3 significantly out-yielded ($P < 0.05$) all selected primary tetraploid plantain hybrids in on-station trials (Table 3). This hybrid was selected after crossing a high-yielding dwarf secondary triploid (SH-3386). SH-3386 was not released by FHIA because of its long fruit-filling period (Phil Rowe, personal communication), but it was crossed with a selected diploid hybrid to obtain FHIA-3. SH-3386 was not available for our trial due to germ plasm quarantine restrictions.

The somaclonal variants of TMBx 612-74, a primary tetraploid derived from the cooking banana Bluggoe, exhibited a highly resistant host response to black sigatoka. They had more than ten fully functional standing leaves at flowering while the maternal parent had only six. However, none of TMBx 612-74 variants nor TMBx 1378 (another primary cooking banana tetraploid hybrid developed at IITA) out-yielded their parental triploid landraces in this trial (Table 1). In a neighbouring experiment, the true-to-type TMBx 612-74 produced bunches weighing an average of 13 kg plant^{-1}. These results demonstrate that bunch weights of the three clonal selections of TMBx 612-74 were adversely affected by somaclonal variation after micropropagation. Hence, these results may suggest that

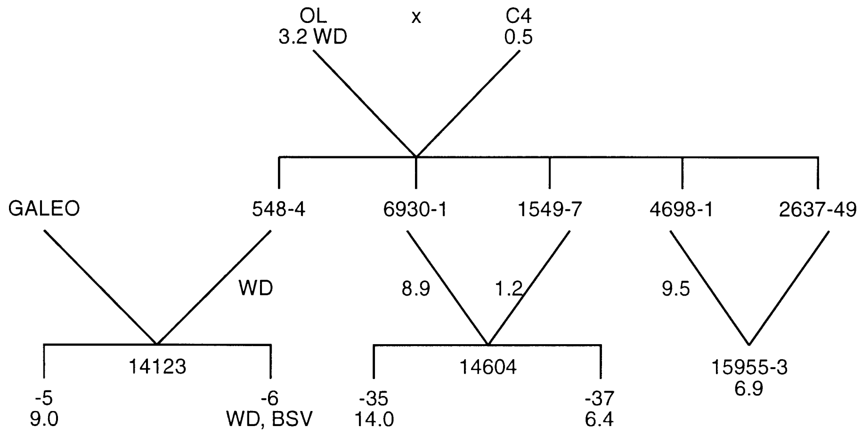


Fig. 2 Progressive polyploid-parent heterosis for bunch weight (kg plant^{-1}) in Obino l' Ewai (OL) × Calcutta 4 (C4). Bunch weights (kg plant^{-1}) are indicated below the respective name or code of parents and offspring. $LSD_{0.05} = 2.0$. Most plants bearing bunches of OL were damaged twice by strong winds (WD) during the fruit-filling time, while all plants of TMPx 548-4 were lost by wind before flowering. The secondary triploid 14123-6 was significantly affected by banana streak virus (BSV), and all mother plants of this clone were rogued prior to harvest. In a neighbouring trial, healthy plants of Obino l' Ewai, TMPx 548-4 and TMP × 2637-49 had bunches weighing on average $\pm$ 9 kg plant^{-1}. Galeo was the diploid banana male parent of secondary triploid hybrids 14123-5 and 14123-6

somaclonal variants are of limited use in the improvement of cooking bananas, as was demonstrated earlier for plantains (Vuylsteke et al. 1996). Meanwhile, the fruits of TMBx 1378, as well as those of its triploid landrace parent Fougamou, were infected by an unknown pest during the fruit-filling time, thereby producing low-yielding bunches.

The late-flowering SH-3362, a selected diploid hybrid from FHIA, had a medium-yielding bunch with many small fruits in this trial (Table 1). Two of its derived TM3x hybrids (TM3x 15108-1 and TM3x 15108-6) showed medium size fruits (16–18 cm × 12–14 cm). The bunches of both hybrids had significantly ($P < 0.05$) more fruits (119–127); however, they were of smaller size than that of TMPx 4479-1 (74 fruits, 20-cm length by 13-cm girth), which was their primary tetraploid female parent.

