Inheritance of Albinism in Banana and Plantain (*Musa* spp.) and its Significance in Breeding

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Abstract. Few genetic markers are available in *Musa* spp. as a result of a lack of inheritance studies. Full-sib diploid ($2n = 2x = 22$) plantain-banana hybrids of the International Institute of Tropical Agriculture were selfed or outcrossed with other diploid bananas, one of which is an improved selection from Central America. Three populations having albinos (complete lack of chlorophyll in any plant tissue) were produced. The segregation ratios for albinism suggested that this deleterious trait is controlled by one or two recessive alleles. The small sample sizes (a problem inherent in the low reproductive fertility of cultivated parthenocarpic *Musa*) in two of these three populations did not allow for conclusiveness between the one or two genes model. However, a distinction was possible with the third population, consisting of 64 seedlings, of which four were albinos. The segregation ratio for albinism fit the 15:1 ratio ($\chi^2 = 0.07$, $P = 0.79$) and not the 3:1 ratio ($\chi^2 = 11.02$, $P < 0.01$), suggesting that albinism in *Musa* spp. is under the genetic control of at least two independent recessive alleles with complementary gene action. This finding also demonstrates that deleterious recessive alleles are present in the cultivated AAB plantain gene pool and in cultivated and advanced AA banana breeding populations. The latter suggests that population improvement through phenotypic recurrent selection for agronomic traits might be based on the elimination of deleterious recessive genes.

Banana and plantain, when considered together (*Musa* spp. L.), are among the 10 most important food crops of the world. They are a principal source of carbohydrates and calories, particularly for domestic consumption in the producing tropical countries, as only 10% of world production (≈ 70 million tons) enters the export market.

Few genetic studies have been undertaken in *Musa* spp. despite the importance of the crop. Simmonds (1953) elucidated the genetic system controlling fruit parthenocarpy (at least three independent dominant P_i genes with complementary gene action) and persistence of bracts and flowers in the male part of the inflorescence axis (complementary gene control).

Several characteristics inherent in the crop constrain the breeding and genetic analysis of *Musa* spp. The bulk of cultivated bananas and plantains are triploid ($2n = 3x = 33$) and have very low reproductive fertility. The low rate of hybrid progenies recovered and the resulting small sample sizes are the major obstacles to

genetic analysis. Simmonds (1986) claimed that "formal genetic studies of nearly or quite sterile triploids [plantains and bananas] are impossible," illustrating the absence of inheritance studies in *Musa* cultivars during the past 40 years. Recently, Ortiz and Vuylsteke (1992, 1994) elucidated the inheritance of resistance to black sigatoka (*Mycosphaerella fijiensis* Morelet) disease, which is under the genetic control of recessive-additive alleles at three loci. Black sigatoka, an airborne fungal leaf spot disease, is the most critical constraint to plantain and banana production worldwide (Buddenhagen, 1987). Considering the importance of this disease, the International Institute of Tropical Agriculture (IITA) initiated

a plantain and banana improvement program aimed at host plant resistance to black sigatoka (Vuylsteke et al., 1993a, 1993b). Alongside this primary target, which is one facet of disease pressure, other traits are also evaluated and analyzed to acquire a better understanding of *Musa* genetics. The Onne station of IITA in Nigeria seems to provide a suitable environment for seed production in cultivated *Musa* (Swennen and Vuylsteke, 1990, 1993), which allows the production of adequate numbers of hybrid progenies necessary for genetic studies.

This paper reports on the occurrence of albinism in *Musa* hybrids, determines the inheritance of this trait, and briefly discusses this finding in relation to the genetic structure and the current breeding methods in *Musa* spp.

Materials and Methods

The full-sib, plantain-derived diploid F_1 hybrids TMPx 1668-7 and TMPx 2829-62 were used as female parents in crosses with the improved diploid banana SH 3362 and the cultivated diploid banana 'Pisang lili'. Also, TMPx 2829-62 was selfed to produce an F_2 . Figure 1 illustrates the crosses and indicates their parentage and progeny identification. These two TMPx clones were selected in 1990 from crosses between the triploid French plantain cultivar Bobby Tannap (BT) from Cameroon (Swennen, 1990) with the wild diploid banana 'Calcutta 4' (C4), a true-breeding line from Burma/Myanmar (Simmonds, 1953). C4 belongs to the subspecies *burmannicoides* of *M. acuminata* Colla. (De Langhe and Devreux, 1960). 'Pisang lili' is an edible diploid banana of Malaysia (Simmonds, 1966) related to *M. acuminata* ssp. *malaccensis*. SH 3362 is an improved diploid line developed by Phil Rowe (Fundación Hondureña de Investigación Agrícola, Honduras) and kindly provided to IITA. This clone was selected in the third cycle of phenotypic recurrent selection (PRS) in a diploid banana breeding population (Stover and Buddenhagen, 1986). PRS was based mainly on agronomic traits such as bunch weight, fruit size and weight, plant height, and disease resistance (Rowe, 1990).

Fig. 1. Pedigree of diploid *Musa* progenies segregating for albinism.

