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GENOTYPE-BY-ENVIRONMENT INTERACTION AND PHENOTYPIC STABILITY OF *MUSA* GERMPLASM IN WEST & CENTRAL AFRICA

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ABSTRACT

A multilocational evaluation trial comprising 18 *Musa* genotypes was carried out from 1991 to 1994 in three representative locations in the Humid Forest (Onne, Nigeria and M'Balmayo, Cameroon) and the Forest-Savanna Transition (Ibadan, Nigeria) zones of West and Central Africa. The main objective was to evaluate the performance of improved *Musa* germplasm under different agro-ecological conditions, thereby assessing the genotype-by-environment interaction (GxE) for specific traits and yield stability. Hybrids, their parental genotypes together with plantain and banana landraces, were included in the trial for comparison purposes. Differences between the genotypes and environments were significant for all traits. Number of days to fruit filling was the only trait not affected by location effects. Due to a large number of fruits and high fruit weight, the improved germplasm showed heavier bunches than their parents, even though they had fewer hands. The GxE affected all traits, except fruit circumference. Genotype-by-location effects were significant for bunch weight, number of hands, number of fruits and fruit weight. Most of the traits were not affected by genotype-by-cycle interaction at Onne and at Ibadan. These observations suggest that multilocational trials may be more efficient than single site trials over several years. Stability analysis of bunch weight and yield potential, based on the phenotypic coefficient of variation, allowed the identification of high and stable yielding genotypes, e.g. the black sigatoka resistant hybrids TMPx 1658-4 and TMPx 2796-5.

Key Words: **Banana, breeding, multi-locational trials, sigatoka resistance, yield stability**

RÉSUMÉ

Une essai multilocal comprenant 18 genotypes de *Musa* a été conduit de 1991 à 1994 dans 3 sites représentatifs dans la forêt humide (Onne, Nigeria and M'Balmayo, Cameroun) et dans la zone de transition Forêt-Savanne (Ibadan, Nigeria) en Afrique de l'Ouest et Centrale. L'objectif principal était d'évaluer la performance de germoplasme amélioré de Musa sous différentes conditions agroécologiques afin de déterminer l'interaction génotype x environement (G x E) pour des traits spécifiques ainsi que la stabilité du rendement. Les hybrides, leurs génotypes parentaux ensemble avec les plantains ainsi que les bananiers locaux ont été inclus dans l'essai pour les comparer. Les différences entre le génotype et l'environnement étaient significatifs pour tous les traits. Le nombre de jour pour le remplissage de fruits était le seul trait qui n'était pas affecté par les effets de sites. A cause du nombre et du poids élevés des fruits, les génotypes améliorés ont donné des régimes plus lourds que leurs parents en dépit du petit nombre des mains. L'interaction G x E a affecté tous les traits, excepté la circonférence des fruits. Les effets de l'interaction génotype x site étaient significatifs pour le poids des régimes, nombre des mains, nombre et poids des fruits. La plupart des traits n'étaient pas affectés par l'interaction génotype x cycle végétatif à Onne et à Ibadan. Ces observations suggèrent que les essais multilocaux sont plus efficients que les essais

en site unique sur plusieus saisons. L'analyse de la stabilité du poids de régime ainsi que du potential productif, basé sur le coéfficient de variation du caractère phénotypique permet l'identification des génotypes stables et plus producteurs, c'est le cas des hybrides TMPX1658-4 et TMPx2796-5 résistants à la cercosporiose noire.

***Mots Clés*: Banane, variétés locales, essais multilocaux, résistance à la cercosporiose, stabilité de rendement**

INTRODUCTION

Bananas and plantains (*Musa* spp.) are among the most important staple crops in the humid forest and mid-altitudes zones of sub-Saharan Africa. Black sigatoka, a leaf spot disease caused by the airborne fungal pathogen *Mycosphaerella fijiensis* Morelet, is considered to be the most critical constraint to plantain and banana production in this region (Vuylsteke *et al.*, 1993a). The pathogen causes yield losses of 30 to 50% (Mobambo *et al.*, 1993). All plantain cultivars and some of the most popular banana cultivars of East Africa, are susceptible to black sigatoka (Swennen and Vuylsteke, 1991). Fungicides are available to control the disease, but they are expensive and pose a health hazard for the smallholders who grow most of the crop. Therefore, the development of durable host plant resistance is considered the most appropriate option for control of black sigatoka.

