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RESEARCH

Genotype × Environment Interactions for East African Orange-Fleshed Sweetpotato Clones Evaluated across Varying Ecogeographic Conditions in Uganda

Silver Tumwegamire,* Patrick R. Rubaihayo, Wolfgang J. Grüneberg, Don R. LaBonte, Robert O. M. Mwanga, and Regina Kapinga

ABSTRACT

African dry and starchy (DS) orange-fleshed sweetpotato [*Ipomoea batatas* (L.) Lam] (OFSP) cultivars, distinct from American moist or medium dry and sweet OFSP, have potential to fight vitamin A deficiency (VAD) in the world. This study assessed the genotype × environment (*G* × *E*) interactions in multienvironment trials (METs), the genetic correlations for total root yield (TYLD), biomass (BIOM), harvest index (HI), root dry matter (RDM), root starch (RST), root sucrose (RSU), root β-carotene, (RBC), root Fe (RFE), root Zn (RZN), root Ca (RCA), and root Mg (RMG) and the potential contributions of the cultivars to fight VAD and mineral deficiencies. Nine DS OFSP cultivars, (Ejumula, Zambezi, Carrot_C, Kakamega, KMI61, Abuket_1, SPK004/6/6, SPK004/6 and Naspot_5/50) and a medium dry and sweet OFSP cultivar (Resisto) were tested in METs in Uganda. The $\sigma^2_{G\times E}$ components were smaller than σ^2_G components for HI, RDM, RST, RSU, and RBC, making it possible to ably select for the traits in the early stages. The $\sigma^2_{G\times E}$ components were larger than σ^2_G components for TYLD and mineral traits. Thus, like yield, breeding for mineral traits in sweetpotato is complex, requiring prior data on the causes of the *G* × *E* interactions. Medium to high positive correlations among mineral traits favor parallel selection, and it merits further study to efficiently improve the mineral trait complex by an index. Clearly, a 50- to 100-g ration of all the cultivars, except Naspot_5/50, can provide 100% recommended dietary allowance of vitamin A for a 5- to 8-yr-old child.

S. Tumwegamire, W.J. Grüneberg, R.O.M. Mwanga, and R. Kapinga, International Potato Center (CIP), P.B. 22274, Kampala, Uganda or P.B. 1556 Lima 12, Peru; P.R. Rubaihayo, Crop Science Dep., Makerere Univ., P.B. 7062 Kampala, Uganda; D.R. LaBonte, Louisiana State Univ., AgCenter, 104B M.B. Sturgis Hall, Baton Rouge, LA 70803, USA; S. Tumwegamire and R. Kapinga, current address, International Inst. of Tropical Agriculture (IITA), Tanzania, P.O. Box 34441, Dar es Salaam, Tanzania. Received 6 Oct. 2015. Accepted 4 Feb. 2016. *Corresponding author (s.tumwegamire@cgiar.org).

Abbreviations: AMMI, additive main effects and multiplicative interaction; BIOM, biomass; CIP, International Potato Center; DS, dry and starchy; ECA, eastern and central Africa; *G* × *E*, genotype × environment; HI, harvest index; MET, multienvironment trial; MS, mean squares; NIRS, near-infrared reflectance spectroscopy; OFSP, orange-fleshed sweetpotato; RBC, storage root β-carotene content; RCA, storage root Ca content; RDA, recommended dietary allowance; RDM, storage root dry matter; RFE, storage root Fe content; RMG, storage root Mg content; RPR, storage root protein content; RST, storage root starch content; RSU, storage root sucrose content; RZN, storage root Zn content; SPVD, sweetpotato virus disease; SSA, sub-Saharan Africa; TYLD, total root yield; VAD, vitamin A deficiency; VYLD, vine yield; WFSP, white-fleshed sweetpotato.

Sweetpotato is grown on ~3.7 million ha annually in sub-Saharan Africa (SSA). From 1990 to 2013, the harvested area of sweetpotato in SSA nearly tripled (FAOSTAT, 2013) and the crop has become a staple in some East African countries. The crop has often been considered as a subsistence crop for marginal conditions and usually ignored for its nutritional value (Woolfe, 1992) and breeding potential (Grüneberg et al., 2009b). Nowadays, there is increasing information about (i) the worldwide public health problems related to vitamin A, Fe, and Zn deficiencies in our food supply (Low et al., 2001, 2007; Pfeiffer and McClafferty, 2007;),

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(ii) the extreme high provitamin A content and substantial root Fe and Zn content in high-yielding OFSP cultivars (Mwanga et al., 2007; Laurie et al., 2012; Grüneberg et al., 2009b; Tumwegamire et al., 2011a), and (iii) the genetics and new cultivars of sweetpotato such as the new DS OFSP type (Mwanga et al., 2007; Grüneberg et al., 2009a; Tumwegamire et al. 2011a,b; Laurie et al., 2015).

Traditional American OFSPs are categorized as moist and sweet, but this type does not meet consumer taste preferences and is usually very susceptible to sweetpotato virus disease (SPVD) in SSA. The sweetpotato in SSA is traditionally white-fleshed (WFSP) with high root dry matter and starch content and no or very low β-carotene content. The CIP and partners are breeding for DS OFSP cultivars in a decentralized breeding approach, which means (i) local parental selection, (ii) intensive recombination, and (iii) selections considering farmer and gender sensitive attributes (i.e., SPVD resistance, sufficient upper biomass production, dry mouth feel, and not too sweet taste [Grüneberg et al., 2009b]). Owing to the close genetic relation among African WFSPs and locally found or bred OFSPs, as well as large genetic distances between American and African OFSP germplasm (Tumwegamire et al., 2011b; Laurie et al., 2015), it is hypothesized that African DS OFSP cultivars are sufficiently genetically diverse to show pronounced $G \times E$ patterns similar to those observed by Grüneberg et al. (2005) for a diverse set of clones comprising WFSP and traditional OFSP evaluated across varying ecogeographic conditions of Peru. A better understanding of $G \times E$ interactions in DS OFSPs in eastern and central Africa (ECA) is required before breeders can confidently decide (i) whether a breeding platform can serve the ECA subregion to conduct population improvement for DS OFSP in ECA and (ii) which locations should be chosen for breeding in early or later breeding stages. Such an understanding would also assist agronomists to make more informed choices as to which DS OFSP cultivars might perform well across different regions of the world. That such clones can be identified has been reported for WFSP (Grüneberg et al., 2005). For example, cultivar Xushu18, a WFSP developed in China, is a widely adapted clone with high yields in environments of Peru (Grüneberg et al., 2005) and Bangladesh (Mohammad Hossain, personal communication, 2012).

