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Effect of the parthenocarpy gene P_1 and ploidy on fruit and bunch traits of plantain–banana hybrids

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Plantain and banana (*Musa* spp. AAB and AAA groups) are perennial giant herbs of the tropics which develop parthenocarpic fruits. At least three independent but complementary dominant genes control vegetative parthenocarpy in *Musa*. One of these genes, P_1, segregates in euploid hybrid progenies derived from crosses between triploid 'French' plantains and a wild nonedible diploid banana. Linear correlation and regression analyses revealed that bunch weight and fruit weight and size were positively influenced by both ploidy increases and change of recessive to dominant alleles at the P_1 locus. Moreover, significant multiple regression models, including ploidy and number of copies of the P_1 allele as independent variables, accounted for most of the phenotypic variation for bunch and fruit traits. The coefficients of determination of the multiple regression analyses were always smaller than estimates of broad-sense heritability for each trait. This implies that ploidy and the effect of allele substitution did not explain all the genetic variation for bunch and fruit traits. Hence, other genetic factors may explain the remaining portion of genetic variation. The potential for indirect marker-assisted selection in the seedling nursery, through the utilization of predictive multiple regression equations, was assessed by the Durbin–Watson test of residuals. The adoption of this breeding method requires the identification of DNA markers linked to the P_1 gene and reliable and rapid methods to determine ploidy in seedlings

Keywords: allele substitution, banana, fruit parthenocarpy, marker-assisted selection, plantain, ploidy.

Introduction

The perennial giant herbs plantain and banana (*Musa* spp. AAB and AAA groups, respectively) are important staple food for rural and urban consumers in the humid forest and mid-altitudes of sub-Saharan Africa (Vuylsteke *et al.*, 1993a). The genomes of the cultivated species are derived from the diploid wild species *M. acuminata* Colla. and *M. balbisiana* Colla., which contributed the A and B genomes, respectively (Simmonds, 1976). Most of the cultivated *Musa* are triploids ($2n = 33$), almost sterile and they develop fruit by parthenocarpy.

Vegetative parthenocarpy occurs when an unpollinated ovary automatically grows into a fruit which has its loculi filled with edible pulp (Dodds & Simmonds, 1948). For Simmonds (1976) 'the key to understanding banana evolution lies in the analysis of parthenocarpy and sterility in the edible diploids'. Hence, he pointed out, seedless edible bananas are the product of two evolutionary processes: parthenocarpy and sterility.

There is a great need for genetic studies in *Musa* as breeding endeavours gain impetus to combat major production constraints (Vuylsteke *et al.*, 1993c). Very few genetic markers are available in banana and plantain as a result of a lack of inheritance studies (for a review see Ortiz, 1995).

Simmonds (1953) and Ortiz & Vuylsteke (1992) elucidated the genetic systems controlling fruit parthenocarpy in bananas and plantains, respectively. Simmonds (1953) established that the autonomous stimulus giving rise to parthenocarpic fruits was a result of at least three independent complementary genes (P_i). He determined that the wild diploid accession 'Calcutta 4' (*M. acuminata* ssp. *burmannica*) lacks one of the three dominant genes (i.e. P_1) and has homozygous dominant genotypes for the other two P_i loci. Ortiz & Vuylsteke (1992) reported that locus P_1 segregated in trisomic ratios in plantain-derived diploid test-crosses derived by crossing triploid 'French' plantains and 'Calcutta 4'.

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Simmonds (1976), based on Vakili (1967), explained that fruits of triploid *Musa* cultivars grow faster and larger than diploids. Indeed, in natural banana germplasm, triploids have heavy bunches of big fruits whereas diploids have bunches with small fruits. Similarly, Vuylsteke *et al.* (1993b) reported that tetraploids and triploids had significantly higher yields than their respective full-sib diploids in segregating euploid plantain–banana hybrid progenies. This could not be explained in terms of bunch characteristics because there were no differences in the number of hands or fruits per bunch. Rather, diploids produced smaller fruits. Diploid fruit was shorter and thinner, resulting in lower fruit mass and thus, with similar number of fruits per bunch, lower bunch weight and yield than in tetraploids and triploids.

This paper reports the effect of the P_1 gene on fruit and bunch traits of euploid hybrids derived from crosses between triploid 'French' plantains and 'Calcutta 4', a wild diploid banana.

