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Ploidy and genomic group effects on yield components interaction in bananas and plantains across four environments in Nigeria

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Abstract

Thirty-six *Musa* genotypes, comprising the three major genomic groups (AAA, AAB, ABB) and their hybrids, were evaluated in four environments in Nigeria. Multiple correlation and path coefficient analysis was performed on phenological and yield traits. Bunch weight was more associated with phenological traits in triploid *Musa,* especially in resource-poor environments. In tetraploid *Musa* hybrids, bunch weight was consistently correlated with fruit traits. Path coefficient analysis demonstrated that, as expected, bunch weight was essentially determined by the number and weight of fruits. Phenological traits such as plant height and number of days to flowering had low direct effects on bunch weight, but their indirect effects via fruit traits were high. We conclude that ideotype breeding should aim at increasing the number of fruits and the fruit weight regardless of the target environment. Additional gains could be achieved by adopting crop management options that improve the expression of these traits.

Keywords: *Musa* species; Bunch weight; Multiple correlation; Path coefficient analysis

1. Introduction

Banana and plantain (*Musa* spp.) are important cash and subsistence crops in most tropical and subtropical regions of the world (Robinson, 1996). Because of

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biotic stresses, considerable efforts have been made to breed for resistance, as well as to broaden the genetic base of these crops (Vuylsteke et al., 1997).

Newly selected genotypes are routinely tested across locations and years to study their adaptation and consistency of performance before releases. This is because genotypes often interact with the environment in an unpredictable manner (Simmonds, 1991), which complicates selection or recommendation of new hybrids (Annicchiarico, 1997).

The ultimate assessment index of genotype performance is yield. However, yield is a complex characteristic, resulting from many growth functions (Pandey and Torrie, 1973). Identification of components which contribute most to yield may be of practical importance for breeding and crop management (Pandey and Torrie, 1973; Bos and Sparnaaij, 1993; Sparnaaij and Bos, 1993; Piepho, 1995).

Path coefficient analysis is a useful tool for dissection of yield into its components. Path analysis permits the separation of correlation among variables into direct and indirect effects (Dewey and Lu, 1959), and it has proven useful for understanding factors contributing to bunch yield in dessert bananas (Baiyeri and Ortiz, 1995). Such information is lacking for other *Musa* groups.

The objectives of this study were to assess the effect of ploidy and genome composition on the interactions between bunch weight and other plant characteristics under different environmental conditions.

2. Materials and methods

Thirty-six *Musa* genotypes belonging to different genomes and ploidy levels (Table 1) were evaluated at three locations in Nigeria, following a north–south gradient of vegetation types: Abuja (southern-guinea savanna zone), Ibadan (forest-savanna transition zone), and Onne (rainforest zone).

Abuja (9°16′N, 7°20′E), at about 300 m altitude above sea level (asl), has a unimodal rainfall pattern with an annual total of about 1300 mm, falling between May and October. The maximum temperature fluctuates between 26 and 34°C and the minimum is between 13 and 21°C. Radiation is about 5846 MJ m^{-2} per year. The soil is ferris luvisol. Ibadan (7°31′N, 3°54′E), at about 150 m asl, has a bimodal rainfall pattern with an annual total of about 1300 mm, most of which falls between May and October. Average temperature fluctuates between 20 and 35°C with an annual mean of 26.5°C. Radiation is about 5285 MJ m^{-2} per year. The soil is slightly acidic alfisol. Onne (7°E, 5°N; 10 m asl) has annual rainfall of 2400 mm that is distributed monomodally from February to December. Relative humidity remains high throughout the year, with average values ranging from 78% in February to 89% in July and September. On average, there are only 4 h of direct sunshine each day. The soil is representative of highly

Table 1
List of genotypes used in this study

Classification[a]	Landraces (3×)	Hybrids (4×)[b]
Dessert bananas	Pisang Ceylan, Valery, Yangambi Km5	FHIA-1, FHIA-2, FHIA-23, SH3436-9, SH3640, EMB 402, EMB 403, EMC 602
Plantains	Agbagba, Obino l'Ewai, UNN.DB	PITA-1, PITA-2, PITA-3, PITA-5, PITA-7, PITA-8, PITA-9, PITA-11, PITA-12, PITA-14, PITA-16, FHIA-21, FHIA-22
Cooking bananas	Bluggoe, Cardaba, Fougamou, Pelipita, Saba	BITA-1, BITA-2, BITA-3, FHIA-3

[a] The classification of *Musa* cultivars is based on the number of A and B genomes they harbor from ancestor species, *Musa acuminata* Colla (donor of A genome) and *M. balbisiana* (donor of B genome), e.g., AAA predominantly for dessert bananas, AAB for plantains, and ABB for cooking bananas (Robinson, 1996; Simmonds, 1962; Stover and Simmonds, 1987). Dessert banana hybrids are denoted as AAA × AA, plantain hybrids as AAB × AA, and cooking banana hybrids ABB × AA.