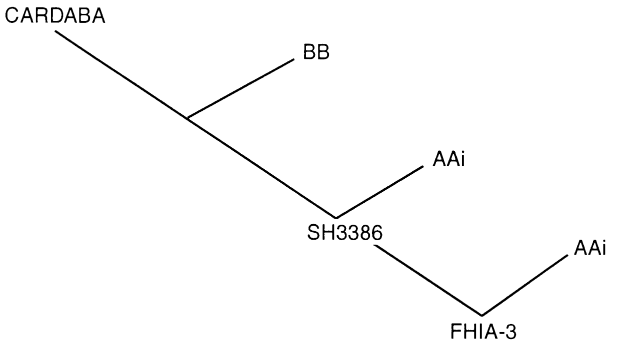
Table 2 Range of high polyploid-parent heterosis for bunch weight (BW, kg plant^{-1}) and yield potential (YLD, t ha^{-1} year^{-1}) in *Musa*

Hybrid group	Obino l'Ewai × Calcutta 4		Bobby Tannap × Calcutta 4	
	BW	YLD	BW	YLD
Primary tetraploids	[a]	[a]	0–25%	0–28%
Secondary triploids				
Full sibs ($n^b = 50$)	0–57 %	0–71 %	Not available	
Not related ($n < 10$)	[c]	[c]	29–60%	24–50%
Secondary tetraploid				
Full sibs ($n = 100$)	0 %	0 %	0–26 %	0–26 %

[a] Biased due to wind damage of 3*x*

[b] Original population size from which secondary polyploid hybrids were selected

[c] Biased due to wind damage of 4*x*



Bunch weight	Cardaba	FHIA 3
Onne	13.6	16.9
West Africa	13.0	17.1

Fig. 3 The development of FHIA-3 through ploidy manipulations and progressive heterosis as tested at the breeding station (Onne) and in multilocational testing in other West African locations. Bunch weights (kg plant^{-1}) of Cardaba and FHIA-3 were significantly ($P < 0.05$) different. *AAi*, improved diploid of *M. acuminata*; *BB*, *M. balbisiana*

Table 3 Bunch weight and its components of the *Musa* hybrids in alley cropping fields (Onne, southeastern Nigeria, 1994–1996). BW = bunch-weight plant^{-1}, H = hands bunch^{-1}, F = fruits bunch^{-1}, FL = fruit length, FG = fruit girth, AFW = average fruit weight, DFF = days for fruit filling, PW = peduncle weight

Hybrid	Parentage[a]	BW (kg)	H (no.)	F (no.)	FL (cm)	FG (cm)	FW (g)	DFF (days)	PW (kg)
Primary tetraploid plantain hybrids									
TMPx 548–9	OL × C4	13.0	6	82	19	12	145	109	0.7
TMPx 1658–4	OL × Pl	15.0	7	102	20	12	132	108	1.2
TMPx 2796–5	BT × Pl	14.6	6	92	19	12	150	112	0.8
TMPx 4698–1	OL × C4	14.5	8	118	19	11	113	113	1.0
TMPx 7002–1	OL × C4	13.8	6	82	20	12	137	114	0.7
TMPx 7152–2	ME × C4	14.2	7	97	20	12	132	109	0.8
Tertiary tetraploid cooking banana hybrid									
FHIA-3	See Fig. 3	18.9	9	134	17	13	125	103	2.0
$LSD_{0.05}$		3.5	1	15	2	1	23	6	0.3
CV (%)		15.4	8.5	10.0	6.0	4.5	11.4	3.8	21.8

[a] OL = Obino l' Ewai, C4 = Calcutta 4, BT = Bobby Tannap, Pl = Pisang lilin, ME = Mbi Egome-1

Discussion

Resistance to biotic and abiotic stresses

Heterosis for bunch weight was expressed only in a resistant background. Single major genes for black sigatoka resistance (Craenen and Ortiz 1996) and fruit parthenocarpy (Ortiz and Vuylsteke 1995 b) enhance fruit size, thereby increasing bunch weight. Therefore, genes for fruit parthenocarpy and resistance should be incorporated (or preserved) in the breeding population(s) to obtain high yields.

Secondary polyploids for further improvement of bunch weight

The outstanding performance of selected TM3x hybrids shows that ploidy per se cannot be regarded as the main cause of high yields in *Musa*. This was confirmed by the relatively low bunch weights of TM4x (Figs. 1 and 2). Although TM4x 15090-102 and 15090-130 had higher bunch weights than the average of their full-sib parents, their yield was lower than that of the selected TM3x. TM4x 15090-102 exhibited significant high polyploid-parent heterosis. However, this hybrid was selected from a large segregating population (>100 sibs), which highlights the inefficiency of this approach for *Musa* improvement.

Re-examining the concept of specific combining ability in polyploid breeding

Specific combining ability (SCA) has been defined for diploid species as the performance of a plant (or genetic strain) in a specific combination as compared with the performance of other cross combinations (Poehlman and Sleper 1995). The results of the present experiment suggests that SCA is very important to obtain high-yielding secondary triploids in *Musa* breeding. However, significant within-family variation for bunch weight has been observed among these secondary polyploid offspring (Figs. 1 and 2). It is likely that this variation occurred because the parents of the secondary triploids are highly heterozygous genotypes. Hence, the concept of SCA should be applied not only to the cross combination (i.e., SCA_{CROSS}) but also to the specific individual hybrid combination ($SCA_{SELECTED\ HYBRID}$). The latter can be calculated as a deviaton of the individual genotypic value from the SCA_{CROSS}.