There is generally little information about $G \times E$ interactions in sweetpotato and no information about $G \times E$ in DS OFSP types in particular. Prerequisites for the analysis of $G \times E$ interactions are estimates of variance components relative to genotypes (σ^2_G), $G \times E$ interactions ($\sigma^2_{G\times E}$), and the error term (σ^2_ε) from METs conducted across locations. The factor environment can include other environmental factors, such as regions, years, seasons, irrigation, or fertilizer inputs, to which the $G \times E$ term can be further partitioned. With the exception of Ngeve (1993) and Grüneberg et al. (2004), there is no information about genotype × year ($\sigma^2_{G\times Y}$) and genotype × location × year interactions ($\sigma^2_{G\times L\times Y}$) in sweetpotato. It can therefore be recommended to use a factor season instead of year because sweetpotato, like many other crops in the tropics, are grown twice within a 12-mo period, and the beginning or the end of a growing season can be in different years. Ngeve (1993) reported TYLD variance component ratios $\sigma^2_G / \sigma^2_{G\times L} / \sigma^2_{G\times Y} / \sigma^2_{G\times L\times Y} / \sigma^2_\varepsilon$ from two sets of METs in Cameroon with the result of 1:0.32:0.06:0.50:1.33 and 1:−0.38:−0.21:1.97:3.34. Grüneberg et al. (2004) reported TYLD variance component ratios for $\sigma^2_G / \sigma^2_{G\times L} / \sigma^2_{G\times S} / \sigma^2_{G\times L\times S} / \sigma^2_\varepsilon$ (where S denotes season), of 1:1.46:0.96:1.83:2.62 for Kenya and Uganda based on 15 cultivars. Information about $G \times E$ considering years and seasons is important to conduct appropriate allocations of test capacities in later breeding stages (Grüneberg et al., 2004). However, it is also informative for allocation of breeding resources in early breeding stages. On the basis of the available $\sigma^2_{G\times L}$, $\sigma^2_{G\times S}$, $\sigma^2_{G\times L\times S}$ or $\sigma^2_{G\times L}$, $\sigma^2_{G\times Y}$, $\sigma^2_{G\times L\times Y}$ estimates, CIP recommends allocating only two seasons or years to later breeding stages before entering into the variety release testing provided that the free test capacity of Year 3 is used to test at more locations in Year 1 and 2. This saves 1 yr of testing in later breeding stages, but using only two series of trials for a final variety release is not a good decision.

There are many studies that have found extreme variability in sweetpotato for nutritional quality traits (Collins, 1990; Woolfe, 1992; Ravindran et al., 1995; Grüneberg et al., 2009b, Laurie et al., 2012). Estimates of variance components for quality traits relative to σ^2_G, $\sigma^2_{G\times E}$, and σ^2_ε from METs show, in nearly all studies, that σ^2_G is considerably larger than $\sigma^2_{G\times E}$ for RDM, RST, RSU, and RBC even in diverse genetic material evaluated across very different environments (Grüneberg et al., 2009a, 2015). For quality traits such as root protein content (RPR) and root mineral content (i.e., RFE, RZN, RCA, and RMG), depending on soil fertility, studies show a more pronounced $\sigma^2_{G\times E}$ but usually not larger or not much larger than σ^2_G. In METs, low $G \times E$ were reported for RDM (Grüneberg et al., 2004); RDM, RST, and RBC (Grüneberg et al., 2005); and RDM, RST, RSU, and RBC (Grüneberg et al., 2009a, 2015). In trials across two environments, low $G \times E$ interactions were reported for RDM, RBC, and RZN; medium $G \times E$ interactions were reported for RPR, RFE, and RMG; and high $G \times E$ interactions were reported for RST, RSU, and RCA (Tumwegamire et al., 2011a); whereas, on the basis of three environments, Grüneberg et al. (2009a) reported medium $G \times E$ interactions for RFE, RZN, RCA, and RMG; and high $G \times E$ interactions for RPR. K'osambo et al. (1998) and Ndirigwe (2005) reported significant $G \times E$ interactions for RBC.

There is not much knowledge on genetic correlations among yield-related and nutritional-quality traits in

Table 1. Description of cultivars used for the genotype × environment analysis.

Cultivar	Type†	Origin	Storage root			SPVD resistance§
			Form	Flesh color‡	Skin color	
Kakamega	FV	Kenya	Long irregular	IO	Pink	Resistant
Resisto	MV	USA	Ovate	DO	Brown	Susceptible
Ejumula	FV	Uganda	Long irregular	DO	Cream	Susceptible
SPK004/6/6	MV	Uganda	Long irregular	DO	Pink	Resistant
Naspot_5/50	MV	Uganda	Long elliptic	LO	Purple red	Resistant
Zambezi	MV	Zambia	Round elliptic	DO	Purple red	Susceptible
KMI61	FV	Uganda	Round elliptic	IO	Cream	Susceptible
Carrot_C	FV	Tanzania	Long irregular	DO	Cream	Susceptible
Abuket_1	FV	Uganda	Long elliptic	IO	Purple red	Susceptible
SPK004/6	MV	Uganda	Obovate	DO	Pink	Resistant

† FV, farmer variety; MV, modern variety.

‡ DO, deep orange; IO, intermediate orange, LO, light orange.

§ SPVD, sweetpotato virus disease.

sweetpotato. Knowledge about negative trait associations is very important in breeding, since these can considerably slow down breeding progress (Wricke and Weber, 1986; Hill et al., 1998). Given the difficulty in estimating genetic correlations, means of phenotypic correlations (average across correlations estimated separately by environments and replications) have been useful to approximate genetic correlations (Hill et al., 1998). Phenotypic correlations among sweetpotato traits, including storage root mineral content, have been reported by Courtney (2007). Grüneberg et al. (2009b) and Tumwegamire et al. (2011a) reported means of phenotypic correlations as approximations of genetic correlation among TYLD and nutritional traits. Critical in breeding for high RDM in OFSP appears to be a negative association between the trait complexes RDM and RST on the one hand and RBC and RSU on the other. However, this correlation pattern changes if WFSP and OFSP are analyzed together or separately (Tumwegamire et al., 2011a). It is hypothesized that negative trait associations between RBC and RDM become so low in DS OFSPs that these do not hamper breeding progress for high RDM, RST, and RBC content and low RSU content, especially when done separately from traditional moist and sweet OFSP and WFSP gene pools.

There were three objectives of this study, namely, (i) to determine the magnitude of $G \times E$ interaction in DS OFSP cultivars of ECA origin for yield and nutritional traits in METs across ecogeographic zones of Uganda in two subsequent seasons, (ii) to determine genetic correlations (on the basis of means of phenotypic correlations) among the traits (for yield components and storage root quality) in the DS OFSP gene pool, and (iii) to determine the potential contribution of DS OFSPs to alleviate vitamin and mineral deficiencies in ECA and other regions of the world.

