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GENOTYPE X ENVIRONMENT INTERACTION AND OPTIMUM RESOURCE ALLOCATION FOR YIELD AND YIELD COMPONENTS OF CASSAVA

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ABSTRACT

Dry yield and yield components from 6 multilocational trials of cassava genotypes conducted for 3 years in Nigeria were used to study the nature and magnitude of genotype x environment (G x E) interaction and to determine the optimum resource allocation for cassava yield trials. The effects of environment, genotype and G x E interaction were highly significant for all yield traits. Variations due to G x E interaction were greater than those due to genotypic differences for all yield traits. Genotype x location x year interactions contributed most to the G x E interaction for all the yield traits. Therefore, to facilitate selection, zonation of cassava growing agroecologies into homogenous ecosystems using multivariate statistical approach should be done to minimise the influence of the G x E interaction. Testing at 3-5 locations for 2-3 years with 3-4 replications per location is the optimum combination that will not jeopardise precision in cassava yield trials.

Key Words: *Manihot esculenta*, Nigeria, yield stability

RÉSUMÉ

Le rendement sec et les composantes du rendement de 6 essais multilocaux de génotype de manioc menés pendant 3 ans au Nigeria ont été utilisés pour étudier la nature et la magnitude de l'interaction génotype x environnement (G x E) ainsi que pour déterminer l'allocation optimum des ressource dans des essais de rendement du manioc. Les effets de l'environnement, du génotype et de l'interaction G x E étaient hautement significatifs pour tous les caractères du rendement. L'interaction génotype x localité x année a contribué le plus à l'interaction G x E pour tous les caractères du rendement. Par conséquent, pour minimiser l'influence de l'interaction G x E et ainsi faciliter la sélection, l'approche statistique multivariée devrait être envisagée dans la zonation des agroecologies où le manioc est cultivé en écosystème homogène. L'évaluation dans 3-5 localités pendant 2-3 ans avec 3-4 répétition par localité est la combinaison optimale qui permet une bonne précision dans les essais de rendement du manioc.

Mots Clés: *Manihot esculenta*, Nigeria, stabilité du rendement

INTRODUCTION

Cassava (*Manihot esculenta* Crantz) is an important food crop in developing countries where it is the fourth source of calories, after rice, sugar cane and maize, for more than 400 million people (El-Sharkawy, 1993). Cassava is grown in agroecologies which differ in rainfall, temperature regimes and soil types. Therefore, a major objective of cassava breeding is the development of high yielding genotypes with broad stability and adaptation over a wide range of environmental conditions.

Genotype x environment (G x E) interaction is the change in a cultivar's relative performance over environments, resulting from differential response of the cultivar, to various edaphic, climatic and biotic factors (Dixon *et al.*, 1994). The G x E interaction has been observed for cassava yields (Dixon *et al.*, 1994; Ngeve, 1994; Makame, 1995; Tan and Mak, 1995). Tan and Mak (1995) demonstrated the existence of G x E interaction for root yield and root number, but did not assess the magnitude of the G x E interaction effect. Ngeve (1994) showed that the yields of some cassava genotypes were unstable across six environments in Cameroon, but did not also estimate the magnitude of the G x E interaction effect. Otoo *et al.* (1994) determined the magnitude of G x E interaction for cassava yields in West Africa, but not for yield components. There is a paucity of information on the magnitude of G x E effect on yield and yield components in cassava.

The objectives of this study were to assess the relative magnitude of G x E and determine the optimum resource allocation for conducting cassava yield trials, with respect to the number of replications, locations and years of testing.

MATERIALS AND METHODS

Eight improved (U/41044, TMS 4(2)1425, TMS 30001, TMS 30555, TMS 30572, TMS 50395, TMS 63397 and TMS 91934) and one local (TME 1) cassava genotypes were evaluated at 6 Nigerian locations from 1989 to 1991 (Table 1). The genotypes were grown under rainfed condition in a randomised complete block design with 4 replications. Planting was done at the beginning of the rainy season, usually between April and May, at each location for the 3 years. Each plot was 10 m long and 4 m wide, with 4 rows (ridges) of plants spaced at 1 m x 1 m, giving a population of 10,000 plants ha^{-1}. No fertiliser or herbicide was applied during the course of the experiment. Hand weeding was done whenever necessary.