The short-term strategy chosen by the International Institute of Tropical Agriculture (IITA) was to identify, multiply and distribute cooking bananas that possess resistance to black sigatoka as a substitute for the susceptible plantain landraces. So far, adoption of these resistant cooking bananas has been limited because West Africans are not familiar with them and prefer plantains. Hence, in 1987 IITA initiated a cross-breeding programme for the long-term improvement of plantains (IITA, 1992).

Tetraploid hybrids were produced at IITA using susceptible triploid plantain ('Obino l'Ewai' and 'Bobby Tannap') or cooking banana ('Bluggoe') landraces as female parents, and 'Calcutta 4' (a wild diploid banana) or 'Pisang lilin' (a cultivated diploid banana) as male partners (Vuylsteke *et al.*, 1993b). The plantain parents were selected because of their high seed-fertility (Swennen and Vuylsteke, 1993), and because they are local plantain cultivars in Nigeria and Cameroon, respectively (Swennen, 1990b). Selection of the tropical *Musa* plantain hybrids (hereafter designated TMPx) was based on equal or higher bunch weight than their fungicide-treated plantain parent, combined with decreased susceptibility or partial resistance to black sigatoka (Vuylsteke *et al.*, 1993c). Recently, the stability of black sigatoka resistance in the TMPx germplasm was reported (Ortiz *et al.*, 1993). The TMPx also showed rapid cycling due to the dominant allele *Ad* for apical dominance that allowed regulated development of suckers (Ortiz and Vuylsteke, 1994a). Resistance to black sigatoka leaf spot disease in TMPx germplasm is controlled by the action of a complex genetic system comprising one recessive gene (*bs1*) and at least two additional independent additive modifier genes (Ortiz and Vuylsteke, 1994b).

The potential utilisation of this improved *Musa* germplasm by African farmers required its testing across different agro-ecologies where black sigatoka has been reported. Hence, multilocational evaluation trials were carried out at IITA stations in the Humid Forest and Forest-Savanna Transition zones of Cameroon and Nigeria to assess the yield stability of the TMPx germplasm compared with their parents and other landraces.

MATERIALS AND METHODS

The multilocational evaluation trial was carried out from 1991 to 1994 in three different locations: the IITA stations at Ibadan (transition zone) and Onne (High Rainfall Station) in Nigeria, and M'Balmayo (Humid Forest Station) in Cameroon (Table 1). The trial consisted of eight plantain or banana hybrids, two known black sigatoka susceptible plantain and banana cultivars ('Agbagba' and 'Valery', respectively), three black sigatoka resistant cooking banana cultivars ('Fougamou', 'Pelipita' and 'Cardaba'), as well as the cultivated triploid parents ('Bluggoe', 'Bobby Tannap' and 'Obino l'Ewai') and the diploid banana parents ('Calcutta 4' and 'Pisang lilin').

A randomised complete block design with two replications was used in each location. Each plot of five plants was surrounded by a border row of the black sigatoka susceptible cultivar 'Valery', to provide inoculum for black sigatoka throughout the field. Field sizes were 54 m x 48 m (Onne and M'Balmayo) or 108 m x 24 m (Ibadan), and plants were spaced at 3 m between rows and 2 m within rows, viz, a plant density of 1,667 per hectare. At Onne and M'Balmayo, alley cropping with natural hedgerows was employed, while at Ibadan the trial was a monocrop. All other crop management practices, with the exception of fungicide treatments, were as recommended by Swennen (1990a).

Data were collected for twelve plant traits. Growth cycle indicated the number of days from planting to harvesting for the plant crop and from harvest to harvest for the ratoon crop. This period was partitioned into days to flowering, and days to fruit filling, from flowering to harvesting. Also, the total number of leaves was recorded, i.e., from the first leaf (the leaf nearest to the bottom with a lamina broader than 10 cm) until flowering. Plant height was measured at flowering and height of tallest sucker (cm) at harvesting. Bunch weight per plant was measured in kilograms to the nearest 0.1 kg. Number of hands and number of fruits per bunch were recorded. Fruit length was measured along the external curve, and fruit circumference in the centre of the fruit. Finally, fruit weight of the middle finger of each hand was taken to the nearest gramme. By using bunch weight (BW) and growth cycle (GC), yield potential (YLD, MT ha^{-1} $year^{-1}$) was obtained as YLD = (BW x 365 x 1667) / (GC x 1000).

