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AMMI analysis of cassava response to contrasting environments: case study of genotype by environment effect on pests and diseases, root yield, and carotenoids content in Cameroon

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Abstract Genotype by environment interaction remains a substantial issue in all breeding programs. Crop genotypes are generally developed in a central breeding location, but always require the evaluation of breeding products in different environments. This is particularly relevant in countries that have a wide range of climates. Eighteen cassava genotypes were evaluated in Cameroon in eight environments—varying in seasonal rainfall and temperature patterns and soil characteristics—over two cropping seasons. Soil nutrient content was analyzed and trials were established in a randomized complete block design in three replications. Response of genotypes to major cassava pests and diseases, yield and carotenoids content was evaluated. It was observed that four genotypes did not show cassava mosaic disease (CMD) symptoms irrespective of the environments. The local check had highest CMD incidence and severity across all environments. Average number of whitefly per plant across all environments was highest on TMS 96/0023. Average cassava green mite (CGM) infestation was low on all the genotypes. Fresh root yield of five genotypes ranged between 25 and 30 tons per ha for both years. Significant and positive correlation was found across locations between fresh root yield and soil K, P and Mg. AMMI analysis revealed highly significant differences among genotypes and environments and significant genotype × environment interaction for most of the estimated traits, indicating variability in genotypes performance with environment.

Keywords Cassava mosaic disease · G × E interaction · Mega-environment · Root yield · Soil nutrient · Whitefly

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Introduction

Genotype by environment interaction remains a substantial issue in all breeding programs. Crop genotypes are generally developed in a central breeding location, but always require the evaluation of breeding products in different environments. This is particularly relevant

in countries that have a wide range of climates. Cassava, a widely-grown crop throughout the tropics and sub-tropics, is continually being improved to respond to changing pest and disease pressure, utilization, changing climate, and improvement in yield. Multilocation trials are conducted to select the best genotypes for a set of environments for parameters such as crop yield and/or crop response to pests and diseases (Egesi et al. 2009; Akinwale et al. 2011). As such, G × E is essential for demonstrating the potential of a genotype in a given environment and for optimizing the production and utilization of that genotype (Nassir and Ariyo 2011). The net effect of G × E can be additive or multiplicative, depending on the significance of the G × E interaction. Significant interaction implies spatial variation, indicating that chosen sites belong to different environments and large magnitude of G × E is expected in contrasting environments for diverse genotypes (Ekanayake et al. 2000).

Several multilocation experiments focus mostly on agricultural biophysical properties dominated by climate but sometimes, social or cultural contexts are also included (Coe 2012). Many of these studies, however, do not specifically quantify environmental factors like soil nutrients that may account for underlying differences in genotype performance. They rely mainly on the physical and climatic description environments in which one or more genotype are stable or has performed best or worst (mega-environments) (Ngeve 1994; Otoo et al. 1994; Dixon and Nukenine 1998; Benesi et al. 2005; Ssemakula and Dixon 2007; Akinwale et al. 2011; Bradbury et al. 2011; Nassir and Ariyo 2011; Maroya et al. 2012; Callist Kundy 2015; Pariyo et al. 2015). Few authors have attempted to report on cassava performance in relation to soil physical properties and their nutrient contents in G × E experiments (Tan and Mak 1995; Mtunguja et al. 2016).

Cassava, *Manihot esculenta* (Crantz), is generally considered a widely-adapted crop; but there are numerous examples that show considerable variations in cassava genotype characteristics under varying environmental conditions (Mkumbira et al. 2003; Fu et al. 2014). In Africa and elsewhere in the world where cassava has largely been a subsistence crop, there has been considerable effort to enhance the cassava crop profile. To this end, several cassava genotypes have been developed by IITA cassava breeding unit in Nigeria with a focus in improving root yields, starch content, and resistance/tolerance to major pests and diseases, nutritional content (e.g., higher provitamin A content), and other characters that will satisfy the requirements of cassava based industry (Dixon and Ssemakula 2008). The deployment of these newly developed varieties into new production areas, requires basic understanding of their performance (root yield and stability, nutritional quality of yellow-root genotypes and response to pests and diseases) in relation to contrasting environments and identify some key elements, mainly soil nutrient content, that may account for the observed differences in their performance. Cameroon with five agroecologies ranging from humid forest with bimodal rainfall pattern in the south to the Sahelian zones in the north, is indicated for the evaluation of these varieties and results could be rapidly disseminated in neighboring countries and locations with similar soil characteristics.

Materials and methods

Cassava genotypes

The present study consisted of advanced multilocation trials with three yellow-root and 15 white-root genotypes received from the cassava breeding unit of IITA-Ibadan and planted at IITA-Cameroon, and LMR, a farmer variety widely grown in Cameroon. Some varieties introduced in the 1980s (8034) and beginning of 1990s (92/0326, 92/0067 and 92/0057) were included for comparison. All the experimental material was collected on virus-free plants (i.e., CMD symptom-less plants) from the IITA cassava multiplication plots. Inoculation in the field was done naturally on this material by the whitefly *Bemisia tabaci,* the vector of the cassava mosaic disease. Subsequent CMD-infection proved to be current-season whitefly-borne infection as only the upper leaves displayed the symptoms (Okao-Okuja et al. 2004).