Harvesting was done 12 months after planting and data were collected from the 2 middle rows. The number and fresh weight of storage roots were recorded. Dry matter percentage of storage roots was determined from a bulk of four randomly selected plants from the inner 2 rows of the plots. Clean storage roots, including the peel were shredded. Two hundred grammes duplicate samples were weighed and dried for 72 hours in a forced air drying oven at 70 °C. The dried samples were then re-weighed to obtain the dry weights, and the dry matter (weight) percentage was obtained as the proportion of the fresh weight. Dry yield was estimated as the fresh root yield multiplied by the percentage dry matter of the roots.

Combined analyses of variance were carried out for fresh weight of storage roots, root weight, percentage dry matter and dry yield using the SAS software (SAS Institute, 1993). Genotypes and location were considered fixed effects while years were considered random. The F-test and significance of the various main effects and interactions were determined using appropriate error terms and degrees of freedom (McIntosh, 1983). Mean separation was done by Fisher's protected least significant difference (LSD). The variance components associated with the genotype (σ^2g), and its interactions with year (y) and/or location (l): (G x L (σ^2gy/y), G x Y (σ^2gl/l), G x L x Y (σ^2gly/ly)), and the error term (σ^2e/rly) where computed for yield and yield components by equating the mean squares to their expected mean squares. The expected variance of a genotype mean (Vx) was calculated as follows (Rasmuson and Lambert, 1961):

$$Vx = \sigma^2gy/y + \sigma^2gl/l + \sigma^2gly/ly + \sigma^2e/rly$$

Where g, y, l and r are the number of genotypes, years, locations, and replicates, respectively.

RESULTS AND DISCUSSION

The combined analyses of variance for number of fresh storage roots, fresh weight of storage roots, dry matter percentage and dry yield revealed highly significant genotypic variation for all the traits (Table 2). The effect due to environment was also highly significant for all the traits. The relative magnitude of the environment was much higher than for the genotype effect. All

TABLE 1. Agroecological characteristics of the locations where testing was performed

Location	Agroecological zones	Soil type	Position	Altitude (m)	Rain (mm) [a]	Wet season	Min/max temperature[a]
Ibadan	Forest-savanna transition	Ferric Luvisols	3° 54' E; 7°26'N	210	1252.8	Mar-Aug Aug-Nov	12-23/28-34°C
Ilorin	southern Guinea savanna	Ferric Luvisols	2° 75' E; 5° 11' N	304	1283.5	Apr-Nov	19-12/28-36°C
Mokwa	southern Guinea savanna	Ferric Luvisols	5° 4' E; 9° 18' N	210	1235.2	Apr-Nov	13-24/28-36°C
Onne	Humid forest Fluvisols4° 46' N	Thionic	7° 10' E;	30	2501.6	Feb-Dec	12-23/28-32°C
Owerri	Humid forest Gleysols	Eutric 3° 31'N	4° 21' E;	67	2385	Mar-Dec	20-22/27-32°C
Ubiaja	Humid forest Nitosols	Dystric 6° 40' N	6° 25' E;	210	1943.5	Mar-Dec	12-22/27-32°C

[a] Long term averages (10 years)
(Source: Jagtap, 1993)

TABLE 2. Combined analyses of variance for yield and its components of nine cassava genotypes grown in 18 environments (6 locations x 3 years) in Nigeria

Source	df	Number of storage roots	Fresh weight of storage roots	Dry matter percentage	Dry yield
Environtment (E)	17	11330.58** (38)	526.48** (27)	511.40** (44)	69.93** (32)
Year (Y)	2	25589.65** (10)	1951.75* (12)	644.44** (6)	295.02** (16)
Location (L)	5	11238.27** (11)	398.33** (6)	1069.72** (27)	84.92** (11)
Y x L	10	8524.92** (17)	305.50** (9)	205.65** (11)	17.41** (5)
Rep (Y x L)	54	569.24** (6)	60.47** (10)	23.38** (6)	4.65** (9)
Genotype (G)	8	9189.68** (15)	588.70** (14)	353.22** (14)	54.93** (12)
G x E	136	711.66** (19)	54.30** (22)	26.02** (18)	5.48** (20)
G x Y	16	329.88** (1)	35.76* (2)	11.62 (1)	4.65* (2)
G x L	40	877.42** (7)	72.61** (8)	44.85** (9)	6.69** (7)
G x Y x L	80	705.14** (11)	48.85** (12)	19.49** (8)	5.04** (11)
Pooled error	432	245.21	21.21	7.74	2.29

*P < 0.05; **P < 0.01

Percentage contribution as a proportion of the total sum of squares in parenthesis environment components (year (Y), location (L) and Y x L interaction) were highly significant for the 4 traits. All the 4 yield traits thus varied from location to location, indicating that final selection has to be done at each location.