[b] FHIA and SH hybrids are from Fundaçion Hondureña de Investigacíon Agricóla, Honduras; PITA and BITA hybrids are from the International Institute of Tropical Agriculture, Nigeria; EMB and EMC hybrids are from EMBRAPA and EMCAPA in Brazil, respectively; others are landraces. Note that PITA16 is a triploid, while others are tetraploids.

leached acid ultisols. Detailed characterization of Onne site has been reported by Ortiz et al. (1997).

Planting was in a sole cropping system at each location, but an additional alley cropping system in a natural multispecies hedgerow (Ortiz, 1995) was used at Onne, giving a total of four environments. The experimental design was a 6 × 6 simple lattice replicated twice with a planting distance of 3 m between rows and 2 m within rows. Each genotype was grown in a single-row plot with five plants per replication. Cultural practices were as recommended by Swennen (1990).

Data collected were number of days to flowering, number of days to harvest, number of days for fruit filling (bulking), plant height at flowering (cm, determined as distance from ground level to the junction of the last two fully expanded leaves), and height of the tallest sucker (cm) at the time of harvest of the mother plant. Cycling index was determined as the ratio of sucker height to plant height multiplied by 100. This ratio is an indication of the interval between two consecutive harvests (Tenkouano et al., 1998). Response to black sigatoka disease was obtained using the youngest leaf spotted criterion (Vakili, 1968). Other characters include bunch weight per plant (kg), number of hands (nodal clusters) per bunch, number of fruits per bunch, fruit weight (g), fruit length (cm) and fruit circumference (cm).

Statistical analysis was carried out on a plot means basis due to an unequal number of observations per plot (Piepho, 1997). Correlation among the traits was assessed using PROC CORR (SAS, 1992). Path coefficient analysis was then carried out with MINITAB software (MINITAB, 1984) using those traits that were significantly correlated with bunch weight and with each other. Thus, the correlation coefficients among these traits were partitioned into direct and indirect effects, and coefficients were calculated as described in Ortiz and Langie (1997).

3. Results

The analysis of variance showed significant differences among environments and *Musa* genotypes for all traits (Table 2). A significant genotype × environment interaction was also found for all traits, except fruit length and fruit circumference (Table 2).

Bunch weight was significantly correlated with several growth and yield traits (Table 3). However, the traits most strongly correlated with bunch weight varied across ploidy groups, genome groups, and environments (Table 3). For example, the number of fruits per bunch appeared to be frequently correlated with bunch weight across environments for dessert banana (AAA) landraces and hybrids. Fruit weight was also consistently correlated with bunch weight of the tetraploid hybrids from dessert bananas at all locations (Table 3). In the plantain (AAB) genomic group, bunch weight was predominantly associated with the number of days to flowering in the triploid landraces but with fruit weight in the tetraploid hybrids (Table 3). In the cooking banana (ABB) genomic group, no trait was consistently associated with bunch weight across the environments for the landraces. However, in the ABB-derived hybrids, bunch weight was correlated with the number of fruits per bunch in all environments (Table 3).

Path coefficient analysis was performed as previously described (Dewey and Lu, 1959; Ortiz and Langie, 1997). There was a strong environmental effect on the paths defined for the different ploidy and genome groups. However, a few traits consistently showed significant correlation with bunch weight, due to their significant direct and indirect contribution to bunch weight, irrespective of ploidy group, genome group, or environment (Fig. 1).

In the dessert banana genomic group (Table 4), no path could be defined at Abuja. At other locations, the number of fruits per bunch, fruit weight and fruit length appeared to be the major contributors to bunch weight. Other characters that had a positive correlation with bunch weight contributed to bunch weight indirectly via fruit weight (Table 4).