Environment, soil characterization and general procedure

The trials were conducted during two consecutive cropping seasons (2014/2015 and 2015/2016) at eight locations representing the four-contrasting cassava

growing agroecologies in Cameroon. During Year 2, Ngaoundere was replaced by Meiganga (highland savannah) for logistical reasons. We used at each location a HOBO data logger (Onset Computing, USA) for continuous temperature and relative humidity. A rain gauge (Tru-chek®) was used to monitor daily rainfall (Table 1).

Cassava was grown for 12 months under natural conditions and without added fertilizer. Each trial consisted of a randomized complete block design with three replicate blocks, with 18 plots within each block. Each plot consisted of 42 plants in a 6 m × 7 m array, with 1 m-spacing within and between rows of plants. Weeds were controlled manually as necessary.

Data collection

A composite soil sample was taken from each plot at the onset of the experiment to determine soil physical and chemical properties (Soil pH, N, P, K, Ca, Mg, Organic C and Total N) relevant to cassava growth and development were determined in the soil laboratory of IITA-Cameroon. The incidence and severity of cassava mosaic disease (CMD), cassava bacterial blight (CBB) and cassava anthracnose (CAD) were scored at 3, 6, and 9 months after planting (MAP) following a 5-level scale where 1 = no symptoms and 5 = severe symptoms. Average incidence and severity score of CMD, CBB, and CAD were calculated based on data recorded at 3, 6, and 9 months after planting (MAP). Cassava green mite (CGM) active stages and whiteflies (both adults and nymphs) individuals were also counted at each evaluation using standard procedures. The presence of the predatory mite (*Typhlodromalus aripo* Bondar) and the parasitism of whitefly nymphs were also determined with standard sampling methods for both species (IITA 1990).

Cassava harvest yield was evaluated at approximately 12 MAP at all locations. We estimated fresh root yield (FYLD) per ha based on average fresh root weight of ten plants per plot, excluding border rows. Root dry matter content (DMC) was determined for each genotype from a random sample of three roots/plot. Roots were washed, sliced with peels and a sample of 500 g was dried for 48 h at 60 °C in an electric oven. Root dry matter content was calculated by dividing the dry weight by the fresh weight. Dry root yield (DYLD) was the product of FYLD and DMC: DYLD = FYLD × DMC.

For the determinations of total carotene concentration (TCC), five roots were collected from roots of the 10 harvested plants and processed following BioAnalyt protocol (Kulakow et al. 2015) and TCC was measured using iCheck™ Carotene device within 24 h after harvest.

Data analysis

Data of all parameters were statistically analyzed using a linear mixed model ANOVA that considered cassava genotype as fixed factor, environment and year as random factors. Replication was nested within environment. The model included genotype by environment (G × E) and genotype by year (G × Y) interactions. Tukey test was used as post hoc for the separation of means. Spearman correlation was used to evaluate relationship between soil nutrient content and

Table 1 Climatic characteristics of the study sites

Environment	Agro-ecology	Latitude (dd.ddd)	Longitude (dd.ddd)	Elevation (m asl)	Temperature range (°C)	Rainfall (mm)
Bambui	Highland/savannah[a]	6.04	10.22	1237	11.8–33.0	2125
Foumbot	Highland/savannah[a]	5.48	10.56	1018	12.2–33.4	1798
Ekona	Lowland/transition[a]	4.21	9.32	450	18.2–33.2	2815
Bertoua	Mid-altitude/forest[b]	4.56	13.85	667	17.8–32.6	1569
Mbalmayo	Mid-altitude/forest[b]	3.46	11.48	671	19.9–29.6	1667
Meyomessala	Mid-altitude/forest[b]	3.09	12.35	660	19.8–30.1	1644
Meiganga	Highland/savannah[b]	6.47	14.16	1007	12.4–33.6	1575
Ngaoundere	Highland/savannah[b]	7.52	13.83	1095	11.7–32.1	1523

[a]Monomodal rain fall pattern, [b]bimodal rainfall pattern

Table 2 Soil pH and nutrient composition in the trial locations in the 2 years

Year	Location	pH Water	K cmol (+/kg)	Ca cmol (+/kg)	Mg cmol (+/kg)	P µg/g	Org C %	Total N %	C/N
Y1	Bambui	4.92^{d}	0.21^{d}	1.45^{e}	0.59^{e}	2.26^{c}	6.33^{a}	0.42^{a}	15.13^{c}
	Bertoua	4.61^{e}	0.14^{d}	1.90^{e}	0.87^{de}	3.45^{c}	2.15^{d}	0.13^{d}	16.51^{b}
	Ekona	5.3^{c}	1.23^{a}	8.50^{c}	4.11^{a}	61.37^{a}	3.18^{b}	0.30^{b}	10.42^{f}
	Foumbot	6.34^{b}	1.02^{b}	12.32^{a}	3.44^{b}	14.55^{b}	6.42^{a}	0.42^{a}	15.18^{c}
	Mbalmayo	7.08^{a}	0.34^{c}	10.46^{b}	2.72^{c}	14.96^{b}	1.94^{e}	0.17^{c}	11.16^{e}
	Meyomessala	6.19^{b}	0.26^{cd}	3.86^{d}	1.11^{d}	12.59^{b}	1.19^{f}	0.09^{e}	12.93^{d}
	Ngaoundere	4.94^{d}	0.23^{cd}	2.70^{de}	1.18^{d}	4.23^{c}	2.53^{c}	0.14^{d}	17.63^{a}
Y2	Bambui	5.03^{e}	0.33^{cd}	2.07^{d}	0.95^{de}	3.52^{b}	6.98^{a}	0.44^{a}	15.87^{b}
	Bertoua	4.64^{f}	0.18^{d}	2.55^{d}	1.21^{d}	4.59^{b}	2.47^{e}	0.16^{d}	15.90^{b}
	Ekona	5.29^{d}	1.55^{a}	8.50^{b}	3.74^{a}	34.39^{a}	3.18^{d}	0.34^{c}	9.42^{e}
	Foumbot	6.08^{b}	1.16^{b}	11.65^{a}	3.44^{a}	13.06^{b}	5.43^{c}	0.40^{b}	13.52^{c}
	Mbalmayo	6.44^{a}	0.21^{d}	6.28^{c}	1.57^{c}	7.55^{b}	1.83^{f}	0.14^{d}	12.75^{d}
	Meiganga	5.66^{c}	0.45^{c}	9.40^{b}	2.45^{b}	33.71^{a}	5.71^{b}	0.32^{c}	17.77^{a}
	Meyomessala	5.45^{cd}	0.17^{d}	2.44^{d}	0.82^{e}	8.97^{b}	1.43^{g}	0.10^{e}	13.94^{c}