Combined analyses of variance (ANOVA) were performed with MSTAT-C (Anonymous, 1990) to determine the environment (i.e, each location-production cycle combination), location, cycle within each location, genotype, genotype-by-environment, genotype-by-location and genotype-by production cycle (plant crop and ratoon) within location effects. Least significant differences (LSD) and the coefficients of variation were calculated for each variable. Combined ANOVAs across environments were carried out for all the traits, following a mixed model (Nevado and Ortiz, 1985). Environments, i.e., the location-cycle combination, locations and cycles within locations were considered as random factors while genotypes were considered as fixed factors in the linear additive model.

The phenotypic coefficients of variation across environments (PCV) of yield potential and bunch weight were calculated for each clone as PCV(%) = (s_i / X_i) x 100, with s_i being a measurement of dispersion and X_i. the genotype mean (Francis and Kannenberg, 1978). PCV is a measurement of static stability, i.e., homeostasis. It measures the dispersion of the data set: the smaller the

TABLE 1. Agro-ecological characterisation of testing sites in MET-1

Location	Onne	M'Balmayo	Ibadan
Latitude	4° 43'N	3° 25'N	7° 30'N
Longitude	7° 01'E	11° 28'E	3° 54'E
Altitude (masl)	5	640	210
Agro-ecozone	Degraded rain forest - swamp	Humid forest	Derived savanna
Soil	Ultisol derived from coastal sediments	Ultisol derived from schist band	Ferric luvisols
Total rainfall (mm / year)	2400	1500	1300
Rainfall pattern	unimodal (+ 1 month dry spell: mainly in Jan)	bimodal (+ 2 month dry spell: Dec-Jan; Jul-Aug)	bimodal (+ 4 month dry spell: Dec-Mar; Jul-Aug)
Resource and crop management practices	Multispecies alley cropping with natural regrowth of hedgerows between trial genotypes		Land clearing in hydromorphic area

TABLE 2. Growth cycle (days) of plantain (P), banana (B), and their black sigatoka resistant plantain hybrids (TMPx) at IITA stations in the humid forest (Onne and M'Balmayo) and forest/savanna transition (Ibadan) zones in Nigeria and Cameroon. Plant (PC) and ratoon (RC) crops, 1991-1994

Hybrid/Cultivar	Onne, Nigeria		Ibadan, Nigeria		M'Balmayo, Cameroon	
	PC	RC	PC	RC	PC	RC
TMPx 548-4	448	184	432	274	430	362
TMPx548-9	456	215	428	243	432	-
597-4	404	245	435	261	445	365
TMPx 582-4	431	204	425	228	396	213
TMPx 2796-5	483	278	379	232	438	337
TMPx 1112-1	537	248	393	209	456	327
TMPx 1658-4	495	356	464	313	434	379
612-74 OFFTYPE	538	303	413	274	448	-
Obino l' Ewai (P)	518	409	446	290	492	408
Bobby Tannap (P)	451	381	431	295	483	413
Valery (B)	442	256	422	271	414	346
Bluggoe (B)	544	249	441	227	471	371
Cardaba (B)	516	267	407	223	454	327
Pelipita (B)	583	335	576	-	509	368
Fougamou (B)	549	257	478	268	-	-
Calcutta 4 (wild B)	308	131	354	217	-	-
Agbagba (P)	532	310	442	322	-	-
Pisang lilin (B)	-	204	-	-	-	-
LSD 0.05	54	122	82	NS	39	45
C.V (%)	5.2	21.1	8.9	18.1	4.0	5.7

TABLE 3. Plant height (cm) of plantain (P), banana (B), and their black sigatoka resistant plantain hybrids (TMPx) at IITA stations in the humid forest (Onne and M'Balmayo) and forest/savanna transition (Ibadan) zones in Nigeria and Cameroon. Plant (PC) and ratoon (RC) crops, 1991-1994