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Results and Discussion

Albinos, i.e., seedlings that show complete lack of chlorophyll in any plant tissue (Fig. 2), were recovered from the three segregating populations. To our knowledge, this is probably the first report on the occurrence of albinism in the genus *Musa*. The segregation ratios observed in the three progenies (Table 1) suggest that albinism may be under the genetic control of independent recessive allele(s). Independent tests for goodness of fit were performed using Yates' correction factor for continuity in small sample sizes, which protects against type I errors. Analysis of segregation data of TMPx 14980 and TMPx 18173 progenies were inconclusive to determine whether one or two genes were involved. This failure may be explained by the small sample sizes of these populations, a problem inherent to the low reproductive fertility of cultivated parthenocarpic *Musa*. However, analysis of data from the TMPx 20369 progeny was unequivocal. The segregation ratio for albinism fit the 15:1 ratio ($\chi^2 = 0.07$, $P = 0.79$) and not the 3:1 ratio ($\chi^2 = 11.02$, $P < 0.01$), suggesting that albinism in *Musa* species is under the genetic control of at least two independent recessive alleles at two loci (hereafter referred to as a_1 and a_2) with complementary gene action. This finding was further corroborated by the test for goodness of fit of the pooled results, which was performed after verifying the distribution homogeneity of the three segregating populations (Table 1). This test provided more statistical evidence to reject the hypothesis of a one-locus model (3 normal : 1 albino) and not to reject the two recessive complementary gene hypothesis (15 normal : 1 albino) for the genetic control of albinism in *Musa*.

'Calcutta 4' is a true-breeding line (Simmonds, 1953). Therefore, it cannot be a carrier of the a_1 and a_2 alleles. The necessary inference that its hybrid progenies TMPx 1668-7 and TMPx 2829-62 are heterozygous for

Table 1. Segregation for green and albino seedlings in three populations of plantain-banana hybrids.

Population	No. germinated seedlings			One gene model ^z		Two genes model	
	Total	Green	Albino	$\chi^2_{(3:1)}$	$P_{(3:1)}$	$\chi^2_{(15:1)}$	$P_{(15:1)}$
TMPx 14980	27	25	2	3.57	0.06	0.02	0.89
TMPx 18173	8	6	2	0.17	0.68	2.13	0.14
TMPx 20369	64	60	4	11.02	0.00	0.07	0.79
Pooled results ^y	99	91	8	14.23	0.00	0.30	0.58

^zChi-square tests for goodness of fit were calculated using Yates' correction for continuity in small sample sizes, where $\chi^2 = [|\text{Obs.} - \text{Exp.}| - 0.5]^2 / \text{Exp.}$

^yTest for homogeneity of ratio of the three populations was not significant ($\chi^2 = 3.85$, $P = 0.15$).

both loci indicates that the female plantain parent BT is a carrier of such recessive alleles. This conclusion is corroborated by the earlier observation of an in vitro-produced phenotypic variant (Vuylsteke et al., 1991) of BT that exhibited a chimeric white band on the green pseudostem. That BT is a carrier of recessive deleterious alleles is possible due to two facts: BT's triploidy and its vegetative propagation. Triploidy allows for at least one dominant normal allele (A_1 or A_2) to mask the deleterious phenotypic expression of the recessive deleterious mutants (a_1 and a_2). The accumulation of recessive deleterious alleles and of such epistatic genetic systems is expected in vegetatively propagated species (Crow and Kimura, 1965), particularly in view of the occurrence of a series of independent mutational events that accumulated during the long history of *Musa* cultivation in Africa (De Langhe, 1964).

That 'Pisang lili' is a carrier of the deleterious recessive alleles for albinism could be expected, because this clone has been described as a structural hybrid (Hutchinson, 1966). Vakili (1965) and R. Ortiz (unpublished data) also found that 'Pisang lili' was heterozygous for the loci examined. Surprisingly, SH 3362, the improved 2x progenitor, is also a carrier of the recessive deleterious a_1 and a_2 alleles. This finding could indicate that the gain of phenotypic recurrent selection applied to diploid banana improvement has been based on the elimination of deleterious reces-

sive alleles or, in other words, on the accumulation of favorable alleles through recurrent cycles of phenotypic selection. However, heterozygosity seems to be important in the development of elite 2x progenitors because SH 3362 is a heterozygous clone not only for the a_1 and a_2 loci but also for another 20 out of 21 loci examined (R. Ortiz, unpublished data).

In conclusion, this albinism study in *Musa* hybrids illustrates that population improvement at the 2x level is effective for eliminating deleterious recessive alleles in selected 2x progenitors for further crosses with cultivated 3x bananas or plantains.

Finally, the production of diploid plantain-derived hybrids via triploid x diploid crosses not only allows the possibility of plantain germplasm enhancement at the diploid level but also provides the material required for simple genetic analyses in a triploid crop that historically has been neglected for such basic studies (Buddenhagen, 1987).

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Fig. 2. Albino seedlings of the TMPx 18173 F₂ progeny, growing in vitro.

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