MATERIALS AND METHODS

Experimental Materials

Ten OFSP cultivars were used for the study (Table 1). These included six farmer cultivars (Ejumula, Zambezi, Carrot_C, Kakamega, KMI61, and Abuket_1) and three modern cultivars (SPK004/6/6, also called NASPOT 10 O or Kabode, SPK004/6, also called NASPOT 9 O or Vita, and Naspot_5/50) of African origin. All the African OFSP cultivars are categorized as DS OFSP. Additionally, one modern cultivar of American origin (Resisto) and categorized as medium dry and sweet OFSP was used as a check. Resisto has medium RDM and RST content, insufficient upper biomass production, and is susceptible to SPVD in SSA. The cultivars are diverse in storage root shape, skin color, and intensity of orange flesh color (Table 1). The storage root orange flesh color has been shown to be correlated with RBC content in sweetpotato (Takahata et al., 1993).

Experimental Sites

The field experiments were conducted for two consecutive seasons at four locations representing the major sweetpotato producing ecogeographic zones in Uganda (Table 2), namely, (i) the tropical montane zone (at the Kachwekano Zonal Agricultural Research and Development Institute [KZARDI]) with bimodal rainfall average of 1319 mm annually, (ii) the tropical rain forest zone (Namulonge, at the National Crops Resources Research Institute [NaCRRI]) with bimodal rainfall average of 1270 mm annually and high SPVD pressure, (iii) the tall savanna zone (Serere, at the National Semi-Arid Resources Research Institute [NaSARRI]), with low rainfall and a high level of weevil infestation, and (iv) the grass savanna zone (at Mobuku Irrigation Scheme) with an annual rainfall of 1000 mm and high evapotranspiration (cropping usually with supplementary irrigation). The experimental sites also differed in soil type and pH. The cultivars were planted at all sites during the first rains in March and April of 2006 and during the second rains in October and November of 2006. At Namulonge, final ridging of plots was done using a tractor, while other sites were manually ridged using hand hoes. Only at the location Mobuku, the crop was irrigated periodically through the growing season using furrow irrigation, where water was directed from distributing channels to the field and let to run in the furrows between sweetpotato crop ridges.

Table 2. Description of locations used for the genotype × environment analysis.

Location	Ecogeographic zone	Elevation	Rainfall	Temperature	Soil	
					Type	pH
		m asl	mm	°C		
Namulonge	Tropical rain forest	1150	1500	22.2	Sandy clay	4.9–5.0
Kachwekano	Tropical montane	2150	≥1750	17.5	Sandy clay loam	5.8–6.2
Serere	Tall savanna	1140	1000–1300	18.0–31.3	Sandy loam	6.2–6.0
Mobuku	Grass savanna	900	≤1000	23.9–30.0	Alluvial	5.5–6.1

Field Layout and Management

In each experiment, a randomized complete-block design with two replications was used. Overall, the METs were complete and orthogonal, respectively (all clones were evaluated in all environments). The experimental plots consisted of three rows, each containing 10 plants. Planting distances were 1.0 m between rows and 0.3 m between plants. The trials were kept weed free and no fertilizers or pesticides were applied.

Data Collection

Harvesting was done 5 mo after planting at Mobuku, Namulonge, and Serere and 7 mo after planting at Kachwekano (note, the cool climate at Kachwekano and surrounding highlands requires a longer growth cycle for sweetpotato). Total storage root yield, vine yield (VYLD), and BIOM production (BIOM = TYLD + VYLD) were recorded in kilograms per plot and converted to tonnes per hectare. Harvest index was calculated as a percentage of the fraction of TYLD to BIOM. From a composite pile of the harvested storage roots of the center row, a sample of four or five roots (each between 100 and 300 g) was taken to prepare a 100-g subsample for determination of RDM, RPR, RST, RSU, RBC, RFE, RZN, RCA, and RMG content. The subsample was freeze-dried at −31°C for 72 h using a vacuum freeze drier YK-118 (True Ten Industrial Co., Ltd.) and weighed to obtain the dry weight in grams. The dry samples were then milled into flour using a stainless steel mill and used to estimate RPR, RST, RSU, RBC, RFE, RZN, RCA, and RMG by near-infrared reflectance spectroscopy (NIRS) (Cozzolino and Moron, 2004; Halgerson et al., 2004). Values for RDM, RPR, RST, and RSU were recorded as percentages on root dry-weight basis, whereas RBC, RFE, RZN, RCA, and RMG were recorded in micrograms per gram on root dry weight basis. Near-infrared reflectance spectroscopy technology has been used to screen for macronutrients in root and tuber crops (Young et al., 1997; Mehrübeoglu and Coté, 1997; and Haase, 2006) including sweetpotato (Lu et al., 2006; Lebot et al., 2009) and to test for mineral concentrations in legumes (Cozzolino and Moron, 2004) and alfalfa (*Medicago sativa* L.) (Halgerson et al., 2004). Also, the technology has become a standard fast-screening method for micronutrients (provitamins A, Fe, and Zn) (Pfeiffer and McClafferty, 2007; Zum Felde et al., 2009) under the HarvestPlus biofortification challenge program. Each milled sample material (2 times 3 g) was analyzed by NIRS within the range of 400 to 2500 nm on a NIRS monochromator model 6500 (NIRSystems, Inc.) using small ring cups with sample autochanger. Near-infrared spectra of each sample were stored in a computer file, and in 2009 these spectra were again used to determine protein, starch, sucrose, β-carotene, Fe, Zn, Ca, and Mg with the latest calibration version for sweetpotato freeze dried samples (Zum Felde et al., 2009). In this version, the correlations in cross-validation between standard laboratory reference methods and NIRS were 0.95, 0.96, 0.80, 0.97, 0.80, and 0.89 for protein, starch, sucrose, β-carotene, Fe, and Zn, respectively (Zum Felde et al., 2009) and 0.92 and 0.78 for Ca and Mg, respectively (Zum Felde, personal communication, 2012). The standard methods for NIRS calibration were done according to Sweeney and Rexroad (1987) for crude protein; polarimetrically by hydrochloric acid dissociation according to the International Association for Cereal Science and Technology No. 123/1 (ICC, 1994) for starch; high performance liquid chromatography according to Rodriguez-Amaya and Kimura (2004) for β-carotene; and inductively coupled plasma–argon optical emission spectrometer according to Bridger and Knowles (2000) and reviewed by Aceto et al. (2002) for Fe, Zn, Ca and Mg. For sucrose determination, a procedure in which a water extract of the freeze-dried samples (0.1 g in 100 mL) was used: (i) the samples were incubated in a water bath at 60°C for 1 h and afterward were treated each with 0.2 mL Carrez I and Carrez II solution to remove proteins; (ii) samples were purified by centrifugation (Sorvall RC-5B Refrigated Superspeed, GMI) for 10 min at 20°C and 166.7 Hz (10,000 rpm); (iii) total sugars were determined from the membrane-filtered supernatant (pores size 0.45 μm); and (iv) sucrose, glucose, fructose, maltose, and galactose were separated using a LiChrospher 100 NH_2 (5 μm) 4- by 4-mm precolumn in combination with a LiChrospher 100 NH_2 (5 μm) 4- by 250-mm separation column (Merck KGaA) and an acetonitrile pure water solution (80:20 v/v) as mobile phase (flow rate 1.0 mL min^{-1}) at 20°C and an injection volume of 20 μL. Sugars were detected with a Knauer differential refractometer 198.00.