There was no significant path to bunch weight for plantain landraces in two of the four environments (Table 5). At Abuja and Onne sole cropping, bunch weight

Table 2
Mean squares from the analysis of variance of phenological and yield traits of 36 *Musa* genotypes grown in four environments in Nigeria

Source of variation	d.f.	Traits[a]							
		PHF	DTF	BWT	FWT	F/B	FLT	FCR	YLSF
Environment	3	80926.1***	36408.3***	678.7***	24021.3***	18082.1***	156.1***	108.2***	26.6***
Blocks (Rep)	10	663.0	5218.9*	10.7	1112.6	161.7	3.8	1.2	1.5
Reps (Environment)	3	12208***	60489.9***	60.3***	1904.4	1218.1***	55.3***	4.8*	3.9
Genotype	35	11407.3***	19172.4***	78.7***	11302.4***	6027.9***	67.4***	15.6***	12.3***
Between groups	5	33606.7***	44910.4***	58.5***	29505.1***	11817.9***	169.7***	48.1*	23.6***
Within groups	30	7228.3***	15265.1***	78.4***	7889.9***	4785.1	46.2***	9.4***	10.4***
Genotype × Environment	104	884.3***	6935.1***	14.9***	1349.4	364***	11.4	1.8	4.1**
Between groups	15	1230.7	2467.6***	21.6**	2138.6*	260.4	15.8	3.0*	5.2*
Within groups	89	812.9	4011.1	13.9**	1209.4	372.9***	10.7	1.5	3.8*
Residual	118	465.8	2454.5	7.3	972.6	177.6	4.0	1.5	2.5

* *F*-test significant at 5% probability level.
** *F*-test significant at 1% probability level.
*** *F*-test significant at 0.1% probability level.
[a] PHF, plant height at flowering; DTF, days to flowering; BWT, bunch weight; FWT, fruit weight; F/B, fruits per bunch; FLT, fruit length; FCR, fruit circumference; YLSF, youngest leaf spotted at flowering.

Table 3
Correlation of bunch weight with growth and yield components in different *Musa* groups grown in four environments in Nigeria

Traits	3× Landraces[a]				4× Hybrids			
	ABJ	IBD	OSC	OAC	ABJ	IBD	OSC	OAC
Dessert bananas								
Days to flowering	−0.72	−0.77	0.15	0.01	0.53*	0.17	0.30	0.83**
Days for fruit filling	−0.84*	−0.20	−0.72	−0.43	−0.56*	−0.51	0.11	−0.49
Plant height at flowering (cm)	0.44	0.75	0.86*	0.09	0.15	0.40	0.21	0.40
Height of tallest sucker at harvest (cm)	0.73	0.29	−0.24	−0.58	−0.73*	−0.30	−0.23	0.02
Youngest leaf spotted at flowering (no.)	0.75	0.01	−0.15	0.46	0.48	0.35	−0.05	−0.34
Fruits per bunch	0.84*	0.72	0.94**	0.63	0.78**	0.74**	0.91**	0.76**
Fruit weight (g)	0.76	0.78	0.55	0.87*	0.77**	0.91**	0.95**	0.86**
Fruit length (cm)	0.76	0.83	0.21	0.84*	0.77**	0.87**	0.90**	0.91**
Fruit circumference (cm)	0.61	0.70	0.76	0.88*	0.59*	0.77**	0.78**	0.79**
Plantains								
Days to flowering	−0.95*	−0.73	−0.93**	0.03	−0.39*	−0.56**	−0.05	0.03
Days for fruit filling	−0.25	0.79	0.26	0.89*	−0.33	0.29	−0.02	0.01
Plant height at flowering (cm)	0.70	0.75	0.99**	−0.10	0.59*	0.59	0.47**	0.71**
Height of tallest sucker at harvest (cm)	0.32	0.40	−0.46	−0.94*	−0.24	0.05	−0.43*	−0.04
Youngest leaf spotted at flowering (no.)	−0.44	−0.80	−0.27	0.76	0.07	0.07	0.10	0.38
Fruits per bunch	−0.19	0.40	0.23	0.27	0.72**	0.79**	0.25	0.47*
Fruit weight (g)	0.71	0.60	0.55	0.24	0.73**	0.77**	0.78**	0.88**
Fruit length (cm)	0.80*	0.59	0.73	0.31	0.71**	0.35	0.71**	0.67**
Fruit circumference (cm)	0.77	0.40	0.57	0.25	0.72**	0.46*	0.72**	0.79**
Cooking bananas								
Days to flowering	−0.32	−0.40	−0.39	−0.07	−0.42	−0.53	−0.96**	−0.30
Days for fruit filling	−0.04	−0.13	0.65*	0.58	−0.63	−0.27	−0.77*	−0.71
Plant height at flowering (cm)	0.21	0.40	0.85**	0.18	0.03	0.30	−0.09	−0.49
Height of tallest sucker at harvest (cm)	0.57	0.09	0.41	0.31	−0.12	0.42	−0.78*	−0.49
Youngest leaf spotted at flowering (no.)	0.75*	−0.31	−0.02	0.56	−0.14	0.71	0.70*	0.77
Fruits per bunch	0.34	−0.14	0.26	0.35	0.72*	0.75*	0.77*	0.86**
Fruit weight (g)	0.15	0.70*	0.56	0.63*	0.44	0.12	0.52	0.17
Fruit length (cm)	0.09	0.65*	0.41	0.58	0.16	0.31*	0.57	0.23
Fruit circumference (cm)	0.11	0.68*	0.40	0.69*	0.67	0.03	0.24	0.35