Hybrid/Cultivar	Onne, Nigeria		Ibadan, Nigeria		M'Balmayo, Cameroon	
	PC	RC	PC	RC	PC	RC
TMPx 548-4	311	408	238	248	316	353
TMPx 548-9	318	398	235	259	342	355
597-4	246	328	224	226	294	347
TMPx 582-4	260	314	202	218	292	319
TMPx 2796-5	313	363	232	258	340	368
TMPx 1112-1	312	348	199	233	259	301
TMPx 1658-4	369	409	246	271	360	366
612-74 OFFTYPE	302	346	253	267	288	328
Obino l' Ewai (P)	376	398	266	282	347	375
Bobby Tannap (P)	316	336	248	238	286	323
Valery (B)	222	244	204	214	215	234
Bluggoe (B)	356	390	274	302	330	390
Cardaba (B)	316	356	264	288	311	366
Pelipita (B)	390	431	302	-	344	426
Fougamou (B)	368	440	308	336	362	427
Calcutta 4 (wild B)	187	246	144	199	206	-
Agbagba (P)	328	353	257	258	-	370
Pisang lilin (B)	201	240	-	-	-	-
LSD 0.05	33	41	36	31	28	40
C.V (%)	5.1	5.5	7.1	5.6	4.3	5.3

phenotypic coefficient of variation, the closer the results around the mean, and thus the more stable the genotype across the environments tested.

RESULTS AND DISCUSSION

Environments. Significant differences ($P<0.001$) between the six environments were found for all traits: i.e., growth cycle (Table 2), plant height (Table 3), bunch weight (Table 4), number of fruits (Table 5), days to flowering, days to fruit filling, total number of leaves, height of tallest sucker, number of hands, fruit length, fruit circumference, fruit weight and yield potential (data not shown).

All traits, except the number of days to fruit filling were significantly ($P<0.05$) affected by location. At Onne, the production cycle was longer than in M'Balmayo and Ibadan (Table 2). In general, plants as well as their tallest suckers were shorter at Ibadan than at the other two locations (Table 3). The total number of leaves was highest at Onne, while plants had more leaves at Ibadan than at M'Balmayo (data not shown). Other indications of location effect were the differences in bunch weight (Table 4) and number of hands (data not shown), which were higher at Onne and M'Balmayo than at Ibadan. High number of fruits (Table 5) and fruit weight (data not shown) were probably the cause of the differences in bunch weight. Fruits were bigger at Onne and Ibadan than at M'Balmayo (data not shown).

Genotypes. For all traits, significant ($P< 0.001$) differences were observed among genotypes in the different environments. The low yields at Ibadan may reflect a lack of adaptation of the hybrids to the dry season at Ibadan, as they were selected at the High Rainfall Station in Onne.

In general, the hybrids were shorter than their plantain parents (Table 3) and had higher bunch weights in the humid forest locations (Table 4). Heavy bunches were due to high number of fruits and fruit weight (Table 5), although they had fewer hands than their plantain parents (data not shown). Short plants also tended to have fewer leaves (data not shown). The tropical *Musa* plantain hybrids (TMPx) exhibited a shorter growth cycle (Table 2), with fewer days needed to

TABLE 4. Bunch weight (kg plant^{-1}) of plantain (P), banana (B), and their black sigatoka resistant plantain hybrids (TMPx) at IITA stations in the humid forest (Onne and M'Balmayo) and forest/savanna transition (Ibadan) zones in Nigeria and Cameroon. Plant (PC) and ratoon (RC) crops, 1991-1994