Data Analysis

Statistical analyses were conducted using PLABSTAT (Plant Breeding Statistical Program) computer package (Utz, 2001), SAS 6.12 (SAS Institute 1988, 1997), and R (R Development Core Team, 2009). Data were classified relative to cultivars or genotypes (*G*), locations (*L*), seasons (*S*), and blocks (bl) or replications (*R*). In an initial analysis of variance (ANOVA), each trait x_i (namely, TYLD, VYLD, BIOM, HI, RDM, RPR, RST, RSU, RBC, RFE, RZN, RCA, and RMG) was analyzed for each location and season separately to determine outliers, experimental means, minimum, and maximum values using the PLABSTAT model statement $x_i = G + R$, which corresponds to the following statistical model:

$$Y_{ijn} = \mu_i + g_{ij} + \mathrm{bl}_{in} + \varepsilon_{ijn} \quad ,$$

where Y_{ijn} is the plot value of the *i*th trait of the *j*th genotype and the *n*th block, μ_i is the trial mean of the *i*th trait, g_{ij} is the effect of genotypes, bl_{in} is the effect of blocks, and ε_{ijn} is the plot error.

For the analysis across locations and seasons, an ANOVA was performed for each trait x_i using PLABSTAT with the model statement $x_i = G + L + S + gl + gs + ls + gls + R{:}ls +$ RGLS, which corresponds to the statistical model

$$Y_{ijkl} = \mu_i + g_{ij} + l_{ik} + s_{il} + gl_{ijk} + gs_{ijl} + ls_{ikl} + gls_{ijkl} + bl(ls)_{in(kl)} + \varepsilon_{ijkln}$$

where l_{ik}, s_{il}, gl_{ijk}, gs_{ijl}, ls_{ikl}, and gls_{ijkl} are the effects of locations, seasons, genotype–location interactions, genotype–season interactions, location–season interactions, and genotype–location–season interactions, respectively, $bl(ls)_{in(kl)}$ is the effect of blocks with locations and seasons, and other effects as designated above. In a first analysis the effects g_{ij} , l_{ik}, and gl_{ijk} in the model were considered as fixed, while the remaining effects were considered as random, to estimate the least significant difference (LSD) and to compare means among cultivars and locations for each trait. In a second analysis, all effects in the model were considered as random to use the ANOVA to estimate the magnitude and significance of variance components for σ^2_L, σ^2_S, $\sigma^2_{G\times L}$, $\sigma^2_{G\times S}$, $\sigma^2_{L\times S}$, $\sigma^2_{G\times L\times S}$, and σ^2_ε.

For the analysis of stability and adaptability, each combination of location and season was considered to be an environment (E). Variance components σ^2_G, σ^2_E, $\sigma^2_{G\times E}$, and σ^2_ε were estimated using PLABSTAT with the model statement $x_i = G + E + GE + R{:}E + RGE$, which corresponds to the following statistical model:

$$Y_{ijk} = \mu_i + g_{ij} + e_{ik} + ge_{ijk} + bl(e)_{in(k)} + \varepsilon_{ijkn}$$

where e_{ik} and ge_{ijk} are the effects of environments and genotype–environment interactions and other effects as designated above.

For all yield traits (i.e., TYLD, VYLD, and BIOM) for which $\sigma^2_{G\times E}$ was significant and larger than σ^2_G or σ^2_E, the dynamic concept of stability (Becker and Léon, 1988) was applied and subdivided the interaction term into heterogeneity resulting from regression and residual deviations. This subdivision was performed with respect to genotypes and environments using the PLABSTAT statement SUBINT GE. For the remaining traits (i.e., HI, RDM, RPR, RST, RSU, RBC, RFE, RZN, RCA, and RMG), the static concept of stability was applied (Becker and Léon, 1988) by calculating the variance of each genotype across environments and the ecovalence of each genotype (Wricke and Weber, 1986).

Operational broad-sense heritability (h^2) of observed traits was calculated by the following:

$$h^2 = \frac{\sigma^2_G}{\sigma^2_G + \frac{\sigma^2_{G\times L}}{k} + \frac{\sigma^2_{G\times S}}{l} + \frac{\sigma^2_{G\times L\times S}}{kl} + \frac{\sigma^2_{error}}{lkn}}$$

where k denotes the number of locations, l the number of seasons, and n the number of replications. Additionally, all stability parameters were calculated separately for Seasons 1 and 2, followed by calculation of operational broad-sense heritability for the stability parameter of each trait by the following equation:

$$h^2_{stab} = \frac{\sigma^2_G}{\sigma^2_G + \frac{\sigma^2_{G\times S}}{l}}$$

For all yield traits for which the dynamic concept of stability was applied (i.e., TYLD, VYLD, and BIOM) and where regression could not explain the majority of $G \times E$ interaction, an additive main effects and multiplicative interaction (AMMI) analysis (Gollob, 1968; Gauch and Zobel; 1988; Zobel 1990) was conducted using R following the R function developed by Onofri and Ciriciofolo (2007).

Correlations among traits were determined by PLABSTAT using the statement GENOT/1 G, which provides genotypic correlations, and by SAS procedure CORR and the optional statement PEARSON. The correlations determined by the procedure CORR were calculated for each location, season, and replication separately followed by calculating the average correlation between each trait pair across locations, seasons, and replications. These correlations (genotypic correlations and average phenotypic correlations as approximations for genotypic correlations [Hill et al., 1998]) were calculated with all African DS OFSP cultivars and the medium dry and sweet cultivar Resisto as well as without Resisto.

In a final step, the contributions of each variety to the recommended dietary allowance (RDA) for RBC, RFE, RZN, RCA, and RMG were calculated by assuming an intake of 250 g fresh storage roots per person per day (comparable to daily per capita intake in Uganda). The RDA intake of 400 μg retinol (corresponds to 4.8 mg of β-carotene), 10 mg of Fe, 5 mg of Zn, 800 mg of Ca, and 130 mg of Mg was assumed for school-age children from 5 to 8 yr old as recommended by the Institute of Medicine in the United States of America (National Academy of Sciences, 2004). Percentage RDA contributions for RBC for each variety were plotted as a function of intake estimates per person per day with reference to sweetpotato intake estimates in different countries of the world. The daily per-person sweetpotato intake estimates in different countries were based on Food and Agriculture Organization (FAO) statistics (FAOSTAT, 2010) except for Malawi, the state of Orissa in India, and southwestern parts of Bangladesh for which the local statistics of 220, 39, and 15 g, respectively, were used.