* Significant at 5% probability level.
** Significant at 1% probability level.
[a] ABJ: Abuja, IBD: Ibadan, OSC: Onne sole cropping, OAC: Onne alley cropping.

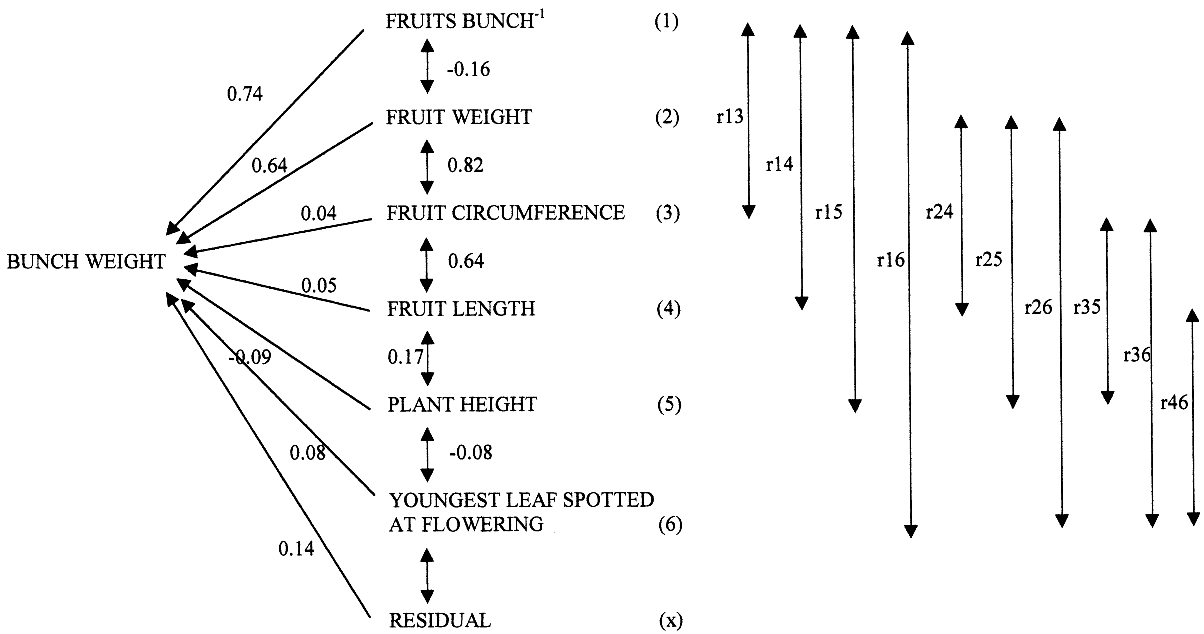

Fig. 1. Path diagram showing causal relationship between bunch weight and six other plant traits. The residual is the undetermined portion. The double-arrowed lines indicate mutual association as measured by correlation coefficient, and the single-arrowed lines represent direct influence as measured by path coefficients.