Materials and methods

F_1 euploid hybrids were derived from interspecific interploidy crosses (Vuylsteke *et al.*, 1993d). The female parents were the locally adapted AAB 'French' plantain cultivars 'Obino l'Ewai' (OL) from Nigeria and 'Bobby Tannap' (BT) from Cameroon (Swennen, 1990). These cultivars were selected as parents because of their relatively high female fertility (Swennen & Vuylsteke, 1993). The diploid male parent was the wild diploid banana 'Calcutta 4' (C4) from Burma (Myammar). The crosses between OL × C4 and BT × C4 have produced the two 'largest' segregating populations in plantain improvement (Ortiz & Vuylsteke, 1994; Vuylsteke *et al.*, 1993d).

'Calcutta 4' has true seeded, fleshless, nonparthenocarpic fruits because it lacks the P_1 gene (Simmonds, 1953). Hence, its genotype is p_1/p_1 P_2/P_2 P_3/P_3. 'Bobby Tannap' and 'Obino l'Ewai' are duplex for the P_1 locus, i.e. $P_1/P_1/p_1$. Euploid progenies from crosses between the above parents segregated as test-crosses for the P_1 locus. Moreover, Ortiz & Vuylsteke (1992) showed that the P_1 locus is about 34 cM from the centromere. This, along with a second division restitution mechanism for $2n$ egg production in triploid plantains (Ortiz & Vuylsteke, 1994), leads to the production of duplex tetraploid hybrids ($P_1/P_1/p_1/p_1$) with parthenocarpic fruits when $2n$ eggs of plantains are fertilized by n pollen from 'Calcutta 4'. Meanwhile, their full-sib diploids are either heterozygous clones with parthenocarpic fruits (P_1/p_1) or homozygous recessive (p_1/p_1) clones with nonparthenocarpic fruits.

Data were collected for 52 euploid hybrids of BT × C4 and 31 of OL × C4 in the first (plant) crop and in the following ratoon at IITA High Rainfall Station in Onne, south-eastern Nigeria. Site characterization has been published elsewhere (Winslow, 1992). Most of the euploid hybrids were diploids, 85 per cent of BT × C4 and 52 per cent of OL × C4, whereas the remaining were mainly tetraploids. The hybrids were planted randomly in single-row plots of 4 or 5 plants each and scored for fruit parthenocarpy to assign respective genotypes. Bunch weight, number of hands and fruits, average fruit weight, length and circumference and time to fruit filling were recorded following Gauhl *et al.* (1993).

Broad-sense heritability (H^2) and repeatibility (R) were calculated, based on plot means, from the ratios of the variance components (Becker, 1975) as $H^2 = \sigma^2_G/(\sigma^2_G + \sigma^2_{GC}/c)$ and $R = \sigma^2_G/(\sigma^2_{GC}+\sigma^2_C)$ (Goodman & Paterniani, 1969), where σ^2_G is the pooled genetic variance across the two types of crosses, σ^2_C is the cropping season variance, σ^2_{GC} is the genotype-by-cropping season variance and c is the number of cropping seasons, i.e. 2; σ^2_{GC} included two components, $[\sigma^2_{GP}+\sigma^2_W/k]$, where σ^2_{GP} is the variance of the genotype-by-production cycle interaction, σ^2_W is the within plot variance and k is the harmonic mean of plants per plot (Goodman & Paterniani, 1969). H^2 provides relative measurements about the proportion of phenotypic variance explained by the genetic variance whereas R measures the relative importance of each variance component in the phenotype.

Linear correlation and regression, and multiple regression analyses (Sokal & Rohlf, 1981) were performed to establish individual and combined associations and relationships between ploidy and copies of the P_1 allele (independent variables) and quantitative variation in bunch and fruit traits for each of the two F_1s, OL × C4 and BT × C4. Analyses were based on means for each genotype across cropping seasons, instead of their respective plot means, to avoid serial correlations from cropping season effects. Residuals from the multiple regression models for each trait within each F_1 cross were tested by Durbin–Watson statistics to determine the reliability of the regression equation as a predictive model for marker-assisted selection.