RESULTS

Environmental effects were significant for all the traits except RDM (Table 3). Differences in the environmental means were large for TYLD (6.6–33.9 Mg ha^{-1}), BIOM (21.5–69.5 Mg ha^{-1}), and HI (29.3–59.0%). Across seasons, Namulonge had the highest TYLD in Season 1 followed by Mobuku in Season 2. However, for Season 2, extreme low yields (i.e., TYLD = 6.6 Mg ha^{-1} and BIOM = 22.1 Mg ha^{-1}) were obtained at Namulonge. Also, at Serere, yields were clearly lower in Season 2 than Season 1. For Namulonge this was associated with lower BIOM and HI. At Serere, the lower TYLD in Season 2 was only associated with lower BIOM, but differences between seasons at Serere were not significant for TYLD and BIOM. At Kachwekano and Mobuku, differences between seasons were less pronounced for yield traits. In all environments, the RDM means were >30.0% and the RBC means >200 μg g^{-1}, except at Namulonge where the RBC mean was slightly below 200 μg g^{-1}. Differences among

Table 3. Environmental means for observed traits across genotypes (TYLD, total root yield; VYLD, vine yield; BIOM, biomass; HI, harvest index; RDM, root dry matter; RPR, root protein; RST, root starch; RSU, root sucrose; RBC, root b-carotene; RFE, root Fe; RZN, root Zn; RCA, root Ca; RMG, root Mg).

Location†	TYLD	VYLD	BIOM	HI	RDM	RPR‡	RST‡	RSU‡	RBC‡	RFE‡	RZN‡	RCA‡	RMG‡
	Mg ha^{-1}		Mg ha^{-1}	%					μg g^{-1}				
MBK 1§	17.6	30.5	48.1	38.7	33.0	3.4	66.0	10.3	221	15.3	9.3	2139	452
MBK 2¶	23.1	15.1	38.2	59.0	32.7	2.7	61.4	12.0	265	13.6	6.4	1637	376
NM 1	33.9	35.6	69.5	48.3	32.4	4.6	68.3	8.1	192	16.1	9.1	1845	515
NM 2	6.6	15.6	22.1	29.3	33.2	6.7	65.8	7.6	232	19.0	10.7	1627	483
SR 1	13.1	29.3	42.4	32.1	32.2	6.0	65.4	9.0	208	18.5	10.7	1899	504
SR 2	9.0	20.1	29.1	34.2	32.6	5.5	66.1	10.6	261	17.2	10.2	1895	305
KA 1	10.5	11.0	21.5	49.5	32.1	6.2	69.9	7.4	225	18.0	10.3	2250	903
KA 2	8.4	14.0	22.5	37.0	32.1	6.4	68.5	8.5	225	18.9	10.1	1738	588
Mean	15.3	21.4	36.7	41.0	32.5	5.2	66.4	9.2	229	17.1	9.6	1879	516
LSD (0.05)	5.1		15.7	10.6	0.9	1.1	1.4	0.7	35	1.9	1.3	289	63.5

† MBK, Mobuku; NM, Namulonge; SR, Serere; KA, Kachwekano.

‡ Storage root dry weight basis.

§ Season 1.

¶ Season 2.

Table 4. Variety means for observed traits across environments (TYLD, total root yield; VYLD, vine yield; BIOM, biomass; HI, harvest index; RDM, root dry matter; RPR, root protein; RST, root starch; RSU, root sucrose; RBC, root β-carotene; RFE, root Fe; RZN, root Zn; RCA, root Ca; RMG, root Mg).

Variety	TYLD	VYLD	BIOM	HI	RDM	RPR	RST†	RSU†	RBC†	RFE†	RZN†	RCA†	RMG†
	Mg ha^{-1}		Mg ha^{-1}	%					μg g^{-1}				
Resisto	15.8	16.6	32.3	47.2	28.0	5.1	60.3	11.6	344	17.0	9.2	1895	494
Kakamega	16.3	21.1	37.3	41.2	33.5	4.9	68.4	8.4	169	15.3	9.0	1669	470
Ejumula	18.8	27.8	46.6	38.5	34.1	5.0	66.4	9.4	283	17.0	9.3	1995	514
SPK004/6/6	17.8	17.6	35.4	52.7	32.3	5.5	66.1	9.2	230	17.8	10.5	1968	462
Naspot_5/50	7.7	23.3	31.0	24.6	32.1	5.2	67.2	9.4	132	17.4	9.3	1824	490
Zambezi	14.2	20.0	34.4	40.2	32.0	5.0	67.1	9.1	238	16.7	9.6	2003	573
KMI61	12.6	25.9	38.4	32.3	32.7	5.1	69.5	7.0	192	16.7	9.3	1522	430
Carrot_C	14.9	20.5	35.4	47.3	35.7	5.4	65.5	10.1	279	17.8	9.7	2154	595
Abuket_1	16.9	26.4	43.9	35.8	32.0	5.2	66.4	9.3	184	17.7	10.1	1899	532
SPK004/6	17.7	14.9	32.6	50.3	32.8	5.4	67.3	8.6	235	17.1	10.2	1860	499
Mean	15.3	21.4	36.7	41.0	32.5	5.2	66.4	9.2	229	17.1	9.6	1879	516
LSD (0.05)	7.0		12.1	12.1	1.7	0.7	2.1	1.6	34.7	1.7	0.9	295	125

† On dry-matter basis.

environments were small and nonsignificant for RPR, RST, and RSU except for differences between Mobuku in Season 2 and the other environments. At Mobuku in Season 2, lowest RPR (2.7%), lowest RST (61.4%), and highest RSU (12.0%) experimental means were observed. However, this was associated with low experimental means for the minerals (i.e., RFE = 13.6 μg g^{-1}, RZN = 6.4 μg g^{-1}, RCA = 1637 μg g^{-1}, and RMG = 376 μg g^{-1}). The ranges for RFE (13.4–18.9 μg g^{-1}), RZN (6.4–10.7 μg g^{-1}), and RCA (1627–2250 μg g^{-1}) were medium to small, whereas those for RMG (305.1–903.1 μg g^{-1}) were large.

The DS OFSP cultivars exhibited high TYLD (up to 18.8 Mg ha^{-1} for Ejumula), which were not significantly different from the medium dry and sweet OFSP cultivar Resisto (15.8 mg ha^{-1}) (Table 4). However, Naspot_5/50 was exceptional with significantly lower TYLD (7.7 Mg ha^{-1}) than Resisto. The low TYLD for Naspot_5/50 was associated with a low HI (24.6%). The BIOM yields were higher for all DS OFSP cultivars (except Naspot_5/50 with 31 Mg ha^{-1}) but only significant for variety, Ejumula (with 46.6 Mg ha^{-1}). Considerably higher RDM and RST levels were observed in DS OFSP cultivars than in medium dry and sweet Resisto. Conversely, RSU levels were clearly lower in DS OFSP cultivars than in medium dry and sweet Resisto. All comparisons to Resisto were significant for RDM, RST, and RSU except the difference between Carrot_C and Resisto for RSU (1.5%). The RBC content of the DS OFSP cultivars were relatively high and significantly different but significantly lower than of the check Resisto. Differences among the cultivars were small and not significant for RPR. No cultivar was consistently highest across all environments in all the mineral traits; Carrot_C was only highest in RFE, RCA, and RMG content. However, RFE and RZN content were associated (i.e., the highest RFE [17.8 μg g^{-1}] and RZN [10.5 μg g^{-1}] content were observed in SPK004/6/6, which

Table 5 Estimated recommended dietary allowance contributions of different sweetpotato cultivars for β-carotene, Fe, Zn, Ca, and Mg (dry-matter basis).

