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Genotype-by-Environment Interaction and Testing Environments for Plantain and Banana (*Musa* spp. L.) Breeding in West Africa

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Keywords: *Musa* - Banana - Black sigatoka - Correlated response across environment - Plantain - Site rationalisation.

Summary

*With reduced budgets allocated for international agricultural research, site rationalisation had become an important issue to consider when carrying out multilocational testing of promising selections. The aim of this paper was to determine the importance of the genotype-by-environment interaction in multilocational trials of plantains and bananas (*Musa *spp.L.) in selected sites of West Africa comprising the humid forest and the forest-savanna transition zones. A sample of plantain-banana hybrids, plantain landraces, exotic banana cultivars and diploid parental banana accessions were evaluated in three locations: Mbalmayo and Onne (humid forest) and Ibadan (forest-savanna transition). The experimental results of our research suggested that multilocational testing is more profitable than single site evaluation over several years in the* Musa *breeding station. Furthermore, based on correlated responses across environments for yield potential, we suggest that one of the selection sites in the humid forest (i.e., Mbalmayo) be dropped since selections in one site (Onne) may be well adapted to the other location in the same agroecozone. Conversely, the relatively poor performance of most genotypes in dry environments (e.g. Ibadan) reinforces the importance of early testing across a wide range of environments. In this way, selections with broad or specific adaptation may be identified for further release to targeted farmers.*

Resumen

Genotipo ambiental interacción y evaluación de entornos para el mejoramiento genético del llantén y del plátano (*Musa* spp. L.) en Africa Occidental

*La selección de localidades para los ensayos de nuevos genotipos se ha convertido en un asunto muy importante en esta época de escasos recursos para la investigación en la agricultura. El objetivo de este experimento fue determinar la importancia de la interacción genotipo-ambiente en los ensayos de plátanos y bananos (*Musa *spp.L.) en el bosque tropical húmedo y en la zona de transición del Africa Occidental. Una muestra de híbridos, cultivares locales de plátanos, cultivares exóticos de bananos y los progenitores bananos diploides de los híbridos fueron evaluados en tres localidades: Mbalmayo y Onne (en el bosque tropical húmedo) e Ibadan (en la zona de transición). Los resultados sugieren que los ensayos repetidos en diferentes ambientes son más importantes que un sólo ensayo repetido en una localidad por varios años. Asímismo, en análisis de correlación genética para rendimiento indica que una de las localidades en la zona del bosque tropical húmedo (Mbalmayo) puede ser eliminada porque las selecciones en la otra localidad (Onne) se adaptan ampliamente en esta zona agro-ecológica. Los rendimientos de varios genotipos en ambientes secos como Ibadan señalan la importancia de ensayos preliminares en un rango amplio de ambientes. De este modo los genotipos con adaptación amplia o específica podrán ser seleccionados para ser posteriormente ofrecidos como nuevos cultivares para los agricultores.*

Introduction

Measurements of the genotype-by-environment (GE) interaction are a very important basis for determining the breeding strategy which is most appropriate for the development of genotypes for specific targeted environments. When GE interactions are not important, breeding materials may be safely tested in the most convenient environment (8). Otherwise, the breeding material must be evaluated in the specific environments where they are expected to be grown by farmers (6).

When the effects of a particular environmental stress are not taken into account, the gains from a selection

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program may decrease as the level of that stress increases. Indeed, segregating populations characteristically exhibit low genetic variances in diverse or stressed environments (4,9). Consequently, this type of selected population is likely to produce low mean yields when grown in non-stressed environments. This type of effect can be accounted for in terms of the high metabolic 'cost' to plant of expressing additional traits for tolerance or resistance to abiotic or biotic stresses.

The environment plays an important role in the identification of promising genotypes adapted or resistant to specific stresses (3). For example, selection for increased efficiency of nitrogen uptake should take place in environments with a low fertility level (7). Optimum environments, where all individuals are phenotypically normal do not allow the differentiation between different genotypes. In contrast, the genetic differences may be masked during growth in extremely poor environments because all the entries tested will have their phenotypes adversely affected by the stress.