Hybrid/Cultivar	Onne, Nigeria		M'Balmayo, Cameroon		Ibadan, Nigeria	
	PC	RC	PC	RC	PC	RC
TMPx 548-4	14.5	15.8	13.4	15.8	7.7	7.1
TMPx 548-9	15.9	16.0	14.6	-	6.2	7.1
597-4	5.1	5.0	7.0	9.6	4.5	3.1
TMPx 582-4	9.3	10.4	11.1	10.6	6.5	6.7
TMPx 2796-5	14.6	16.9	12.6	12.1	8.9	6.6
TMPx 1112-1	14.6	15.0	9.8	12.2	6.2	5.8
TMPx 1658-4	19.5	14.5	16.3	19.4	9.4	6.5
612-74 OFFTYPE	9.4	10.0	6.2	-	6.2	7.0
Obino l' Ewai (P)	12.0	9.6	9.7	12.8	7.6	6.4
Bobby Tannap (P)	9.2	9.1	8.5	11.9	8.8	6.6
Valery (B)	8.5	7.3	9.6	12.0	7.0	7.3
Bluggoe (B)	13.8	12.5	7.4	12.2	11.7	9.6
Cardaba (B)	14.1	13.2	9.2	19.7	9.0	7.6
Pelipita (B)	12.1	12.0	9.3	16.2	2.2	-
Fougamou (B)	11.1	13.6	-	20.7	5.6	4.2
Calcutta 4 (wild B)	0.3	1.2	-	-	0.4	0.5
Agbagba (P)	3.5	5.6	-	4.9	5.7	4.1
Pisang lilin (B)	4.0	5.1	-	-	-	-
LSD 0.05	3.1	5.8	2.8	5.1	4.5	3.3
C.V (%)	13.8	24.9	12.7	17.7	28.6	27.4

TABLE 5. Number of fruits of plantain (P), banana (B), and their black sigatoka resistant plantain hybrids (TMPx) at IITA stations in the humid forest (Onne and M'Balmayo) and forest/savanna transition (Ibadan) zones in Nigeria and Cameroon. Plant (PC) and ratoon (RC) crops, 1991-1994

Hybrid/Cultivar	Onne, Nigeria		Ibadan, Nigeria		M'Balmayo, Cameroon	
	PC	RC	PC	RC	PC	RC
TMPx 548-4	85	105	58	54	94	75
TMPx 548-9	88	120	55	54	100	-
597-4	66	80	62	60	92	90
TMPx 582-4	75	106	59	59	90	101
TMPx 2796-5	84	115	56	57	88	69
TMPx 1112-1	101	97	50	58	85	75
TMPx 1658-4	112	109	68	61	116	97
612-74 OFFTYPE	57	68	62	52	60	-
Obino l' Ewai (P)	77	70	60	47	73	86
Bobby Tannap (P)	83	80	72	61	84	86
Valery (B)	102	101	86	86	137	106
Bluggoe (B)	59	63	61	58	49	56
Cardaba (B)	69	78	74	60	78	79
Pelipita (B)	92	89	44	-	80	92
Fougamou (B)	123	136	107	87	-	146
Calcutta 4 (wild B)	89	135	60	117	-	-
Agbagba (P)	14	16	16	14	-	13
Pisang lilin (B)	71	86	-	-	-	-
LSD 0.05	16	22	21	14	21	33
C.V. (%)	9.4	11.2	15.6	10.8	11.2	17.3

flowering but a longer fruit filling period (data not shown), in comparison to their plantain parents.

GxE interaction. The genotype-by-environment interaction (GxE) affected all traits significantly (P<0.001), except fruit circumference. The ANOVA for genotype and location indicated that genotype by location interaction (GxL) was important (P<0.001), especially for bunch weight, number of hands, number of fruits and fruit weight. Significant GxE effects (P<0.05) were also found for days to fruit filling, plant height, and fruit length. These results indicated the importance of and need for multilocational testing of improved germplasm prior to release to farmers.

Combined ANOVA showed that most of the traits were not affected (P>0.05) by genotype-by-production cycle (crop plant and ratoon) interaction (GxC) at Onne. Traits such as bunch weight, number of hands, fruit length and circumference, as well as the growth parameters (plant height, height of tallest sucker and total number of leaves) did not show a significant GxC in this location (P>0.05). These data suggest that at IITA's *Musa* Breeding Station (Onne) trials might not need to be spread over several years before selection of promising hybrids takes place. The same can be stated for Ibadan, where all the parameters, except the number of fruits, were unaffected by GxC interaction (P>0.05). These observations suggest that multilocational trials should be prioritised over trials spanning several years at the same location.