Genotype	Recommended dietary allowance				
	β-carotene	Fe	Zn	Ca	Mg
	%				
Resisto	501.7	10.6	12.5	14.4	25.0
Kakamega	294.9	14.0	15.2	19. 6	31.4
Ejumula	502.6	14.4	15.8	21.1	33.5
SPK004/6/6	386.9	14.0	16.5	19.3	27.9
Naspot_5/50	220.7	13.8	14.8	18.1	30.0
Zambezi	396.7	13.8	15.9	20.8	36.5
KMI61	327.0	14.1	15.7	16.0	27.9
Carrot_C	518.8	15.9	17.3	24.1	40.9
Abuket_1	306.7	14.2	16.2	19.1	32.9
SPK004/6	401.6	14.1	16.8	19.2	31.7

was also associated with high RCA content and RMG content below the respective averages across all cultivars]). Differences among cultivars for RFE were small and not significant across environments. Differences among cultivars for RZN content were more pronounced (i.e., the RZN content in SPK004/6/6, Abuket_1, and SPK004/6 were significantly higher than those in Resisto).

Percentage RDA contributions of different cultivars for RBC, RFE, RZN, RCA, and RMG are shown in Table 5. At high sweetpotato daily intakes of 250 g by a 5- to 8-yr-old child (compared with estimated 240 g daily per capita intake in Uganda), the percentage RDA estimates were high for RBC across the cultivars and ranged between 220.7 and 518.8% for RBC, 10.6 and 15.9% for RFE, 12.5 and 17.3% for RZN, 14.4 and 24.1% for RCA, and 25.0 and 40.9% for RMG (Table 5). For RBC, the percentages RDA was highest in Carrot_C (518.8%), followed by Ejumula (502.6%) and Resisto (501.7%). Contrastingly, percentage RDA estimates for all minerals were lowest in Resisto and highest in Carrot_C. Even at lower daily intakes (i.e., 50–100 g), all the DS OFSP cultivars, except Naspot_5/50, showed the potential to meet 100% RDA requirements for a 5- to 8-yr-old child (Fig. 1).

The σ^2_G variance component estimates were small and not significant for TYLD (4.58 Mg^2 ha^{-1}), BIOM (5.0 Mg^2 ha^{-1}), and HI (37.9%^{2}), but $G \times E$ interactions were clearly pronounced and significant for all yield traits (Table 6). The $\sigma^2_{G\times L\times S}$ estimates were significant for TYLD and BIOM while $\sigma^2_{G\times S}$ was significant for HI. This was associated with a significant $\sigma^2_{L\times S}$ variance component for all yield traits (i.e., TYLD, BIOM, and HI). The $\sigma^2_{G\times S}$ variance component was significant for RDM, RST, RSU, and RBC. This was associated with no significant $G \times E$ interactions, except RSU whose $\sigma^2_{G\times L}$ was significant. The σ^2_G variance was not significant for RPR and all mineral traits and often negative or estimates close to zero were observed. No significant $G \times E$ interactions were observed for RPR and mineral traits, except RFE and RMG whose $\sigma^2_{G\times L\times S}$ values were significant. The magnitude of the variance components and the number of locations, seasons, and replications resulted in low to medium operational broad sense heritability for yield traits (i.e., TYLD, BIOM, and HI). High broad sense heritability was observed for RDM, RST, RSU, and RBC. Extremely low or zero broad sense heritability was observed for RPR, RFE, and RMG, whereas RZN and RCA had low to medium operational broad sense heritability.

In an ANOVA in which the factors season and location were aggregated into the factor environment the σ^2_G estimates were positive for all traits, except for RPR (−0.02%^{2}) (Table 7). The σ^2_G estimates were close to zero for RFE and RZN. All broad-sense heritability estimates were larger than 24, except RPR. The σ^2_G estimates for TYLD (4.33 Mg^2 ha^{-1}) and BIOM (6.40 Mg^2 ha^{-1}) were not significant. In contrast, the σ^2_G was more pronounced and significant for HI, RZN, and RCA, compared with the ANOVA, in which three factors (i.e., genotype, season, and location) were considered individually. The σ^2_E was significant for all traits, except RDM. The estimated ratios of $\sigma^2_G/\sigma^2_{G\times E}/\sigma^2_\varepsilon$ were 1:6.12:10.62, 1:12.77:19:98, and 1:0.00:3.14 for TYLD, BIOM, and HI, respectively. The ratios of variance components were 1:0.42:0.83, 1:0.26:1.14, 1:1.19:2.58, 1:0.10:0.45, 1:10.44:18.39, 1:2.28:7.45, 1:2.15:3.96, and 1:13.69:23.04 for RDM, RST, RSU, RBC, RFE, RZN, RCA, and RMG, respectively. The $\sigma^2_{G\times E}$ variance components were significant for TYLD, BIOM, HI, RDM, RSU, RFE, RZN, RCA, and RMG.

The subdivision of $G \times E$ sums of squares (Table 8) into heterogeneity of regression and deviations from regressions for all traits that had ratios $\sigma^2_{G\times E}/\sigma^2_G > 2$ (Table 7) showed that the variance components relative to regression for genotypes (Het.R.G) were significant for TYLD ($p = 0.1$) and RMG content ($p = 0.01$). The heterogeneity of regression with respect to genotypes explained about one-fifth of the total $G \times E$ interaction for TYLD and about two-fifths of the total $G \times E$ interaction for RMG content. The variance component relative to heterogeneity of regression with respect to environments (Het.R.E) was negative or close to zero for all traits except RCA (6188.1 [μg g^{-1}]^2) and RMG (884.3 [μg g^{-1}]^2), but also for these two traits the regression explained no significant part of the variance component as a result of $G \times E$ interactions. However, the deviations from regression lines with respect to genotypes (Dev.R.G) and environments (Dev.R.E) were significant for all the traits in the subdivision analysis of the $G \times E$ interactions. For TYLD, all the cultivars had slopes of regression lines >0.55 (Table 9). High regression slopes ($b > 1$) associated with low mean square (MS) deviations were observed for the cultivars Resisto and Kakamega (Table 9), whereas lower regression slopes (b < 1) and MS deviations were observed for