The ideal environment for breeders' selections would be the one which maximises phenotypic differences among genotypes, i.e., where breeders are able to do visual "genotyping" (8). For example, selection for resistance to black sigatoka (caused by the fungus *Mycosphaerella fijiensis* Morelet) in plantain seems to be more efficient during the rainy than in the dry season. This is probably related to the optimum environment for fungal infection prevailing during the rainy season. However, phenotypic differences between resistant and susceptible genotypes can be observed equally well during the dry season of certain environments (16), where there was no genotype-by-environment interaction. For example, there was no change in the ranking of order or in magnitude differences between the resistant hybrids and the susceptible landraces, in their host response to black sigatoka when evaluated in different seasons in a humid lowland environment in Cameroon (16).

The objective of this study was to determine what could be the best environments for multilocational testing of plantain and banana genotypes in West Africa. This will lead to rationalisation of testing sites for germplasm evaluation wherever possible, thereby improving the efficiency by reducing the costs of the breeding program.

Material and Methods

Eight plantain-banana tetraploid hybrids developed by the International Institute of Tropical Agricultura (IITA) (17,18), four exotic triploid cooking banana cultivars, three triploid plantain landraces, two diploid banana parents, and one dessert banana of world-wide cultivation ('Valery') were evaluated in the plant (PC) and ratoon (RC) crops at IITA stations in the humid forest (Mbalmayo in Cameroon and Onne in Nigeria) and forest-savanna transition (Ibadan in Nigeria) zones (Table 1). These locations have different rainfall patterns, soil characteristics and crop management practices. Mbalmayo has a bimodal annual rainfall (total 1500 mm) and an Ultisol derived from a schist band with low extractable P; whereas Onne, has a monomodal annual rainfall (2400 mm) and an Ultisol derived from coastal sediments, well drained and with high extractable P. Ibadan has a bimodal annual rainfall (1250 mm) and the experiment was planted in a hydromorphic area of a Ferric Luvisol with a water table (30-40 cm) during the rainy season. The trials at Mbalmayo and Onne were carried out under alley cropping with multispecies hedgerows while the experiment at Ibadan was on a sole crop. Cultural practices within each crop management system have been described elsewhere (11).

Table 1
Clones tested in multilocational trials in West Africa

Genotype	Genome[1] or parentage	Black sigatoka response
Diploid bananas (2n = 22)		
Calcutta-4	AA	Highly resistant
Pisang lilin	AA	Resistant
Triploid landraces (2n = 33)		
Agbagba	AAB False Horn plantain	susceptible
Bluggoe	ABB cooking banana	less susceptible
Bobby Tannap	AAB French plantain	susceptible
Cardaba	ABB cooking banana	less susceptible
Fougamou	ABB cooking banana	partially resistant
Obino l'Ewai	AAB French plantain	susceptible
Pelipita	ABB cooking banana	less susceptible
Valery	AAA export dessert banana	susceptible
Tetraploid hybrids (2n= 44)		
TMPx 548-4	Obino l'Ewai (OL) X Calcutta 4 (C4)	partially resistant
TMPx 548-9	OL X C4	partially resistant
TMPx 582-4	Bobby Tannap (BT) X C4	partially resistant
TMPx 597-4	OL X C4	susceptible
TMPx 1112-2	Agbagba French Reversion X C4	partially resistant
TMPx 1658-4	OL X Pisang lilin (P1)	less susceptible
TMPx 2796-5	BT X P1	partially resistant
TMBx 612-74-OT	Bluggoe X C4	highly resistant

[1] AA for *Musa acuminata* Colla., and BB for *Musa balbisiana* Colla.

The experimental layout was the recommended randomised complete block design with two replications of five plants per location (13). Distance between plants within the same row was 2 m and between rows 3 m, thus 1667 plants ha^{-1} was the planting density. All plots were surrounded by the same plantain landrace to assure uniform inoculum pressure for black sigatoka disease. Plant height at flowering (PH, cm), total number of leaves (TNL), days for fruit filling (DFF), days to harvest (DH), height of tallest sucker at harvest (HTS, cm), bunch weight (BW, kg), number of fruits per bunch (F), number of hands per bunch (H), fruit length (FL), circumference (FL) and weight (FW), were recorded in each individual plant.