Maximum heterozygosity and progressive heterosis in bunch weight and yield potential

The results suggest that it will be possible to achieve polyploid-parent heterosis either by maximizing heterozygosity through crossing unrelated parents (e.g. TMPx 4479-1 × SH-3362, which are parents of 15108 hybrids), and/or through progressive heterosis (Groose et al. 1989) by proper selection within crosses even of hybrids derived from full-sib parents, e.g. TM3x 14604-35 was derived from the cross between the full-sibs TMPx 6930-1 and TMP2x 1549-7. The high bunch weight and yield potential of the secondary polyploid germ plasm demonstrated that high polyploid-parent heterosis may be achieved through proper manipulation of the *Musa* genome. For example, FHIA-3 was derived from a complex crossing scheme (Fig. 3). This tertiary tetraploid has performed very well not only in Africa, but also in tropical America (Jones and Tezenas du Montcel 1994).

Gene action and heterosis

In tetrasomic potato and other polysomic crops, yield increases have been associated with increased heterozygosity due to non-additive intra- and inter-locus interactions (reviewed by Peloquin and Ortiz 1992). In contrast, progressive heterosis has been achieved in tetraploid alfalfa (Groose et al. 1989) by accumulating chromosome segments linking favorable dominant alleles. This "linkat" (Demarly 1979) usually confers coadapted functions. The results from our experiment suggest that both maximum heterozygosity and linkats may be exploited in *Musa* to obtain high-yielding bunches. For example, the yield recorded in the cross TMPx 4479-1 × SH-3362 could be the result of maximum heterozygosity by crossing unrelated parents. Similarly, the selection of TM3x 14604-35, from a full-sib cross, demonstrates that progressive heterosis could be exploited in *Musa*. However, progressive heterosis in *Musa* may require a relatively large population size ($\geqslant 50$ sibs) to identify, through phenotypic selection, the right genetic combination. Conversely, maximum heterozygosity was achieved in a relatively small population size, e.g. TM3x 15108-1, TM3x 15108-2 and TM3x 15108-6 were selected from a family of only nine full-sibs.

Evolution and domestication of the *Musa* crop in the tropics

The hybridization of diploid species of *Musa*, and subsequent recombination events and mutations, generated sufficient genetic diversity to allow the domestication of diploid cultivars bearing parthenocarpic fruits (Simmonds 1962). Sexual polyploidization ($2n \times n$) resulted in almost-sterile triploid species, which multiplied through vegetative sucker propagules in the centers of origin. During the long history of cultivation of triploid landraces, new mutants originated and farmers selected among these diverse clones for specific genetic combinations showing the desirable phenotypes. *Musa* germ plasm also moved from the Asian-Pacific centers of origin to Africa, facilitated by vegetative propagation. Mutations provided a means for the secondary diversification of the triploid plantains in West African lowlands (De Langhe 1969) and of the triploid cooking and beer bananas in the highlands of East Africa (Shepherd 1957).

As shown by the evolutionary history of *Musa*, "instant domestication" (Zohary and Spiegel-Roy 1975) could have occurred after the vegetative propagation of a few selected high-yielding phenotypes. Nevertheless, linkats containing favorable combinations, especially in linkage disequilibrium, were preserved through asexual propagation (Wright 1956; Crow and Kimura 1965).

After Columbus' voyages, bananas and plantains moved to Tropical America and the Caribbean (Simmonds 1995 b), where the dessert banana became an important export commodity. The first breeding operations started in the early 1920s in the West Indies (Ortiz et al. 1995 a) aiming to develop improved diploid stocks for further hybridization with dessert bananas. The main objective of this approach was to release pest-resistant cultivars. Later in Honduras, germ plasm was developed through the recombination of available diploid accessions collected in Asia and the Pacific. Today diploid hybrids are routinely used in the production of high-yielding tetraploid bananas and plantains by *Musa* breeders in Honduras (Rowe and Rosales 1993).

Improving diploid germ plasms as parental stocks

The development of SH-3362 through phenotypic recurrent selection (PRS) was based on the elimination of deleterious recessive alleles and the accumulation of favorable additive alleles (Ortiz and Vuylsteke 1994 c). Hence, PRS for population improvement and the individual selection of highly heterozygous clones seems to be effective for the production of improved diploid germ plasms. However, the breeding value of potential male diploid parents should be established through progeny testing since non-additive gene action may be important in order to achieve heterosis for yield in vegetatively propagated *Musa* (Ortiz 1995a).