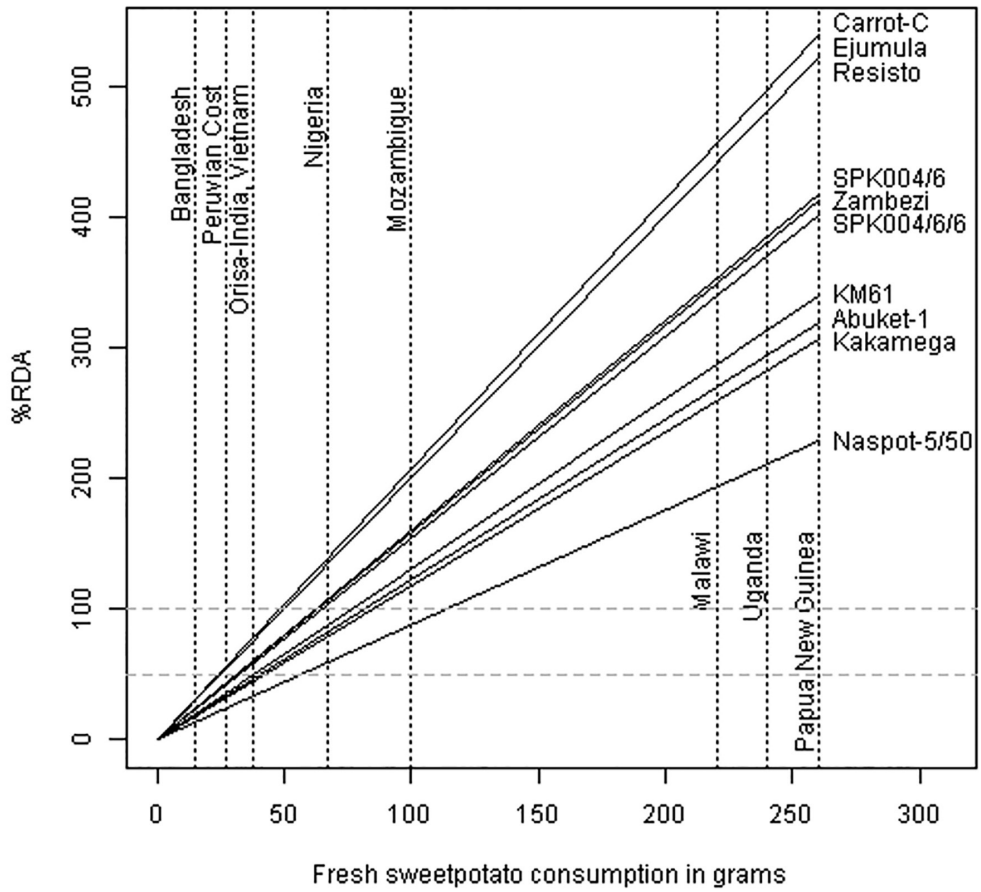

Fig. 1. Recommended dietary allowance contributions (as a percentage) of different orange-fleshed sweetpotato cultivars at different levels of daily per capita intake.

Table 6. Variance components and operational broad-sense heritabilities (h^2) for observed traits when location and season are considered independent factors.

Trait†	σ^2_G	σ^2_L	σ^2_S	$\sigma^2_{L\times S}$	$\sigma^2_{G\times L}$	$\sigma^2_{G\times S}$	$\sigma^2_{G\times L\times S}$	σ^2_s	h^2
TYLD, Mg^2 ha^{-1}	4.58 (1)	−16.72 (−3.65)	−0.07 (−0.02)	95.53** (20.86)	10.14 (2.21)	−3.97 (−0.87)	20.09* (4.39)	46.04 (10.05)	43.6
VYLD, Mg^2 ha^{-1}	9.19 (1)	10.79 (1.17)	42.06 (4.58)	30.96†† (3.37)	6.11 (0.67)	−1.47 (−0.16)	40.68** (4.43)	65.14 (7.09)	48.0
BIOM, Mg^2 ha^{-1}	5.00. (1)	0.40 (0.08)	98.0 (19.6)	189.9** (37.98)	42.81†† (8.56)	−10.88 (−2.18)	51.27* (10.26)	127.84 (25.57)	20.1
HI‡	37.88 (1)	−31.11 (−0.82)	−40.41 (−1.07)	138.46** (3.66)	−9.90 (−0.26)	48.56** (1.28)	37.54 (0.99)	179.66 (4.74)	50.1
RDM‡	3.37** (1)	−0.03 (−0.01)	−0.00 (0)	−0.03 (−0.01)	0.92†† (0.27)	−0.03 (−0.01)	0.70 (0.21)	2.91 (0.86)	87.4
RPR§	−0.03 (1)	1.70†† (−56.7)	−0.16 (5.33)	0.70** (−23.33)	0.06 (−2.0)	0.00 (0)	0.09 (−3.0)	0.64 (21.33)	0.0
RST§	5.40** (1)	3.92 (0.73)	1.30 (0.24)	2.21** (0.41)	0.64 (0.02)	−0.16 (−0.17)	0.92 (0.17)	6.15 (1.14)	90.3
RSU§	0.96* (1)	2.14* (2.23)	0.35 (0.36)	0.46* (0.48)	1.04* (1.08)	−0.13 (−0.14)	0.44 (0.46)	2.73 (2.84)	69.6
RBC¶	3,711.4** (1)	13.0 (<0.01)	526.3* (0.15)	137.4 (0.04)	283.5 (0.08)	−16.3 (<0.01)	136.8 (0.04)	1,670.4 (0.45)	95.3
RFE¶	0.02 (1)	2.02 (101.0)	−0.55 (−27.5)	1.80* (90.0)	0.53 (26.5)	0.16 (8.0)	1.10* (55.0)	2.91 (145.5)	2.8
RZN¶	0.11 (1)	0.53 (4.82)	−0.30 (−2.72)	1.59** (14.46)	0.16 (1.45)	0.02 (0.18)	0.18 (1.64)	1.06 (9.64)	45.1
RCA¶	11,141 (1)	−5,896 (−0.53)	38,734†† (3.48)	20,424†† (1.83)	22,709†† (2.04)	15,837†† (1.42)	16,968 (1.52)	83,804 (7.52)	34.7
RMG¶	−196 (1)	21,045†† (−107.4)	9,895†† (−50.48)	7,122** (−36.34)	1,189 (−6.07)	1,511 (−7.71)	6,629* (−33.82)	14,322 (−73.1)	0.0

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

† TYLD, total root yield; VYLD, vine yield; BIOM, biomass; HI, harvest index; RDM, root dry matter; RPR, root protein; RST, root starch; RSU, root sucrose; RBC, root β-carotene; RFE, root Fe; RZN, root Zn; RCA, root Ca; RMG, root Mg.

‡ Percentage squared.

§ Percentage dry matter.

¶ Dry matter as micrograms per gram squared.