Genotype x environment effects were highly significant for all the traits, indicating differential genotypic responses for yield and yield component across environments. The proportion of total sum of squares (SS) due to environments ranged from 32 to 44%, while that due to genotypes was from 12 to 15% and that due to G x E ranged from 18 to 22%. The magnitude of G x E interaction obtained in this study and elsewhere (Otoo *et al.*, 1994) exceeded that of the genotypes for the 4 traits. Thus, relative ranking of genotypes will differ across environments and can complicate the evaluation and selection of genotypes. However, the magnitude of G x E was smaller for dry matter percentage (18%) and root number (19%), than for dry yield (20%) and fresh root weight (22%). After partitioning of the G x E into its various components, both the first and second order interactions were highly significant for all traits except G x Y effect for dry matter percentage. There is, therefore, the need to use appropriate multivariate analysis such as the Additive Main Effects and Multiplicative Interactions (AMMI) model to zone cassava growing agroecologies into homogenous sub-units. Grouping into such sub-units would minimise the interaction effects.

The presence of G x E interaction generally altered genotypic rankings for dry yield in different environments (Table 3). The best dry yields were produced by 91934 (at Ibadan), 30572 (at Ilorin), 91934 (at Mokwa), 30572 (at Onne), 63397 (at Owerri), and TME 1 (at Ubiaja). Overall, 63397 and TME 1 produced the highest dry yield, while 30001 and U/14044 produced the lowest. Of all 3 years the best yields were obtained in 1990 and least in 1991. In 1989, 1990 and 1991, the best locations for dry yield were Ubiaja, Ubiaja and Owerri, respectively. The year 1990 was most productive for Ibadan, Mokwa, Onne and Ubiaja while 1991 was the most productive year for Ilorin and Owerri. In general, the genotypes produced the highest dry yield in 1990 and the lowest in 1989. Of the 6 locations, Ubiaja was the most productive for dry yield.

The genotypes that produced the highest root numbers were 63397 at Ibadan, 30572 at Ilorin, 91934 at Mokwa, 30572 at Onne, 63397 at Owerri, and 30572 at Ubiaja (Table 4). Overall, 30572 and 63397 produced the highest number of roots while 30555 and 4(2)1425 produced the least. Of the 6 locations, Ibadan and Mokwa produced the highest and the least root numbers, respectively. The genotypes that produced the highest root weight were 91934 (at Ibadan), 50395 (at Ilorin), 4(2)1425 (at Mokwa), 50395 (at Onne), 50395 (at Owerri), and TME 1 (at Ubiaja). Overall, 50395 and 91934 produced the highest while 30001 and U/14044 produced the lowest root weight. Of the 6 locations, Ubiaja was the most productive while Mokwa was the least. For each location, 4(2)1425 (Ibadan), 63397 (Ilorin), 63397 (Mokwa), 30572 (Onne), 63397 (Owerri), and 63397 (Ubiaja) were the best genotypes for dry matter percentage, with 50395 being the worst genotype for this trait in all the locations. Genotype 63397 produced the highest dry matter percentage while 50397 and 91934 produced the lowest across environments. Of the 6 locations, Onne and Ubiaja were the most productive for dry matter percentage.