Statistical analyses and site rationalisation

Analysis of variance. The data were analysed for each trait following the random model of the combined analysis of variance (ANOVA) for series of trials across environments (10). The following combined ANOVA were carried out: (i.) across environments, where environments were defined as location X growth cycle, i.e. six environments; (ii) across locations (over production

cycles), i.e., three locations, and (iii) within locations, i.e. two production cycles per location. All statistical analyses were performed with MSTAT-C (2), but F-tests were adjusted according to the random model (10).

Correlated responses across environments. The performance across two environments was considered as two different but correlated traits (5). The direct response to selection in the targeted environment Y is (R_y) is $\tau_y H_y \sigma G_y$, where τ_y is the intensity of selection, $H_y Y$ is the square root of the heritability of the trait under selection in the targeted environment Y, and σG_y is the genetic standard deviation. The correlated response to selection (CR_y) is $\tau_X H_X H_y \rho_G \sigma P_X$, where τ_x is the intensity of selection in alternative environment X, H_x and H_y are the square roots of the heritability of the trait under selection in each environment, ρG is the genetic correlation between the two performances, and σP_x is the phenotypic standard deviation of the trait under selection in environment Y. The efficiency of selection in alternative environment X was measured by the ratio CR_y/R_y, i.e., $\rho G(\tau_X H_X)/(\tau_y H_y)$. This methodology allowed the testing of whether or not selection in on environment may be efficient to develop cultivars adapted to other environments (i.e., correlated response across environments).

Yield potential of *Musa* germplasm (landraces and hybrids) was estimated using data from three IITA stations in the humid forest (Onne and Mbalmayo) and in the transition zone (Ibadan) to establish a strategy for site rationalisation in multilocational testing. Yield potential (YLD, t ha^{-1} $year^{-1}$) was calculated on a per plot basis as:

$$YLD = BW \times 365 \times 1667 / (DH \times 1000)$$

Results and Discussion

Significant differences ($P < 0.05$) between locations were observed for several characters (Table 2). In general the production cycle was longer at Onne than at Mbalmayo. Furthermore, the total number of leaves was generally highest at Onne, lower at Ibadan, and lowest at Mbalmayo. However, height of the tallest sucker was generally shorter at Ibadan than at the other two locations.

Table 2
Means for growth and yield parameters in each environment (location/cycle)

Location	Cycle	DH	DF	DFF	TNL	PH	HTS
Onne		382	273	109	37	329	251
	PC	488	376	112	38	305	242
	RC	261	163	106	36	353	261
Ibadan		348	242	108	32	248	179
	PC	432	320	113	32	241	175
	RC	259	157	103	32	256	183
M'Balmayo		405	298	114	31	328	249
	PC	450	348	109	28	306	235
	RC	348	228	119	35	353	264
$LSD_{0.05}$ (L)		13	12	NS	1	6	11
$LSC_{0.05}$ (C/L)		18	17	4	1	9	NS
Location	Cycle	BW	H	F	FL	FC	FW
Onne		10.8	7	87	16	12	126
	PC	10.6	6	80	17	12	129
	RC	11.0	7	95	16	12	123
Ibadan		6.4	5	62	17	11	103
	PC	6.8	5	62	17	11	111
	RC	6.0	5	62	17	11	96
M'Balmayo		12.3	6	87	15	13	144
	PC	10.3	6	88	14	12	111
	RC	14.3	7	86	16	14	179
$LSD_{0.05}$ (L)		1	0.2	3	0.5	0.4	8
$LSD_{0.05}$ (C/L)		1	0.2	5	1	1	11

PC = plant crop; RC = ratoon crop; DH = days to harvest; DF = days to flowering; DFF = days for fruit filling; TNL = total number of leaves; PH = plant height, cm; HTS = height of tallest sucker at harvest, cm; BW = bunch weight, kg; H = number of hands; F = number of fruits; FL = fruit length, cm; FC = fruit circumference, cm; FW = fruit weight, g; $LSD_{0.05}$ (L) = least square difference between locations at the 5% level; $LSD_{0.05}$ (C/L) = least square difference between environments at the 5% level.