Within columns, means followed by the same letter are not significantly different according to LSD (0.05)K

CMD, and cassava agronomic yield. Analysis was done using SAS 9.2 package (SAS 2009).

There are several tools used to analyze G × E interaction data. We selected the Additive Main effects and Multiplicative Interaction (AMMI), widely used to analyze main effects and genotype by environment interactions in multilocation variety trials (Jalata 2011). This function generates biplots by plotting the first principal component (PC1) scores of the genotypes and the environments against their respective PC2 scores, resulting from the singular value decomposition of environment-centered or standardized G × E data (Crossa 1990; Yan et al. 2000; Yan and Kang 2003; Yan and Tinker 2006; Maroya et al. 2012; Pacheco et al. 2015). The generated plots graphically display environments in which genotypes performed best or worst.

Results

Soil nutrient analysis

Soil nutrient composition differed between environments and within environment for the 2 years (see Table 1 for description of environments). Greater variation was found in P and K content with Ekona having the highest levels. Soils were less acidic in Mbalmayo (Mid altitude forest with bimodal rainfall) and Foumbot. Soils in Foumbot and Bambui had higher Organic C while higher values of Mg were found in Ekona and Foumbot soils (Table 2).

Cassava mosaic disease incidence, severity and whitefly abundance

Four genotypes (TMS 01/0098, 95/0211, 98/0581 and 01/1086-55) did not show any visible CMD symptoms (Table 3). The local check LMR (G15) had the highest incidence (> 72% for both season), followed by 8034 (16%) and 92/0326 (15%) and 01/1814-9 (13%). The remaining genotypes had less than 9% infection across all the environments over the 2 years. Average CMD incidence across all environments was 13.0 ± 4.7 for year 1 and 12.6 ± 4.9 for year 2 while mean severity was 2.5 for both years (Table 3). Highest CMD incidence was recorded in Bertoua (26%), followed by Mbalmayo (22%), Ekona (18%), Bambui (17%), Meyomessala (16%) and Foumbot (16%), Meiganga (15%) and Ngaoundere (15%).

Average densities of whiteflies were higher on genotypes TMS 96/0023 and TMS 01/0098-36 (24/plant each) and lowest on TMS 95/0211 (8/plant). Whitefly density/plant across season and environment was higher in Bambui (47/plant) followed Meiganga (24/plant), Foumbot (18/plant), Bertoua (13/plant),

Table 3 Average CMD incidence, severity and whitefly population of 18 cassava genotypes across the eight environments and for each location across genotypes

Genotypes		CMD incidence (%)		CMD severity		Whiteflies count	
		Year 1	Year 2	Year 1	Year 2	Year 1	Year 2
01/0040-27[a]	G1	7.9	8.1	2.4	2.6	7.4	13.1
01/0098	G2	0.0	0.0	1.0	1.0	17.7	20.2
01/0098-32	G3	3.3	2.8	2.7	2.8	18.0	25.3
01/0098-36	G4	5.3	4.4	2.3	2.3	24.6	23.2
01/1086-55	G5	0.0	0.0	1.0	1.0	14.9	16.9
01/1814-9[a]	G6	14.1	12.4	2.4	2.4	8.1	10.7
92/0057	G7	6.7	6.7	2.5	2.5	8.0	10.0
92/0067	G8	4.7	5.0	2.5	2.7	19.7	25.9
92/0326	G9	15.7	14.3	2.4	2.3	21.6	22.3
95/0109	G10	3.9	3.9	2.1	2.1	11.7	14.2
95/0211	G11	0.0	0.0	1.0	1.0	6.7	9.0
96/0023	G12	9.2	7.5	2.6	2.6	23.0	25.0
96/1414	G13	8.1	7.4	2.7	2.7	14.1	16.1
98/0581	G14	0.0	0.0	1.0	1.0	16.2	16.4
LMR[b]	G15	72.4	74.7	2.9	2.9	12.4	13.3
MM97/JW2-2[a]	G16	6.7	6.7	2.0	2.0	10.7	11.9
TME 419	G17	7.3	6.3	2.5	2.5	13.0	16.4
8034	G18	16.2	16.0	2.8	2.8	11.6	13.8
Mean		13.0	12.6	2.48	2.51	14.4	16.9
SE		4.7	4.9	0.16	0.16	1.3	1.3
CV		135.8	145.5	10.2	10.5	38.0	32.6

[a]Yellow root cassava, [b]Local variety used as check

Ekona (9/plant), and Mbalmayo, Meyomessala and Ngaoundere with less than 5/plant. Whitefly density on plants has no effect on CMD incidence and severity (Spearman correlation: $r = -0.01$ and $r = -0.02$ respectively).