Increasing the number of replications, locations or years decreases Vx for all 4 yield traits (Fig. 1). However, increasing the number of replications, locations and/or years will lead to increased costs for testing cassava genotypes. The best option, therefore, is to use the least number of replications, locations and years that will not jeopardise precision. Although the lowest Vx is obtained when 6 replications and 6 years were used, irrespective of location, this combination can not be recommended owing to the high cost involved, slow progress from selection and resulting decrease in gain from selection. Also, when numbers of replications and years are kept constant, the Vx decreases as the number of locations is increased. However, a critical point is reached as the curve starts to plateau; beyond which an increase in the number of test locations provides only a negligible gain in precision. Depending on the numbers of replications and years combination, this critical point is generally attained when the number of locations is between 3 and 5 for all the yield traits, representing the optimum number of locations required in cassava yield trials. With

TABLE 3. Mean dry yield in t ha^{-1} of nine cassava genotypes in six locations and across the six locations over three years in Nigeria

Location	Year	Genotypes									Mean	LSD (5%)
		30001	30555	30572	4(2)1425	50395	63397	91934	TME 1	U/14044		
Ibadan	1989	1.5	2.0	3.6	1.8	3.5	2.6	4.1	3.1	2.5	2.7	
	1990	4.6	5.5	6.3	6.3	7.2	6.3	7.5	4.4	3.1	5.7	G = 1.57
	1991	2.9	3.3	4.3	6.9	4.7	5.4	6.2	4.1	2.8	4.5	G x Y = 1.66
	Mean	3.0	3.6	4.7	5.0	5.1	4.8	5.9	3.9	2.8	4.3	
Ilorin	1989	3.0	3.9	4.7	3.6	6.5	6.0	3.9	4.1	2.7	4.3	
	1990	3.4	6.2	7.9	4.4	5.2	6.0	5.5	7.5	6.3	5.8	G = 1.40
	1991	5.3	5.3	7.6	7.2	6.9	7.0	5.7	6.5	6.6	6.4	G x Y = 1.73
	Mean	3.9	5.1	6.7	5.0	6.2	6.3	5.0	6.0	5.2	5.5	
Mokwa	1989	2.6	2.4	2.3	3.3	3.2	4.5	4.1	2.6	2.4	3.0	
	1990	4.7	4.8	7.5	7.9	5.0	6.1	7.6	6.8	5.5	6.2	G = 1.88
	1991	2.7	4.2	3.9	6.8	4.3	8.0	7.2	6.1	4.0	5.3	G x Y = 2.63
	Mean	3.3	3.8	4.6	6.0	4.2	6.2	6.3	5.2	4.0	4.8	
Onne	1989	4.5	5.2	6.1	3.4	5.3	5.1	6.7	6.0	1.9	4.9	
	1990	4.6	7.2	7.1	7.7	5.3	7.9	4.1	7.3	6.0	6.4	G = 1.75
	1991	3.4	4.4	6.5	4.0	8.1	5.6	5.9	4.7	6.1	5.4	G x Y = 2.64
	Mean	4.2	5.6	6.6	5.0	6.2	6.2	5.5	6.0	4.6	5.6	
Owerri	1989	2.6	5.0	4.6	5.8	6.4	7.2	3.9	3.0	3.2	4.6	
	1990	3.1	5.9	5.3	5.0	8.0	6.3	6.8	7.6	5.6	5.9	G = 1.62
	1991	5.5	5.2	8.4	7.9	5.2	7.9	6.7	6.6	5.0	6.5	G x Y = 2.34
	Mean	3.8	5.4	6.1	6.2	6.5	7.1	5.8	5.7	4.5	5.7	
Ubiaja	1989	2.9	5.7	6.4	5.1	5.2	7.3	4.8	7.2	5.7	5.6	
	1990	5.3	8.1	8.5	9.0	8.5	10.0	9.4	13.6	7.8	8.9	G = 1.87
	1991	2.7	5.9	7.1	5.4	7.6	5.9	6.3	8.6	7.5	6.3	G x Y = 2.47
	Mean	3.6	6.6	7.3	6.5	7.1	7.7	6.8	9.8	7.0	6.9	
Across locations	1989	2.9	4.0	4.6	3.8	5.0	5.5	4.6	4.3	3.0	4.2	G = 0.74
	1990	4.3	6.3	7.1	6.7	6.5	7.1	6.8	7.8	5.7	6.5	G x Y = 1.16
	1991	3.7	4.7	6.3	6.4	6.1	6.6	6.3	6.1	5.4	5.7	G x L = 1.66
	Mean	3.6	5.0	6.0	5.6	5.9	6.4	5.9	6.1	4.7	5.5	G x Y x L = 2.29