Results

Estimates of variance components, their statistical significance, heritability and repeatibility values are shown in Table 1. There were significant differences

Table 1 Estimates of variance components of cropping seasons (σ^2_C), genotypes (σ^2_G), genotype-by-cropping seasons (σ^2_{GC}), broad-sense heritability (H^2) and repeatibility (R) for bunch and fruit traits of banana–plantain euploid hybrids at Onne (1990–93)

Trait	σ^2_C	σ^2_G	σ^2_{GC}	H^2 (%)	R
Bunch weight	2.05	13.41***	3.65**	88.0	2.35
Hands per bunch	5.52**	2.32***	1.57	74.8	0.33
Fruits per bunch	3283.58***	1265.09***	539.84	82.4	0.33
Time to fruit filling	10129.24***	74.37	906.78	14.1	0.01
Fruit weight	1701.41**	2699.55***	344.50***	94.0	1.32
Fruit length	0.00	25.31***	3.23**	94.0	7.84
Fruit circumference	3.38*	9.24***	1.19***	94.0	2.02

*$P \leqslant 0.05$, **$P \leqslant 0.01$, ***$P \leqslant 0.001$.

($P<0.01$) between the euploid hybrids for all the traits except time to fruit filling ($P>0.05$). The cropping season affected significantly the phenotypic expression of time to fruit filling ($P<0.001$), number of hands ($P<0.01$) and fruits ($P<0.001$) per bunch, and average fruit weight ($P<0.01$) and circumference ($P<0.05$). The genotype-by-cropping season interaction was significant ($P<0.01$) for bunch weight and average fruit weight, length and circumference. The values of H^2 and R were high for these traits because of large and significant differences among the genotypes. Conversely, the lack of genetic differences explained the very low values of H^2 and R for time to fruit filling. Despite the significant genetic effects, the higher and significant cropping season effects explained the low values of R for number of hands and fruits. This implies that significant differences among euploid hybrids in the plant crop and the ratoon were the result of environmental effects rather than actual genetic differences. However, the lack of a significant genotype-by-cropping season interaction resulted in high values of H^2 for these two components of bunch weight, which are commonly used in plantain taxonomic grouping.

The gene P_1 significantly affected fruit development in terms of fruit weight and size in both F_1s as indicated by the linear correlation and regression coefficients (Table 2). Both characteristics are components of bunch weight, hence the effect of allele substitution, i.e. the change of a copy of the recessive to a dominant at the P_1 locus indirectly accounted for the phenotypic variation of bunch weight. This gene did not affect time to fruit filling as indicated by the nonsignificant regression model. Similarly, an increase in ploidy resulted in high yielding bunches as a result of concomitant increases mainly in fruit weight and size in both F_1s (Table 2).

The coefficient of determination of the multiple regression model (r^2 in Table 3) indicated the percentage of quantitative trait variation explained by the combined effect of allele substitution at the P_1 locus and the ploidy of the euploid hybrid. Regression models were validated by the significant F-values of the ANOVA (Table 3). The analysis of residuals (Durbin–Watson test at the 5 per cent level) showed that multiple regression models based on ploidy and the effect of allele substitution at the P_1 locus may predict bunch weight in OL × C4, and number of fruits, fruit length and circumference in BT × C4. The Durbin–Watson test, which detects serially correlated data even in significant multiple regression models, was inconclusive for fruit sizes in OL × C4 and for bunch weight and number of hands per bunch in BT × C4. In the multiple regression models for fruit weight both F_1s were based on serially correlated data; therefore, they should not be considered as predictive models. Standard errors (in respective units) of each predictive equation are shown in Table 3.

Discussion

Continuous variation in fruit traits, the effect of the gene P_1 *and* Musa *domestication*

Quantitative polygenic traits often exhibit continuous phenotypic variation; however, this may be observed in the expression of a single major gene affected by environmental variation, for example the effect of the gene H on chlorophyll-A content of the flag leaf in wheat (Simmonds, 1979). Also, single genes may explain most of the variation as revealed by conventional (Sax, 1923) and DNA (Paterson *et al.*, 1991) genetic markers, and proper statistical approaches (Dudley, 1993). Few studies have been undertaken to map loci controlling quantitative trait

Table 2 Effect of allele substitution and ploidy effect at the fruit parthenocarpy locus (P_1), as measured by regression (b), in fruit and bunch characteristics of two euploid plantain–banana populations in the plant and ratoon crops at Onne (1990–93). The coefficient of determination (r^2) indicates the percentage of the total phenotypic variation explained by the regression model $Y = a + bX_i$