Table 4
Path coefficients of bunch weight showing components of direct and indirect effects for dessert bananas landraces (3×) and hybrids (4×) in different environments

Environment and trait		Path coefficients, by trait[a]						
		DTF	PHF	FWT	FL	FC	F/B	Correlation[b]
Abuja								
4×	FWT			*0.82*[c]	0.21	−0.26		0.77
	FL			0.79	*0.22*	−0.24		0.77
	FC			0.71	0.18	*−0.30*		0.59
	Residual							0.37
Ibadan								
4×	FWT			*0.83*	0.47	−0.39		0.91
	FL			0.77	*0.51*	−0.41		0.87
	FC			0.74	0.47	*−0.44*		0.77
	Residual							0.14
Onne sole crop								
3×	PHF		*−0.20*				1.06	0.86
	F/B		−0.19				*1.13*	0.94
	Residual							0.11
4×	FWT			*0.82*	−0.05	−0.14	0.32	0.95
	FL			0.79	*−0.06*	−0.13	0.30	0.90
	FC			0.72	−0.05	*−0.16*	0.26	0.78
	F/B			0.64	−0.04	−0.10	*0.41*	0.91
	Residual							0.03
Onne alley crop								
3×	FWT			*0.93*	0.06			0.87
	FL			0.90	*−0.07*			0.84
	Residual							0.26
4×	DTF	*0.53*		0.05	0.59	−0.36		0.82
	FWT	0.34		*0.07*	0.92	−0.47		0.86
	FL	0.33		0.07	*0.96*	0.45		0.91
	FC	0.38		0.07	0.85	*−0.51*		0.79
	Residual							0.04

[a] DTF, days to flowering; PHF, plant height at flowering; FWT, fruit weight; FL, fruit length; FC,fruit circumference; F/B, fruits per bunch.

[b] Correlation coefficients between growth and yield components (row) and bunch weight.

[c] Values on the diagonal (italics) are direct effects of the components on bunch weight; off-diagonal values are indirect effects through the specific path.

was predominantly controlled by vegetative growth. The path to yield in tetraploid plantain hybrids was significantly controlled by fruit weight in most of the environments (Table 5).

The relationship of bunch weight to other plant characteristics was not clear for the ABB genomic group. For example, no path could be defined for plants at

Table 5
Path coefficients of bunch weight showing components of direct and indirect effect for plantains landraces (3×) and hybrids (4×) in different environments

Environment and trait		Path coefficients, by trait[a]					
		DTF	PHF	FWT	FL	FC	Correlation[b]
Abuja							
3×	DTF	*−0.92*[c]				−0.03	−0.95
	FL	0.76				*0.04*	0.80
	Residual						0.09
4×	PHF		*0.30*	0.02	0.04	0.23	0.59
	FWT		0.17	*0.03*	0.08	0.45	0.73
	FL		0.16	0.03	*0.08*	0.44	0.71
	FC		0.15	0.03	0.07	*0.47*	0.72
	Residual						0.04
Ibadan							
4×	DTF	*−0.08*	−0.07	−0.59		0.19	0.56
	PHF	0.04	*0.15*	0.56		−0.16	0.59
	FWT	0.05	0.09	*0.90*		−0.28	0.77
	FC	0.04	0.07	0.70		*−0.36*	0.46
	Residual						0.34
Onne sole crop							
3×	DTF	*−0.21*	−0.72				−0.93
	PHF	0.18	*0.81*				0.99
	Residual						0.00
4×	FWT			*0.58*	0.00	0.20	0.78
	FL			0.52	*0.00*	0.19	0.71
	FC			0.47	0.00	*0.25*	0.72
	Residual						0.36
Onne alley crop							
4×	PHF		*0.25*	0.72	−0.27	0.01	0.71
	FWT		0.17	*1.04*	−0.35	0.02	0.88
	FL		0.17	0.89	*−0.41*	0.01	0.67
	FC		0.18	0.89	−0.30	*0.02*	0.79
	Residual						0.17

[a] DTF, days to flowering; PHF, plant height at flowering; FWT, fruit weight; FL, fruit length; FC, fruit circumference.

[b] Correlation coefficients between growth and yield components (row) and bunch weight.

[c] Values on the diagonal (italics) are direct effects of the components on bunch weight; off-diagonal values are indirect effects through the specific path.

Abuja. Fruit characteristics appeared to be most closely associated with the determination of bunch weight at Ibadan and Onne alley cropping for the landraces, and Onne sole cropping for the tetraploid hybrids (Table 6).