All genotypes expressed mild CBB and CAD symptoms and CGM infestations were generally low. Less than 20% of the whitefly nymphs were parasitized. *T. aripo* presence were recorded on 12 genotypes, but its abundance was generally low probably due to low CGM infestations (see supplementary table for others pest and disease score).

The combined analysis of variance for CMD incidence and severity revealed that G contributed 84% and 19% respectively to the total sum of squares while E contributed 3% and 6% respectively. G × E contributed to 9% and 22% to the total sum of squares of CMD incidence and severity respectively (Table 4).

In the GGE biplot analysis of CMD incidence, PC1 and PC2 together explained 85% of the total variation and graphically summarized genotypes performance in relation to the eight environments. The genotypes located on the vertex of the polygon were TMS 92/0326 (G9), LMR (G15), and 8034 (G18) and were the most

Table 4 Combined analysis of variance of G, E, year G × E and year contributions to the sum of squares of CMD incidence and severity on 18 cassava genotypes

	DF	MS	SS	%SS
CMD incidence				
Genotype	17	44.1***	179,651	83.7
Environment	7	888***	6216	2.9
Year	1	20.7***	20.7	0.0
GE	119	169.2***	19,716	9.2
GY	17	1.6	27.7	0.0
Rep (ENV)	17	48.2***	771	0.4
Residual	568	14.7	8348	3.9
CMD severity				
Genotype	17	1.1***	14.8	19.4
Environment	7	0.6	4.3	5.6
Year	1	0	0	0.0
GE	119	0.4***	16.5	21.6
GY	17	0	0	0.0
Rep(ENV)	17	0.2	2.5	3.3
Residual	568	0.1	38.3	50.1

*Significant at the 0.05 probability level; **Significant at the 0.01 probability level; ***Significant at the 0.001 probability level

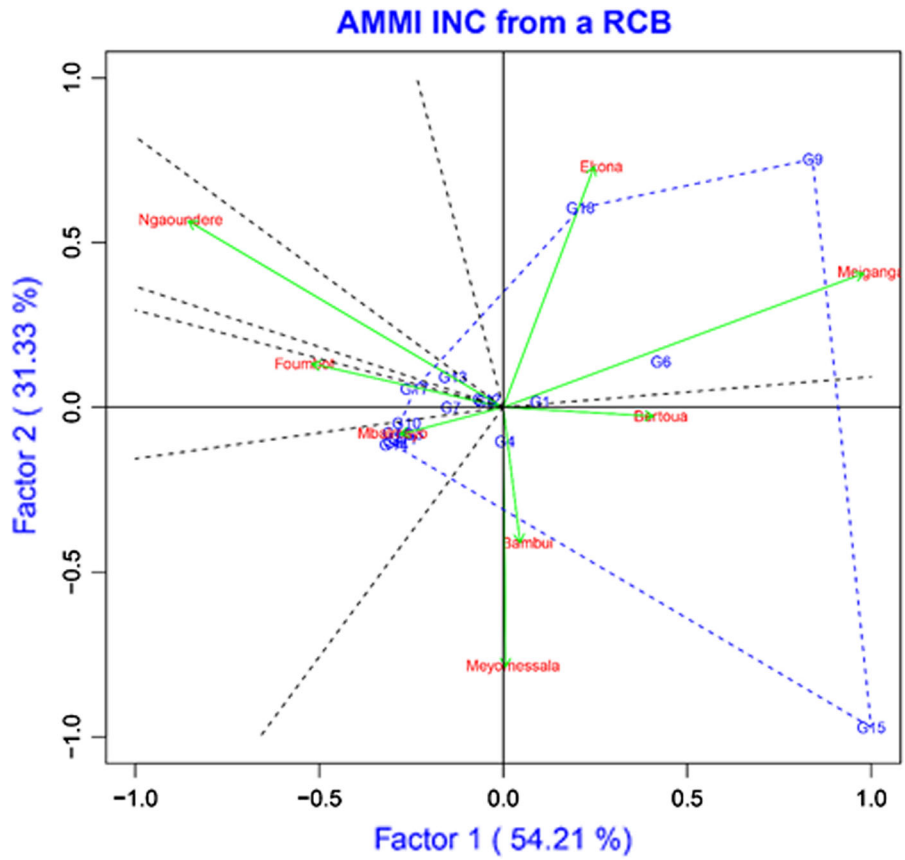

Fig. 1 Mega-environment defined by different winning genotypes tested for the average CMD incidence

responsive with higher incidence. Two mega-environments could be defined: (1) Ekona and Meiganga where genotypes TMS 92/0326 (G9) and 8034 (G18) had higher CMD incidence; and (2) Bertoua, Bambui, and Meyomessala where genotype LMR (G15) had higher incidence. Mbalmayo with the shortest vector from biplot origin was less discriminating of the genotypes while Ngaoundere, Meiganga, Ekona, and Meyomessala were more discriminating (Fig. 1).