TABLE 4. Mean root number ha^{-1}, root weight ha^{-1} and percentage dry matter in thousands of nine cassava genotypes in six locations and across the six locations in Nigeria

Location	Genotype									Mean	LSD (5%)
	30001	30555	30572	4(2)1425	50395	63397	91934	TME 1	U/14044		
Root number											
Ibadan	43.8	32.4	51.5	31.2	46.1	54.2	52.8	32.3	30.1	41.5	12.72
Ilorin	21.1	24.4	38.9	21.2	35.7	31.4	32.9	32.5	28.6	29.6	6.38
Mokwa	20.0	18.5	31.6	25.6	22.5	31.3	32.9	30.2	23.8	26.3	10.37
Onne	31.1	31.1	43.0	23.5	36.7	40.2	38.9	30.4	27.4	33.6	10.25
Owerri	30.0	28.9	36.5	27.0	37.9	40.3	33.0	27.5	30.9	32.4	8.92
Ubiaja	23.2	30.4	41.5	22.5	34.1	41.0	34.2	39.6	33.2	33.2	7.13
Across locations	28.2	27.6	40.5	25.1	35.4	39.6	37.4	32.0	29.0	32.8	4.22
Root weight											
Ibadan	28.0	28.6	36.6	36.2	47.2	37.1	48.9	32.8	23.9	35.5	10.09
Ilorin	25.1	37.3	42.4	35.5	48.7	37.3	36.9	38.2	35.5	37.4	7.80
Mokwa	21.5	26.1	32.0	41.4	32.5	34.8	39.2	32.0	25.3	31.6	12.72
Onne	28.4	31.3	38.1	27.5	41.2	37.0	41.0	38.5	30.2	34.8	10.07
Owerri	25.7	33.6	35.5	36.2	50.3	40.4	38.6	34.4	31.7	36.3	9.04
Ubiaja	23.5	40.8	46.3	36.6	51.1	41.6	43.4	56.4	49.4	43.2	10.57
Across locations	25.4	33.0	38.5	35.6	45.2	38.0	41.3	38.7	32.7	36.5	4.39
Percentage dry matter											
Ibadan	21.6	24.4	25.2	26.6	20.9	25.8	24.4	23.4	23.4	24.0	2.90
Ilorin	31.0	27.6	31.2	28.3	25.6	34.1	27.2	31.4	28.6	29.4	3.60
Mokwa	31.6	31.1	29.4	29.7	25.7	35.9	32.8	33.8	32.5	31.4	3.51
Onne	29.8	35.9	35.0	35.6	30.5	33.4	27.0	31.3	29.9	32.0	3.23
Owerri	29.2	31.7	33.5	34.3	26.3	35.6	27.9	32.3	28.5	31.2	3.12
Ubiaja	31.8	32.1	32.1	35.6	27.5	37.6	30.9	34.5	28.6	32.3	3.22
Across locations	29.2	30.4	31.7	31.7	26.1	33.7	28.7	31.1	28.6	30.1	1.68