Table 6
Path coefficients of bunch weight showing components of direct and indirect effects for cooking bananas (ABB) landraces (3×) and hybrids (4×) in different environments

Environment and trait		Path coefficients, by trait[a]							
		DTF	PHF	FWT	FL	FC	F/B	YLSF	Correlation[b]
Ibadan									
3×	FWT			*0.91*[c]	−0.13	−0.08			0.70
	FL			0.86	*−0.14*	−0.07			0.65
	FC			0.89	−0.13	*−0.08*			0.68
	Residual								0.51
Onne sole crop									
4×	DTF	*−0.85*					−0.15	0.04	−0.96
	F/B	0.60					*0.21*	−0.04	0.77
	YLSF	0.59					0.16	*−0.05*	0.70
	Residual								0.05
Onne alley crop									
3×	FWT			*−1.17*		1.80			0.63
	FC			−1.14		*1.83*			0.69
	Residual								0.48

[a] DTF, days to flowering; PHF, plant height at flowering; FWT, fruit weight; FL, fruit length; FC, fruit circumference; F/B, fruits per bunch; YLSF, youngest leaf spotted at flowering.
[b] Correlation coefficients between growth and yield components (row) and bunch weight.
[c] Values on the diagonal (italics) are direct effects of the components on bunch weight; off-diagonal values are indirect effects through the specific path.

4. Discussion

Path coefficient analysis indicated that the relationship of bunch weight to other plant characteristics varied across ploidy groups, genome groups, and environments. Paths could not be defined for some ploidy groups under certain environments because traits that correlated with bunch weight were not intercorrelated. This might be related to trait sensitivity to stressful conditions at certain developmental stages in those environments. For example, the number of fruits per bunch and the fruit weight often exhibit complementary and/or compensatory effect on bunch weight. Thus, occurrence of moisture stress during fruit bulking could make the relationship between these two traits competitive, and would have negative effect on fruit weight (Ndubizu and Okafor, 1976).

Path analysis suggests that the bunch weight of dessert bananas (AAA) could be improved using a breeding strategy aimed at selecting for increased fruit length and fruit weight. The adoption of crop management options that maximize the expression of these fruit traits constitutes another strategy to increase bunch weight in dessert bananas.

Flowering of plantains (AAB) and other *Musa* genotypes is non-seasonal (Simmonds, 1966). When flowering and fruit bulking coincide with periods of high soil moisture, bunch weight is high (Ndubizu and Okafor, 1976; Obiefuna, 1986). Late flowering, especially among the plantain triploid genotypes, would make fruit bulking coincide with low moisture periods, resulting in low bunch weight via reduced fruit length, fruit circumference and fruit weight. Robinson (1996) attributed seasonal variation in bunch mass of dessert bananas to the prevailing temperature during the flowering period rather than soil moisture. Adequate vegetative growth with large leaf area of plantains will increase photosynthetic products directed into fruit formation (Dewey and Lu, 1959). Therefore, factors that enhance early vegetative growth will also enhance bunch weight in this genome group.

No clear path relationships could be established for the ABB genome group probably due to poor adaptation, since they are new introduction from Asia into Nigerian environments (Vuylsteke et al., 1997). However, crop management practices that enhance the fruit characteristics will increase yield in this genome.

As expected, in all the environments the number of fruits per bunch and fruit weight appeared to be the most important components associated with heavy bunch in tetraploid *Musa* genotypes. In triploid genotypes, however, phenological traits appeared to also contribute significantly to determination of bunch weight in addition to fruit weight.

Moisture availability was the most important abiotic factor of growth in Abuja and Ibadan, whereas in Onne, poor soil characteristics, especially high porosity and acidity (Ortiz et al., 1997), constituted the major limitations to growth. The number of fruits per bunch, which was an important path to bunch weight under sole cropping at Onne, is determined before inflorescence emergence (Barker and Steward, 1962). These poor soil conditions depressed bunch weight via its effect on the number of fruits per bunch. In contrast, the alley cropping system has both high organic matter build-up and high moisture retention capacity, which was more conducive to growth. Therefore, breeding objectives will vary for the two cropping systems since limitations to yield are different. Selection for tolerance to abiotic stress should enhance yield under sole cropping.

These results support the suggestion of Ortiz and Langie (1997) that ideotype selection should be based on path relationships for specific production systems. The path analysis revealed that phenological traits and components of bunch weight that had a high direct effect on yield varied with *Musa* genomic groups and the cropping environments. However, our study indicates that fruit weight and number of fruits per bunch should be essential components of ideotype breeding. Hence, selection of parents with good combining ability for number of fruits and fruit weight would assure production of high yielding hybrids that also have big fruits. This is of particular importance in *Musa*-growing regions of West and Central Africa, where fruit size is an important consumer preference trait.

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