	'Bobby Tannap' × 'Calcutta 4' ($N = 52$)			'Obino l' Ewai' × 'Calcutta 4' ($N = 31$)		
Trait	a	b	r^2 (%)	a	b	r^2 (%)
Effect of allele substitution (X_1)						
Bunch weight (kg)	1.20	2.55***	31.6	−2.77	6.79***	61.0
Hands per bunch	6.52	0.21	0.8	5.25	0.88*	12.6
Fruits per bunch	98.59	1.93	0.1	84.55	8.28	2.2
Time to fruit filling (days)	127.25	−4.50	0.9	120.07	2.00	0.6
Fruit weight (g)	10.12	27.59***	41.6	−27.72	69.60***	63.4
Fruit length (cm)	7.65	3.17***	32.6	5.54	5.82***	62.6
Fruit circumference (cm)	4.87	2.42***	47.6	3.30	3.74***	67.7
Ploidy effect (X_2)						
Bunch weight (kg)	−0.18	1.70***	20.0	−5.70	4.22***	62.7
Hands per bunch	7.57	−0.38	4.1	6.10	0.12	0.6
Fruits per bunch	127.09	−11.96*	8.1	102.50	−2.34	0.5
Time to fruit filling (days)	143.43	−9.16	5.6	123.66	2.19	2.0
Fruit weight (g)	−15.97	23.35***	42.6	−62.45	44.94***	70.2
Fruit length (cm)	7.25	1.52*	10.8	3.68	3.40***	56.6
Fruit circumference (cm)	3.54	1.62***	30.6	1.84	2.27***	66.6

Magnitude of b measures either units of increase (+) or reduction (−) in phenotypic expression of quantitative traits when one unit changes in either the P_1 locus or ploidy.

Table 3 Multiple regression models to explain the combined effects of allele substitution (no. of copies of the P_1 allele) and ploidy (X) at the fruit parthenocarpy locus which affected bunch and fruit characteristics (Y) of two euploid plantain–banana populations in the plant and ratoon crops at Onne (1990–93). The coefficient of determination (r^2) indicates the percentage of the total phenotypic variation explained by the regression model $Y = a + b_1X + b_2P_1$

Multiple regression equation	SE prediction	r^2 (%)	Calculated F (P) ANOVA	Durbin–Watson statistics (d)[a]
'Bobby Tannap' × 'Calcutta 4' ($N = 52$)				[$d_L = 1.47$, $d_U = 1.63$]
Bunch weight (kg) = $0.70 + 0.4X + 2.2P_1$	2.0	32.0	11.53 ($P < 0.001$)	2.51
Hands per bunch = $8.0 - 1X + 1.1P_1$	1.2	15.4	4.47 ($P = 0.016$)	2.38
Fruits per bunch = $137 - 27X + 25P_1$	25.0	20.1	6.16 ($P = 0.004$)	2.05
Time to fruit filling (days) = $146 - 13X + 7P_1$	25.0	6.6	1.74 ($P = 0.186$)	1.72
Fruit weight (g) = $-10 + 14X + 16P_1$	47.0	49.2	23.68 ($P < 0.001$)	2.60
Fruit length (cm) = $8.7 - 0.8X + 3.8P_1$	2.5	33.9	12.59 ($P < 0.001$)	2.37
Fruit circumference (cm) = $4.4 + 0.4X + 2.1P_1$	1.4	48.3	22.93 ($P < 0.001$)	2.12
'Obino l'Ewai' × 'Calcutta 4' ($N = 31$)				[$d_L = 1.30$, $d_U = 1.57$]
Bunch weight (kg) = $-5.2 + 2.5X + 3.4P_1$	3.2	66.8	28.21 ($P < 0.001$)	1.65
Hands per bunch = $6.5 - 1.2X + 2.6P_1$	1.3	30.8	6.23 ($P = 0.006$)	2.07
Fruits per bunch = $10.9 - 24X + 42P_1$	32.0	16.3	2.73 ($P = 0.082$)	2.36
Time to fruit filling (days) = $124 - 4X + 4P_1$	15.0	2.6	0.37 ($P = 0.694$)	3.15
Fruit weight (g) = $-59 + 31X + 26P_1$	29.0	72.6	37.09 ($P < 0.001$)	1.16
Fruit length (cm) = $4.3 + 1.3X + 4.0P_1$	2.7	64.8	25.78 ($P < 0.001$)	1.35
Fruit circumference (cm) = $2.2 + 1.2X + 2.1P_1$	1.5	72.5	36.99 ($P < 0.001$)	1.55

[a]Residual analysis. If $d_U < d < 4 - d_U$, the null hypothesis 'data not serially correlated' is not rejected; however, if $d < d_L$ or $d > 4 - d_L$, the null hypothesis is rejected. When $d_L < d < d_U$ or $4 - d_U < d < 4 - d_L$ the test is inconclusive.

variation in polysomic polyploids, although methods and models have been proposed recently (Ortiz & Peloquin, 1992; Wu *et al.*, 1992; Ortiz *et al.*, 1993; Tai, 1994).