In addition, bunch weight and the number of hands per bunch were generally higher at Onne and Mbalmayo than at Ibadan (Table 3). This might reflect a limitation of the selections at Onne. Hybrids selected under a high rainfall regime cannot be expected to be well adapted to the longer dry season at Ibadan. These differences in bunch weight are likely to be a result of a

Table 3
Analysis of variance for growth and yield parameters of 18 *Musa* accessions grown in six environments (= location x production cycle)

Source of Variation	DH	DF	DFF	TNL	PH	HTS
	Probability of F-test for respective source of variation					
Environment (E)	P≤0.001	P≤0.001	P≤0.001	P≤0.001	P≤0.001	P≤0.001
Genotype (G)	P≤0.001	P≤0.001	P≤0.001	P≤0.001	P≤0.001	P≤0.001
GxE interaction	P≤0.001	P≤0.001	P≤0.001	P≤0.001	P≤0.001	P≤0.05
Coefficient of Variation (%)	10.1	13.9	7.8	6.9	6.2	14.4
Source of Variation	BW	H	F	FL	FC	FW
	Probability of F-test for respective source of variation					
Environment (E)	P≤0.001	P≤0.001	P≤0.001	P≤0.001	P≤0.001	P≤0.001
Genotype (G)	P≤0.001	P≤0.001	P≤0.001	P≤0.001	P≤0.001	P≤0.001
GxE interaction	P≤0.001	P≤0.001	P≤0.001	P≤0.05	P>0.05	P≤0.001
Coefficient of Variation (%)	20.1	8.8	13.0	8.6	9.5	19.2

DH = days to harvest; DF = days to flowering; DFF = days for fruit filling; TNL = total number of leaves; PH = plant height, cm; HTS = height of talles sucker at harvest, cm; BW = bunch weight, kg; H = number of hands; F = number of fruits; FL = fruit length, cm; FC = fruit circumference, cm; FW = fruit weight, g.

Table 4
Analysis of variance for growth and yield parameters of 18 *Musa* accessions grown in three locations

Source of Variation	DH	DF	DFF	TNL	PH	HTS
	Probability of F-test for respective source of variation					
Location (L)	P≤0.001	P≤0.001	P>0.05	P≤0.001	P≤0.001	P≤0.001
Genotype (G)	P≤0.05	P≤0.01	P≤0.001	P≤0.001	P≤0.001	P≤0.001
GxL interaction	P>0.05	P>0.05	P≤0.05	P>0.05	P≤0.05	P>0.05
Coefficient of Variation (%)	29.0	38.9	10.1	3.4	9.4	15.9

Source of Variation	BW	H	F	FL	FC	FW
	Probability of F-test for respective source of variation					
Location (L)	P≤0.001	P≤0.001	P≤0.001	P≤0.001	P≤0.001	P≤0.001
Genotype (G)	P≤0.001	P≤0.001	P≤0.001	P≤0.001	P≤0.001	P≤0.001
GxL interaction	P≤0.001	P≤0.001	P≤0.001	P≤0.05	P>0.05	P≤0.001
Coefficient of Variation (%)	23.4	9.1	16.4	10.0	10.6	25.0

DH = days to harvest; DF = days to flowering; DFF = days for fruit filling; TNL = total number of leaves; PH = plant height, cm; HTS = height of tallest sucker at harvest, cm; BW = bunch weight, kg; H = number of hands; F = number of fruits; FL = fruit length, cm; FC = fruit circumference, cm; FW = fruit weight, g.

Table 5
Analysis of variance for growth and yield parameters of 18 *Musa* accessions grown in three locations in two cycles for each location.

ONNE

Source of Variation	DH	DF	DFF	TNL	PH	HTS
	Probability of F-test for respective source of variation					
Cycle (C)	P≤0.001	P≤0.001	P≤0.01	P≤0.05	P≤0.001	P>0.05
Genotype (G)	P≤0.001	P≤0.001	P≤0.001	P≤0.001	P≤0.001	P≤0.001
GxC interaction	P≤0.01	P≤0.01	P≤0.01	P>0.05	P>0.05	P>0.05
Coefficient of Variation (%)	10.9	13.8	6.3	7.0	5.3	15.0