Fresh and dry root yield and correlation with soil properties

The highest mean for FYLD across locations was recorded from genotype TMS 01/0040-27 (28.4 t/ha) follow by TMS MM97/Jw2-2 (28.2 t/ha) in year 1 while in year 2 highest yield was obtained from genotype 01/0098 (28.8 t/ha) followed by TME 419 (26.7 t/ha). The highest mean for DYLD were recorded by TMS 01/0098-36 (12.5 t/ha) in year 1 and TMS 01/0098 (10.6 t/ha) in year 2. The highest mean for FYLD and DYLD was recorded in Ekona, followed by Foumbot and Bertoua for both years while Meiganga and Ngaoundere were the less favorable environments (Table 5).

The combined analysis of variance of FYLD and DYLD revealed that G contributed 5% and 7% respectively to the total sum of squares while E contributed 46.6% and 40.8% respectively. G × E contributed 12.8% and 12.7% to the total sum of squares (Table 6).

The two principal components (PC1 and PC2) of the biplot together explained 66.1% of the total variation of genotype performance in the eight environments. Most responsive genotypes were 01/1814-9 (G6), 92/0326 (G9), 95/0211 (G11), 98/0581 (G14), and TME 419 (G17) with the highest yield compared to other genotypes. The oldest genotype 8034 was less responsive in all environments except in Ekona for both years. Three mega-environments could be defined: (1) Foumbot, Meyomessala, Bambui, and Ngaoundere which were the winning niche of 98/0581

Table 5 Average yield of 18 cassava genotypes across the eight environments for FYLD, DMC, and DYLD

Genotypes	GEN	Fresh root yield		Dry matter		Dry root yield	
		Y1	Y2	Y1	Y2	Y1	Y2
Genotype							
01/0040-27[a]	G1	28.4	25.9	31.8	27.7	8.7	7.3
01/0098	G2	27.5	28.8	36.0	33.6	9.9	10.6
01/0098-32	G3	22.4	19.8	34.5	28.0	7.8	5.6
01/0098-36	G4	30.0	25.5	42.3	31.2	12.5	8
01/1086-55	G5	22.5	21.3	41.4	32.9	9.2	7.3
01/1814-9[a]	G6	25.3	20.3	33.0	31.9	8.2	6.6
92/0057	G7	26.1	26.0	35.7	32.5	9.1	7.9
92/0067	G8	18.0	17.9	31.5	29.8	5.6	5.1
92/0326	G9	23.0	23.5	31.6	29.7	7.3	7
95/0109	G10	28.3	22.3	35.8	31.3	9.9	7.1
95/0211	G11	17.1	22.6	33.9	26.0	5.6	5.8
96/0023	G12	22.1	25.6	32.4	27.9	6.9	7.2
96/1414	G13	22.5	21.5	35.4	30.8	7.9	6.7
98/0581	G14	23.2	20.0	37.1	31.4	8.5	6.6
LMR[b]	G15	18.4	14.9	34.0	27.3	6.3	4.4
MM97/JW2-2[a]	G16	28.2	26.2	37.7	31.4	10.2	8.3
TME 419	G17	26.7	26.7	41.8	33.3	11	9.5
8034	G18	15.7	19.4	33.9	26.7	5.5	5.1
Mean		23.6	22.6	35.5	30.2	8.3	7
SE		1	0.8	0.8	0.6	0.5	0.4
CV		18.1	15.9	9.6	7.9	23.5	22.1
Environment							
Bambui	E1	12.1	16.0	36.5	35.3	4.4	5.7
Bertoua	E2	25.9	26.7	35.6	25.9	9.2	6.9
Ekona	E3	38.8	47.0	34.3	34.7	13.5	16.6
Foumbot	E4	32.9	22.7	32.2	29.6	10.8	6.8
Mbalmayo	E5	22.4	14.6	40.5	26.3	8.9	3.8
Meyomessala	E6	24.9	18.4	34.8	25.5	8.7	4.7
Ngaoundere	E7	10.1		35.5		3.6	
Meiganga	E8		13.1		34.1		4.5
Mean		23.9	22.6	35.6	30.2	8.5	7.0
SE		3.9	4.4	1.0	1.7	1.3	1.7
CV		43.3	51.8	7.1	14.6	41.1	62.8

[a]Yellow root cassava,
[b]Local variety used as check

(G14); (2) Ekona for 92/0326 (G9) and TME 419 (G17); and (3) Bertoua and Mbalmayo for 95/0211 (G11). Ekona and Bertoua were more discriminating of the genotypes FYLD while Bambui and Meyomessala were less discriminating (Fig. 2).

Significant and positive correlation was found across locations between FYLD and soil K (r = 0.67; n = 140; $p < 0.0001$), soil P (r = 0.52; n = 140; $p < 0.0001$), and soil Mg (r = 0.60; n = 140; $p < 0.0001$), and significant negative correlation between FYLD and soil C/N (r = − 0.59; n = 140; $p < 0.0001$). A non-significant negative correlation was found between FYLD and CMD severity (r = − 0.14; n = 143; $p = 0.09$); however, when genotypes were pooled across locations, this correlation was significant (r = − 0.55; n = 18; $p = 0.02$).