Multiple regression analysis may reveal associations between genetic markers (independent variables) and phenotypic variation (dependent variables). Moreover, stepwise multiple regression analysis has the advantage of controlling Type II error or the failure to reject an incorrect null hypothesis (Cowen, 1989), i.e. there are no significant effects of the markers included in the model on quantitative trait variation. However, it does not provide direct information regarding the cause of such a relationship.

The regression models, which should be reasonable according to prior knowledge (Cowen, 1989), partially explained the pattern of variation and fruit traits. Ploidy and the effect of allele substitution at the P_1 locus partially accounted for phenotypic changes in fruit and bunch traits in *Musa* hybrids. Their significant direct effects on fruit traits, and thereby on bunch weight, were not surprising because in natural *Musa* germplasm triploid bananas have larger fruits than diploid cultivars (Simmonds, 1976). Also, fruit parthenocarpy played a major role in the domestication of the crop (Simmonds, 1962), probably because increases in fruit sizes and weight resulted in high yielding bunches, as suggested by the multiple regression model. The P_1 gene may have direct pleiotropic effects on quantitative phenotypic variation of fruit characters or indirect action through linkage with quantitative trait loci controlling these traits. The only means to identify such linkage would be by determining the occurrence of segregation during the course of breeding experimentation or the selection effort.

A regression model, such as the one explained in this paper, would be the statistical interpretation of the quantitative trait, i.e. the regression model explains what fraction of the phenotypic variance (dependent variable) in fruit traits was contributed by ploidy and the effect of allele substitution at the P_1 locus. Likewise, genetic effects, which are included in the model as independent variables, cannot explain more quantitative trait variation than that expressed by H^2 or the ratio of genetic to phenotypic variance. Indeed, the coefficients of determination of the multiple regression models (r^2 in Table 3) were always smaller than H^2 (Table 1). This was expected because ploidy and allele substitution at the P_1 locus explained some but not all the genetic variation in fruit and bunch traits. Hence, other genetic factors also affect these traits in plantain–banana hybrids, e.g. pleiotropic effects of genes for black sigatoka resistance (K. Craenen & R. Ortiz, unpublished data). Also, the regression approach considers only additive effects, while H^2 includes additive and nonadditive genetic variance. Nevertheless, ploidy and allele substitution at the P_1 locus accounted for more than 50 per cent of the H^2 value for traits such as fruit weight and sizes, which had $H^2 > 0.80$ and $R > 1$. Genetic differences resulting from the individual or combined effects of ploidy and allele substitution at the P_1 locus were significantly high for these traits (Tables 2 and 3), and the cropping season and the genotype-by-cropping season interaction, although significant (Table 1), had relative minor importance.

Feasibility of marker-assisted selection for fruit traits and high yields in Musa

The efficiency of a breeding programme may be enhanced by the identification of the major genes affecting quantitative trait variation (Paterson *et al.*, 1991; Edwards, 1992; Dudley, 1993). Thus, selection based on major genes, which are normally easier and cheaper to manipulate than complex polygenic systems, may facilitate and accelerate the genetic improvement of perennial crops like plantains and bananas. Therefore, the predictive value of genetic models should be examined before they are adopted as a regular practice for indirect selection in the breeding programme. In this way the reliability of this breeding method could be assessed.

Durbin–Watson statistics provide the means to determine how adequately the data obtained from the reference population fit the statistical model. Because the multiple regression models were based on the average for each genotype over the two cropping seasons no serial environmental correlation across levels of the independent variables (copies of the P_1 gene and ploidy) might be expected. It seems most likely that any serial correlation would result from genetic effects not explained by the model, e.g. nonadditive genetic effects.

It seems that information about copies of the P_1 gene and ploidy for each hybrid might suffice to select in the seedling nursery genotypes with potential heavy bunches, because of increases in fruit sizes, in OL × C4. Similar information could assist in the early selection of hybrids with many large fruits, thereby increasing bunch weight, in BT × C4. The adoption of this method, which may increase the efficiency of *Musa* breeding, at early stages of plant development relies on the identification of molecular markers (Faure *et al.*, 1993) linked to the P_1

locus and molecular (Afza *et al.*, 1993) and cytological (Vandenhout, 1993) techniques to detect ploidy in seedlings.

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