With the availability of DNA markers in *Musa* (Faure et al. 1993; Howell et al. 1994; Jarret et al. 1994), diploid populations could be developed in a relatively short time. Ortiz and Vuylsteke (1995 b) and Craenen and Ortiz (1996) have demonstrated the importance of specific gene markers to enhance bunch and fruit size. Ortiz and Vuylsteke (1994 d, 1995 c) and Ortiz et al. (1995 b) also showed that single Mendelian morphological markers accounted for a significant portion of the total phenotypic variation in sucker growth, plant height, and pseudostem waxiness. By speeding up the process of recurrent selection, molecular markers tightly linked to these Mendelian markers will facilitate, the development of improved *Musa* germ plasms.

An evolutionary approach for plantain and banana improvement

Several TMPx hybrids set seed through open-pollination at Onne (PBIP 1996). Their open-pollinated seed set (87 ± 22 seeds bunch^{-1}) seems to be very similar to that obtained through artificial hand pollination (90 ± 18 seeds bunch^{-1}). Natural pollination in *Musa* occurs mainly through animal vectors (Mutsaers 1993). This natural breeding system, along with the assessment of specific combining ability in tetraploid-diploid crosses, will provide a means to establish "controlled" interploidy polycrosses for further improvement of

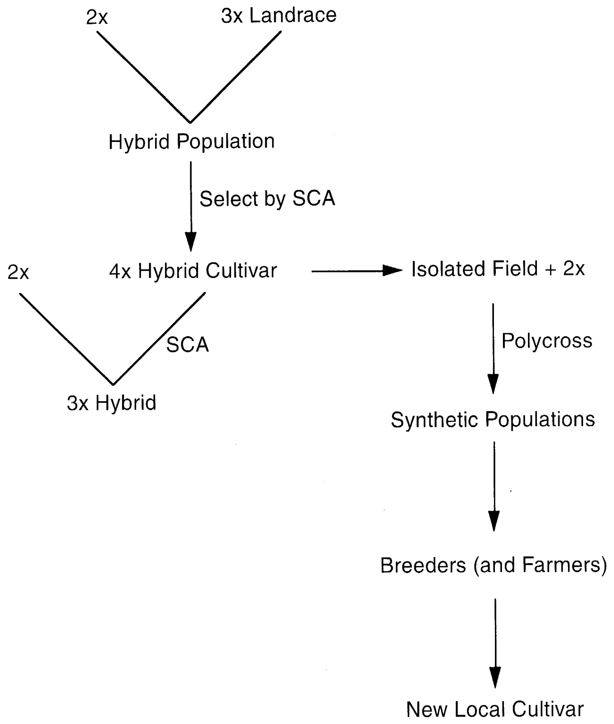


Fig. 4 Proposed scheme for evolutionary crop breeding in *Musa*. *SCA* = specific combining ability

this crop following an evolutionary crop-breeding approach (Fig. 4). For example, TMPs 548-9, an open-pollinated black sigatoka-resistant offspring was selected due to its heavy bunch (19.5 kg plant^{-1}) bearing six hands with 110 large fruits (173 g, 20-cm length by 14-cm girth) (Vuylsteke et al. 1993a).

Figure 4 shows an evolutionary approach for *Musa* breeding. The heterozygous triploid landraces are the source of allelic diversity since their ploidy and mode of evolution have allowed them to retain genetic diversity at individual loci. This diversity is released after crossing the triploid landraces with the diploid parent contributing the desirable trait of interest. Selection for SCA on the segregating population results in the production of high-yielding tetraploid hybrids. This primary tetraploid germ plasm could be used for further improvement of the *Musa* genome through crosses with selected diploids. Secondary triploids are obtained through controlled artificial hand-pollination or through polycrosses among selected parents. Tetraploid and diploid parental genotypes should be selected for isolated polycrosses based on their previously determined SCA in artificial tetraploid-diploid crosses. Synthetic populations derived from these polycrosses may be released to other breeders, who can identify promising clones for further cultivar release in cooperation with their local farmers in on-station and on-farm trials. Local selections are required since genotype-by-environment interaction affect the performance of *Musa* clones across environments (De Cauwer et al. 1995; Ortiz and Vuylsteke 1995d).

This evolutionary approach for the genetic betterment of plantain and banana, through cross breeding, will widen the genetic base of the crop. A broad-based germ plasm with pest resistance will be the best tool to achieve sustainable production in a perennial vegetatively propagated crop affected by many biotic constraints.

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