Stability analysis. The identification of high and stable yielding cultivars and hybrids was possible by plotting yield potential and bunch weight versus the coefficient of variation (Fig. 1). 'Cardaba' and 'Bluggoe' were cultivars with high stable yields and stable heavy bunches. However, 'Bluggoe' might be affected by cigar end rot in regions where this disease occurs (Ortiz *et al.*, 1994). The results were surprising for 'Cardaba' because it is an Asian cultivar only recently introduced into Africa. However, it could explain why IITA, in cooperation with the National Agricultural Research System (NARS), was successful in distributing this cultivar to farmers from 1988 in southeastern Nigeria (IITA, 1992). Similarly, the plantain derived hybrids of the parthenocarpic banana 'Pisang Lilin', TMPx 1658-4 and TMPx 2796-5, were high stable yielders with high and stable bunch weights. TMPx 548-4 showed high unstable yields although it had stable heavy bunches. A short growth cycle for the ratoon crop (Table 2) could explain its unstable yield potential. A very long growth cycle places the cooking banana cultivars 'Fougamou' and 'Pelipita' in the group of 'low unstable yielders' with unstable heavy bunches. The plantain cultivars in the lower left quarter of the yield potential graphs ('Agbagba', 'Obino l'Ewai' and 'Bobby Tannap') (Fig. 1) showed stable low to medium yields. It is not surprising that these plantain landraces have stable yields being widely grown in West and Central Africa (Swennen, 1990b). The low yields may be due to their susceptibility to black sigatoka.

Widely adapted banana and plantain cultivars became low yielders when affected by the black sigatoka. Hence, *Musa* breeding programmes should develop black sigatoka resistant cultivars with stable high yields by using locally adapted plantain or banana landraces as female parents. Similarly, plantain hybrids derived from a parthenocarpic edible cultivated diploid banana (e.g. 'Pisang Lilin') also showed high and stable yields. This may suggest that human selection for fruit parthenocarpy during the domestication of the crop (Simmonds, 1962) did not only result in edible fruits but also in stable productivity. This

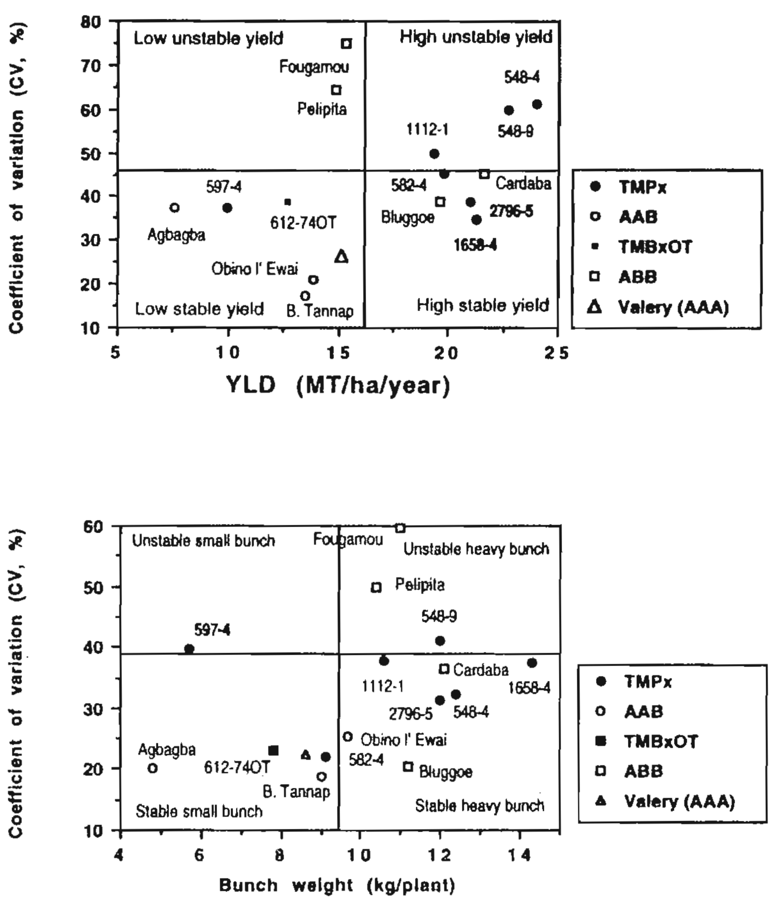

Figure 1. The relationship between bunch weight (kg plant^{-1}) and yield potential (MT ha^{-1} year^{-1}) and phenotypic stability (CV%) among banana and plantain parents and their sigatoka resistant hybrids.

suggests that *Musa* breeders should increase the frequency of fruit parthenocarpy alleles in their breeding populations.

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