Source of Variation	BW	H	F	FL	FC	FW
	Probability of F-test for respective source of variation					
Cycle (C)	P>0.05	P≤0.001	P≤0.001	P≤0.001	P>0.05	P>0.05
Genotype (G)	P≤0.001	P≤0.001	P≤0.001	P≤0.001	P≤0.001	P≤0.001
GxC interaction	P>0.05	P>0.05	P≤0.01	P>0.05	P>0.05	p≤0.05
Coefficient of Variation (%)	18.9	7.1	10.0	7.3	6.0	16.4

IBADAN

Source of Variation	DH	DF	DFF	TNL	PH	HTS
	Probability of F-test for respective soruce of variation					
Cycle (C)	P≤0.001	P≤0.001	P≤0.001	P>0.05	P≤0.001	P>0.05
Genotype (G)	P≤0.01	P≤0.001	P≤0.001	P≤0.001	P≤0.001	P≤0.001
GxC interaction	P>0.05	P>0.05	P>0.05	P>0.05	P>0.05	P>0.05
Coefficient of Variation (%)	12.6	17.4	10.1	7.5	8.7	14.1

Source of Variation	BW	H	F	FL	FC	FW
	Probability of F-test for respective source of variation					
Cycle (C)	P≤0.01	P>0.05	P>0.05	P>0.05	P>0.05	P≤0.001
Genotype (G)	P≤0.001	P≤0.001	P≤0.001	P≤0.001	P≤0.001	P≤0.001
GxC interaction	P>0.05	P>0.05	P≤0.01	P>0.05	P>0.05	P>0.05
Coefficient of Variation (%)	29.9	10.8	15.3	10.6	15.1	27.5

M'BALMAYO

Source of Variation	DH	DF	DFF	TNL	PH	HTS
	Probability of F-test for respective source of variation					
Cycle (C)	P≤0.001	P≤0.001	P≤0.05	P≤0.001	P≤0.001	P>0.05
Genotype (G)	P≤0.001	P≤0.001	P≤0.001	P≤0.001	P≤0.001	P≤0.001
GxC interaction	P≤0.01	P≤0.001	P≤0.01	P≤0.001	P>0.05	P>0.05
Coefficient of Variation (%)	4.8	7.4	6.4	5.5	4.9	13.4

Source of Variation	BW	H	F	FL	FC	FW
	Probability of F-test for respective source of variation					
Cycle (C)	P≤0.001	P>0.05	P>0.05	P≤0.001	P≤0.001	P≤0.001
Genotype (G)	P≤0.001	P≤0.001	P≤0.001	P≤0.001	P≤0.001	P≤0.001
GxC interaction	P≤0.05	P>0.05	P>0.05	P≤0.01	P≤0.01	P≤0.01
Coefficient of Variation (%)	15.6	8.7	14.3	6.8	5.3	14.7

DH = days to harvest; DF = days to flowering; DFF = days for fruit filling; TNL = total number of leaves; PH = plant height, cm; HTS = height of tallest sucker at harvest, cm; BW = bunch weight, kg; H = number of hands; F = number of fruits; FL = fruit length, cm; FC = fruit circumference, cm; FW = fruit weight, g.

higher number of fruits and a higher fruit weight (Table 2). Differences were also observed in fruit length; i.e., fruits were bigger in Onne and Ibadan than in Mbalmayo (Table 2).

The genotype-by-environment interaction did not affect fruit circumference (Table 3). There were significant differences between entries in different environments for all characters measured. The analysis of variance for location (L) and genotype (G) indicated that GL interaction was important, especially for bunch weight, number of hands, number of fingers and fruit weight ($P \leq 0.001$) (Table 4). Significant interaction effects ($P \leq 0.05$) were also observed for days for fruit filling, plant height and fruit length. These results showed the need for multilocational testing of cultivars before release. In contrast to all other parameters the number of days for fruit filling was not significantly affected by location.