Genotypes TMS 01/1086-55(G5), TMS 92/0057 (G7), TMS 95/0109 (G10), TMS 98/0581 (G14), and

Table 6 Combined analysis of variance of G, E, and G × E contributions to the sum of squares of roots yields of 18 cassava genotypes in eight environments

	DF	MS	SS	%SS
FYLD				
Genotype	17	437**	7435	5.0
Environment	7	9908***	69,356	46.6
Year	1	630*	630	0.4
GE	119	161***	19,080	12.8
GY	17	1320	1320	0.9
Rep(ENV)	16	167*	2673	1.8
Residual	549	87	48,190	32.4
DYLD				
Genotype	17	85.4**	1451	7.0
Environment	7	1203***	8422	40.8
Year	1	532*	532	2.6
GE	119	22.1***	2610	12.7
GY	17	22*	292	1.4
Rep(ENV)	16	20.9*	335	1.6
Residual	549	12.7	6980	33.8

*Significant at the 0.05 probability level; **Significant at the 0.01 probability level; ***Significant at the 0.001 probability level

TME 419 (G17) were the most yielding and most stable across the environments for DYLD. Genotypes TMS 01/0040-27 (G1), TMS 01/0098 (G2), TMS 01/0098-36 (G4), and TMS MM97/JW2-2 (G16) also high yielding but their yield varied across the environments (Fig. 3).

Root total carotenoids content (TCC)

The mean TCC in fresh roots ranged from 3.62 µg/g for genotype TMS 01/0040-27 to 4.52 µg/g for TMS MM97/JW2-2 with an average of 4.1 ± 0.1 µg/g.

The combined analysis of variance of the three genotypes showed significant differences among G and Y but not among environments. The G × E and G × Y interaction were not significant. G, E, Y, and G × E contributed respectively 43.6%, 6.6%, 4.5% and 8.9% of the total sum of squares (Table 7).

In the GGE biplot analysis, PC1 and PC2 explained together 100% of the total variation and graphically summarized genotypes performance in relation to the eight environments. Three mega-environments could be defined: Bambui, Foumbot, and Mbalmayo which were the winning niche of TMSMM97/JW2-2 (G16); Meiganga, Ngaoundere, and Meyomessala for TMS 01/0040-27 (G1); and Ekona and Bertoua for TMS 01/1814-9 (G6). Foumbot, Bertoua, and Ngaoundere were more discriminating of the genotypes TTC; Bambui, Meiganga, and Mbalmayo were less discriminating (Fig. 4).

Discussion

Differential responses observed for the measured parameters to different environments justified the importance of testing genotypes in contrasting environments, to identify good performers for specific locations or those that are stable across locations. The large sum of square attributed to genotypes for CMD incidence showed that the susceptibility is more related to the genotype than on the environment (Thresh and Cooter 2005). The genotype however interacted significantly with the environment for the severity of the disease. This interaction accounted for 22% of the CMS severity sum of square and which could be attributed to the virus strain present in the environment. Bertoua and Meiganga are among environments where the virulent strain EACMV-UG virus was first recorded in Cameroon in 2009 (Akinbade et al. 2010). It has been demonstrated that virus has negative impact on genotypes by the severity of the infection varies greatly between genotypes, bringing evidence that the presence of a virus strain in the environment can impact the G × E interaction (van Mölken and Stuefer 2011). There was a negative correlation between CMD severity and fresh root yield. Some genotypes were heavily hit by the virus strain in those environments and the severity was often more than 3 (moderate mosaic pattern throughout the leaf, narrowing and distortion of the lower one-third of leaflets). Other varieties were not affected and these can be considered as good candidate for introduction in such areas. It is also an indication that they can be used in further cassava selection to improve resistance to CMD giving that finding a resistant or tolerant variety remain a major focus for CMD mitigation in cassava production areas (Chikoti et al. 2009).

Whitefly densities per plant were higher in environment with altitudes above 1000 m (Meiganga, Ngaoundere and Bambui). This finding contrasts with previous studies in western and eastern Kenya where