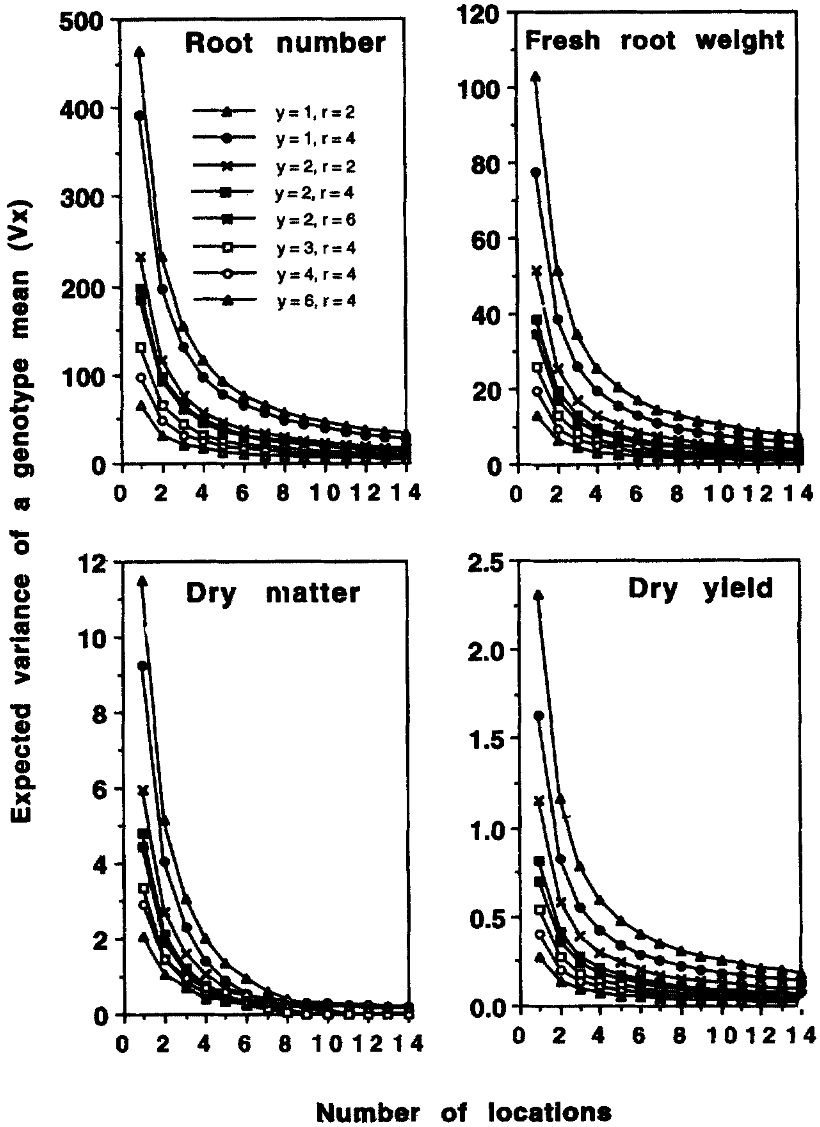

Figure 1. Expected variance of a genotype mean (Vx) for various assumed replicates per test (r), years (y) and locations, for root number 20 m^{-2}, fresh storage root weight (t ha^{-1}), dry matter percentage and dry yield (t ha^{-1}) of cassava.

TABLE 5. Variance component estimates from combined analysis for root number, fresh storage root weight, dry matter percentage and dry yield of cassava

Yield component	Variance component				
	$\sigma^2 g$	$\sigma^2 gl$	$\sigma^2 gy$	$\sigma^2 gly$	$\sigma^2 e$
Number of roots	132.73	0	0	323.76	278.95
Fresh root weight	35.48	0	0	51.69	102.49
Dry matter percentage	4.68	0.39	0	7.77	9.09
Dry yield	0.69	0.02	0	0.93	2.71

respect to numbers of replications and years in Figure 1, fewer than 3 locations will result in inaccurate selection for any of the yield traits, whereas more than 5 locations will only increase cost without any significant gain in precision. It is also clear from the figure that, increase in the number of locations is the most effective in reducing Vx for all the 4 yield traits. Apart from root number where an increase in the number of years is more important in reducing Vx, an increase in the number of years and replications have similar importance in reducing Vx for all other traits. When between 3 and 5 locations are used, the difference in Vx between the combination of 1 year and 2 replications and 6 years with four replications is large for all 4 yield traits, hence one-year testing involving 2 replications is inadequate for field experiments to select for any of the traits. For the same number of locations, 2 years with 2 replications appear to be adequate for all 4 yield traits. However, because of the high error variance component for each yield trait (Table 5), lower cost per replication, and the possible but unpredictable factors which may ruin one or more of the replications used (Liang *et al.*, 1966), very few replications generally is not advisable. Therefore, 3 to 4 replications in each of 3 to 5 locations and 2 or 3 years should suffice for cassava yield evaluation.

CONCLUSIONS

The G x E interaction is sufficiently large for yield and yield components of cassava and could complicate selection. The G x L x Y interactions contributed most to the G x E interactions. Zonation of cassava growing agroecologies into homogenous ecosystems using multivariate statistics such as the Additive Main Effect and Multiplicative Interaction (AMMI) analysis is desirable to minimise the influence of G x E interaction and facilitate efficient breeding for yield and yield components in cassava and in understanding patterns of the interactions. Testing at 3-5 locations for 2-3 years using 3-4 replications per location is the optimum combination that will not jeopardise precision in cassava yield trials.

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