Most of the characters were not affected by genotype-by-cycle interaction (GC) at Onne (Table 5). Bunch weight, number of hands, fruit length and circumference, as well as plant height, height of tallest sucker and total number of leaves did not show a significant GC in this location. These results suggest that trials at Onne do not necessarily need to be spread over several years to enable efficient selection of elite breeding material. Similarly at Ibadan, all of the characters, except the number of fruits, were not affected by GC. However, at Mbalmayo there was a significant GC for most traits, inferring that it may be necessary to also carry out early selection trials in this location. Hence, we might conclude that there is more need for multilocation trials than single site evaluation over several years in the *Musa* breeding station of IITA at Onne. This view agrees with Sandison (15), and Allard and Bradshaw (1) who indicated that it would be more important to cover the main environmental conditions than to achieve great precision in individual trials. This breeding philosophy may hold true for early selection and for later evaluation of elite material.

Correlated responses across environments. The need to select and evaluate *Musa* breeding material in all the target environments where new cultivars might be grown by farmers has been clearly shown above. However, budget constraints will ultimately compromise this ideal situation. Similarly, the identification or development of an environment which allows the optimum expression of all desirable characters, is equally difficult. The genetic parameters of yield potential were calculated as shown in Table 6. Based on this, CR_y and R_y were found to be 0.80 and 0.89, respectively, in the humid forest locations. These results suggest that selections at Onne will only effectively select genotypes capable of performing well in Mbalmayo when the intensity of selection at Onne is 10% higher than at Mbalmayo. This would seem considerably easier than establishing a separate site specifically for the selection of genotypes targeted at farmers in the Mbalmayo region. Similarly, selections from Onne or Mbalmayo are not expected to express their potential at Ibadan due to poor correlated reponses (0.40 and 0.13 for Onne and Mbalmayo, respectively). Hence, selection in breeding stations at different agroecozones may lead to the development of different cultivars or populations. Indeed, *Musa* breeders should restrict their selection operations to their specific environments. In this regard, clustering of similar environments may assist in making recommendations for cultivar release across similar environments. When improving multiple traits, *Musa* breeders should locate their selection trials in the environment where they obtain the greatest heritability for all traits, or by independent culling in the optimum environment for each trait. For example selection for yield potential will be more efficiently pursued at Onne than in Mbalmayo (Table 6). However, when there is distinct priority ranking of traits for improvement, *Musa* breeders should pursue a tandem selection scheme. In this regard, selection for black sigatoka resistance, a highly heritable trait and easy to score (12), could be carried out in a location with high and uniform disease pressure (e.g., Onne) and later only black sigatoka resistant selections should be tested at specific location (e.g., Mbalmayo) for cultivar release in the targeted agroecozone.

Table 6
Genetic parameters of yield potential (t ha^{-1} year^{-1}) measured in *Musa* germplasm (landraces and hybrids) in three IITA stations in the humid forest (Onne and Mbalmayo) and in the forest-savanna transition zone (Ibadan) of sub-Saharan Africa

Agroecozone/Location	σ^2_G	σ^2_{GE}	σ^2_P	H^2 (%)
Humid Forest				
Onne	13.43	1.80	14.34	93.71
M'Balmayo	13.84	3.31	15.50	89.29
Transition Zone				
Ibadan	3.86	0.64	4.18	92.30

Genetic correlations (ρG)	M'Balmayo	Ibadan
Onne	0.80	0.40
M'Balmayo		0.13

$\sigma 2_G$, $\sigma 2_{GE}$ and σ^2_P are the genetic, genotype-by-environment, and phenotypic variance, respectively, while H^2 is the broad sense heritability.

Conclusions

The results suggest that one of the two sites used in for multilocational testing of *Musa* genotypes in the humid lowlands of West Africa (e.g. Mbalmayo) could be dropped. This finding appears very important in terms of site rationalisation for germplasm testing, especially in these days of short budgets allocated for agricultural research elsewhere. Also, since selections at Onne (humid lowland) did not perform well in a dry environment like Ibadan (forest-savanna transition zone), *Musa* breeders should identify genotypes adapted to drier conditions using testing sites in both the transition zone and the moist savanna. Currently, multilocational trials consisting of *Musa* hybrids (from Africa and Latin America) and African and Asian landraces are being carried out at IITA stations in Abuja (Southern Guinea Savanna of Nigeria), Ibadan and Onne (14). In this way, genotypes with wide stability across environments as well as specific adaptation to dry environments may be identified for further testing and release by national programs elsewhere.

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