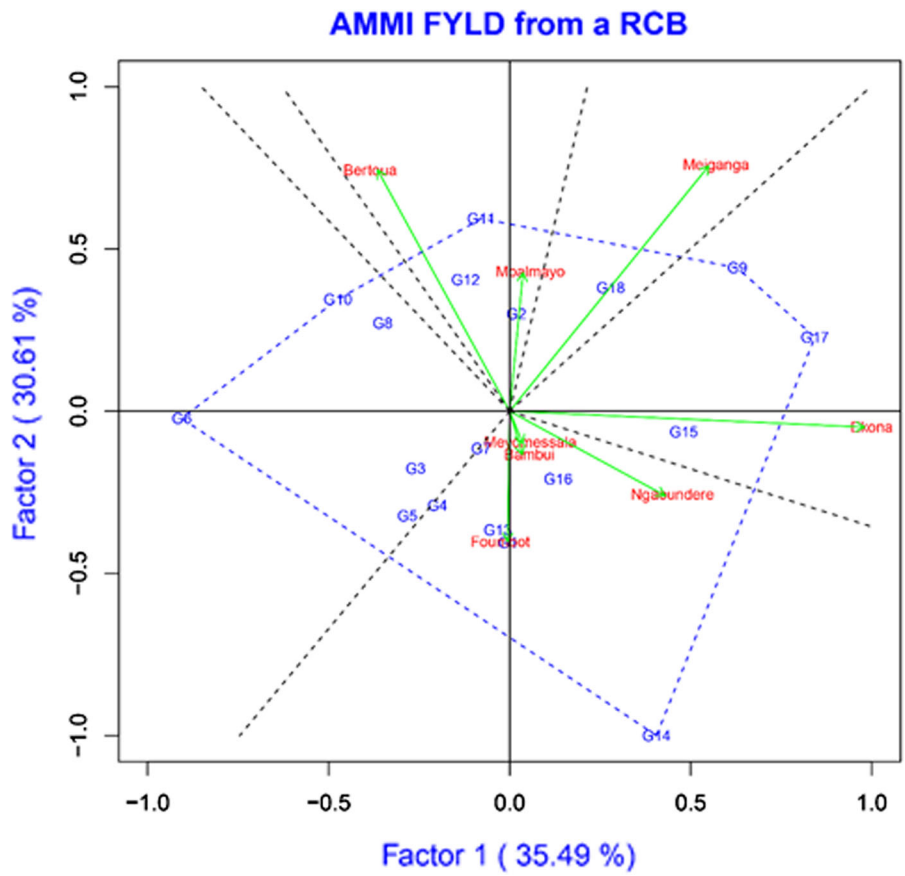

Fig. 2 Mega-environments defined by different winning genotypes tested in eight environments for average FYLD

whiteflies densities were higher in low midlands compared with highlands (Njoroge et al. 2016). Whitefly densities in savannah highlands (Ngaoundere and Meiganga) could have been higher without the impact of bacterial blight which defoliated the tip of many plants.

Five genotypes showed wider adaptability for root yield while others exhibited specific adaptation or performed well in specific environment (e.g. 8034). These difference in performance per environment justifies the large sum of square attributed to environments for roots yields (Kota et al. 2013). The pronounced effect of E on root yield was expected as many authors have indicated that root yield is a polygenic trait (Easwari and Sheela 1998; Cach et al. 2006). Aligning these observations to soil analysis results, Ekona and Foumbot had greater K content, while P content in Ekona was more than 20 folds that of Bambui. The nutrient element K is very important for cassava growth and low K level constitute a limiting factor to the uptake of other nutrients such as N and P (Boateng and Boadi 2010). Also, there is a linear increase in cassava fresh root yields with NPK uptake by plant (Byju et al. 2012; Temegne et al. 2015) and therefore, the high rate of K in Foumbot and Ekona could have played a major role in the uptake of other nutrients, resulting in greater root yields compared with other locations. Meiganga also had high P level but also low K content, negating therefore the effect of high P by reducing uptake (Boateng and Boadi 2010).

Cassava yield in Meiganga, Ngaoundere and Bambui was lower compared with other environments. Average minimal temperature in these locations ranged between 11.7 °C and 12.4 °C. Some authors have reported that cassava at higher altitude experience yield loss potential compared to lowland or mid-altitude environments due to low temperature and reduced solar radiation (Manrique 1992; Noerwijati and Budiono 2015).

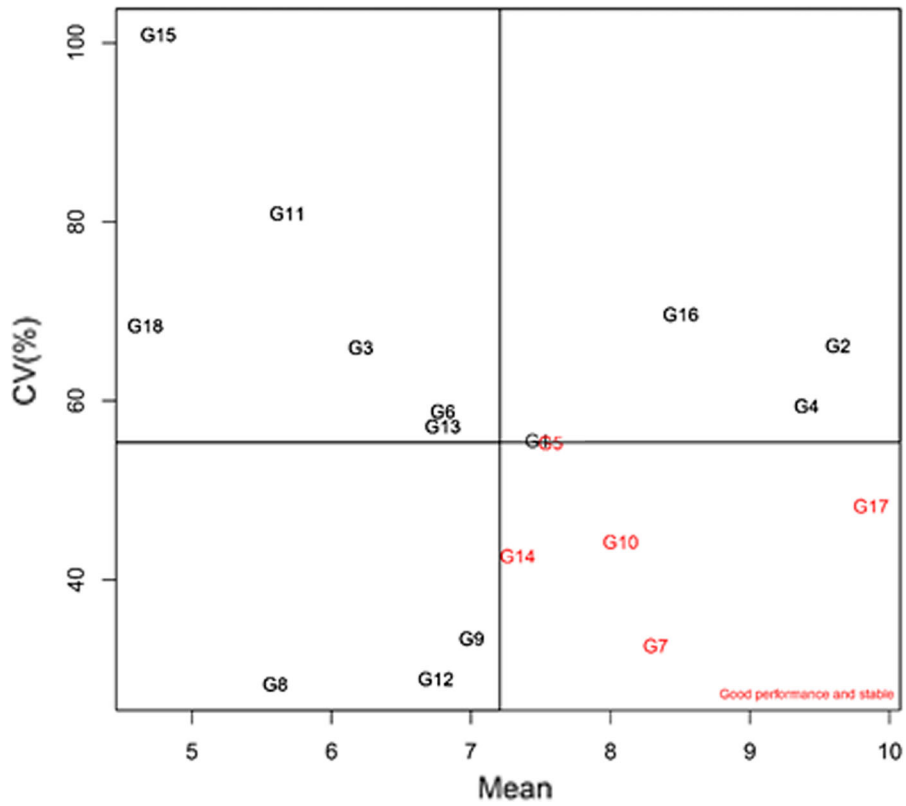

Fig. 3 Performance and stability of genotypes tested in eight environments for the average DYLD

Table 7 Combined analysis of variance table of G, E, year, G × E and year × E contributions to the sum of squares of fresh root TTC of three cassava genotypes in eight environments

TCC	DF	MS	SS	%SS
Genotype	2	5.8*	11.7	43.6
Environment	6	0.7	1.6	6.6
Year	1	1.2***	1.2	4.5
GE	12	0.2	2.4	8.9
GY	3	0	0	0.0
Rep	7	0.1	0.7	2.8
Residual	47	0.2	9.2	34.3

*Significant at the 0.05 probability level; **Significant at the 0.01 probability level; ***Significant at the 0.001 probability level

Five genotypes—TMS 01/1086-55(G5), TMS 92/0057 (G7), TMS 95/0109 (G10), TMS 98/0581 (G14), and TME 419 (G17)—were stable for DYLD across the environments. Dry root yield is an important and favorable characteristic since cassava root dry matter has become an important character for acceptance by researchers and consumers, especially for processed cassava (Teye et al. 2011). These genotypes could therefore be promoted for industrial use.

The environment did not significantly affect the total carotenoid content (TCC) in biofortified genotypes and G × E interaction was not significant, but a small yet insignificant year effect was observed. The reverse was observed by Maroya et al. (2012) in Nigeria with other biofortified genotypes. TCC is known to be affected by the environment, especially in sweet potato (Manrique and Hermann 1999). In the present study, we used three genotypes with relatively low TTC content. The highest TTC recorded by the genotype MM97/JW2-2, was very low compared with more advanced clones such as TMS 07/0593 with TTC of 11 µg/g. The latter has already shown good performance and stability and is recommended for the food technologist and nutritionist (Maroya et al. 2012).

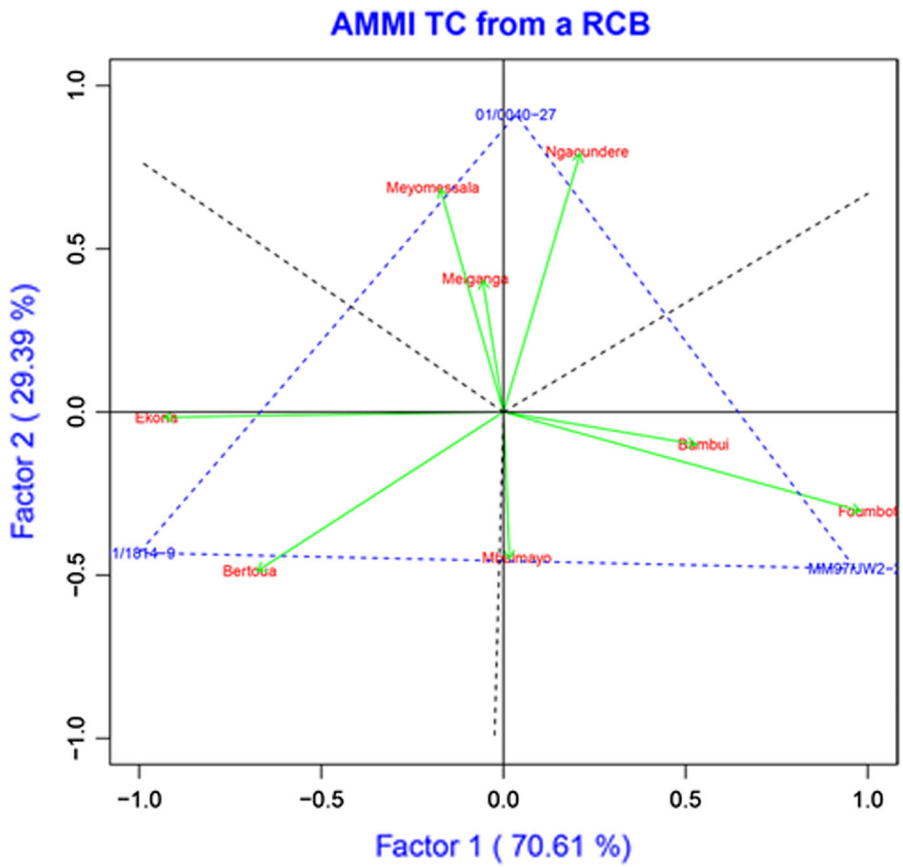

Fig. 4 Mega-environments defined by different winning yellow-fleshed genotypes tested in eight environments for the average root carotenoids content

Conclusion

Newly developed cassava genotypes differed in their performance in tested environments. However, five genotypes (TMS 01/1086-55, TMS 92/0057, TMS 95/0109, TMS 98/0581, and TME 419) were high yielding and stable across the environments, and should be promoted in cassava development programs in regions sharing similar soil and climate characteristics as in our experiment. Four genotypes (TMS 01/0098, TMS 95/0211, TMS 98/0581 and TMS 01/1086-55) did not show CMD symptoms in any environment and constitute a good asset for cassava integrated pest management. Observed difference in genotypes performance could be predicted given the difference in soil nutrient content and virus strain found in each environment. The diffusion of CMD-resistant, high yielding and stable genotypes should promote the change of cassava from subsistence crop associated with low value and poor-quality products to an important commodity in a market-oriented agriculture, pending the evaluation of various utilization by consumers and industries.

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Compliance with ethical standards

Conflict of interest The authors declare that there is no conflict of interest.

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