†† Significant at the 0.10 probability level.

Table 7. Variance components and operational broad-sense heritabilities (h^2) for observed traits when factors location and season are aggregated to single factor environment.

Trait†	σ^2_G	σ^2_E	$\sigma^2_{G\times E}$	σ^2_S	h^2
TYLD, Mg^2 ha^{-1}	4.33 (1)	83.81** (19.36)	26.50** (6.12)	46.0 (10.62)	41.15
VYLD, Mg^2 ha^{-1}	9.44†† (1)	68.74* (7.28)	45.07** (4.77)	65.14 (6.90)	49.29
BIOM, Mg^2 ha^{-1}	6.40 (1)	254.41** (39.75)	81.75** (12.77)	127.84 (19.98)	26.00
HI‡	57.28** (1)	94.38** (1.65)	56.81* (0.99)	179.66 (3.14)	75.76
RDM‡	3.49** (1)	0.09 (0.03)	1.47** (0.42)	2.91 (0.83)	90.50
RPR§	−0.02 (1)	2.08** (–104)	0.15 (–7.5)	0.64 (32)	0.0
RST§	5.42** (1)	6.46** (1.19)	1.38†† (0.26)	6.15 (1.14)	90.69
RSU§	1.06** (1)	2.62** (2.47)	1.26** (1.19)	2.73 (2.58)	76.37
RBC¶	3744.9** (1)	486.3** (0.13)	370.4†† (0.10)	1,670.4 (0.45)	96.13
RFE¶	0.158 (1)	3.381** (21.40)	1.649** (10.44)	2.906 (18.39)	28.96
RZN¶	0.142* (1)	1.909** (13.44)	0.323* (2.28)	1.0581 (7.45)	57.13
RCA¶	21,172.5** (1)	42,052.2** (1.99)	45,481.9** (2.15)	83,804.4 (3.96)	65.97
RMG¶	621.7 (1)	31,666.6** (50.94)	8,512.1** (13.69)	14,322.1 (23.04)	24.09

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

† TYLD, total root yield; VYLD, vine yield; BIOM, biomass; HI, harvest index; RDM, root dry matter; RPR, root protein; RST, root starch; RSU, root sucrose; RBC, root β-carotene; RFE, root Fe; RZN, root Zn; RCA, root Ca; and RMG, root Mg

‡ Percentage squared.

§ Percentage dry matter.

¶ Dry matter as micrograms per gram squared.

†† Significant at the 0.10 probability level.

SPK004/6/6 and Naspot_5/50. Only cultivars with large or low *b*-values were significantly different for slopes of regression lines (i.e., Ejumula [b = 1.592] or Kakamega [b = 1.397] were significantly different than Naspot_5/50 [b = 0.595] or Zambezi [b = 0.567]). Although the slopes of regression lines were not significantly different (P = 0.05) it is worth noting that steep slopes ($b > 2$) of regression lines were observed for Namulonge Season 1 and Mobuku Season 2. However, medium and very low slopes of regression lines were observed for Mobuku Season 1 (b = 0.949) and Namulonge Season 2 (b = 0.322), respectively. With respect to genotypes and nutritional traits (Table 9), no significant differences were observed among slopes of regression lines for RFE and RZN. The RCA did differ for two cultivars, Kakamega (b = −0.037) and Carrot_C (b = 1.838). However, several significant differences of slopes of regression lines were observed for RMG across genotypes. For example, Naspot_5/50 and Carrot_C, with steep regression slopes, were significantly different from most cultivars with *b*-values < 1. The MS deviations were not significantly different among genotypes and environments for all mineral traits. Although there are striking differences among genotypes and environments for the stability parameters, variance of genotype j across environments, variance of environment k across genotypes, and the ecovalence (Table 10), it appears that low values (high stability) were associated with low performance in yield or low levels in minerals.

Moderate to high positive correlations (0.6 to 0.9) were observed between trait pairs TYLD and HI, RFE and RZN, and RCA and RMG on the basis of all clones used in the study (Table 11). On the other hand, high negative correlations (−0.762) were observed between RST and RSU content. Moreover, a moderate negative correlation between RST and RBC (−0.477) and less pronounced negative correlation between RDM and RBC (−0.2) were observed. However, a separate analysis without the check clone Resisto (N = 9 clones) revealed that the negative correlation between RST and RBC and RDM and RBC disappears or nearly disappears.

For TYLD, the first (PC1) and second (PC2) principal components of the AMMI analysis explained 48.0 and 28.4% of $G \times E$ interaction, respectively. The AMMI biplot (Fig. 2a) displays a pattern of $G \times E$ interaction. Low-yielding environments exhibited positive PC1 and PC2 values, whereas high-yielding environments exhibited positive PC1 and negative PC2 values (Namulonge Season 1) or negative PC1 and PC2 values (Mobuku Season 2). The seasons of each location were associated for Kachwekano, Serere, and tentatively at Mobuku but were not clearly associated at Namulonge. Namulonge Season 2 grouped with Kachwekano and Serere in Season 2. High-yielding cultivars with small differences to the zero PC1 and PC2 values (SPK004/6/6, Kakamega, and Resisto) were observed as well as large differences to the zero PC1 and PC2 values (Abuket_1 and SPK004/6). Also low-yielding cultivars exhibited small differences to the zero PC1 and PC2 values (Naspot_5/50, KMI61) as well as large differences to the zero PC1 and PC2 values (Zambezi). For RFE, PC1 and PC2 components of the AMMI analysis explained 36.7 and 30.0% of $G \times E$ interaction, respectively (Fig. 2b). The environments of Namulonge showed smaller differences to

Table 8 An ANOVA for genotype (*G*) × environment (*E*) interaction with subdivision (SUB) of *G* × *E* interaction using regression analysis for storage root yield, Fe, Zn, Ca, and Mg contents of storage roots (Het.R., heterogeneity due to regression; Dev.R., deviation from regression lines.

Trait†	Effect‡	df	Mean square	σ^2	Relative σ^2
TYLD	*E*	7	1724.75	83.81**	1,935
	G	9	168.31	4.33	100
	G × *E*	63	99.05	26.51**	612
	SUB Het.R.G	9	163.19	4.68+	18
	Dev.R.G	54	88.36	21.16**	80
	Het.R.E	7	90.99	−0.45	−2
	Dev.R.E	56	100.06	27.01**	101
RFE	*E*	7	74.05	3.38**	2,113
	G	9	8.73	0.16	100
	G × *E*	63	6.20	1.65**	1,031
	SUB Het.R.G	9	4.92	−0.09	−6
	Dev.R.G	54	6.42	1.76**	107
	Het.R.E	7	6.61	0.02	1
	Dev.R.E	56	6.15	1.62**	98
RZN	*E*	7	41.10	1.91**	1364
	G	9	3.97	0.14*	100
	G × *E*	63	1.70	0.32*	228
	SUB Het.R.G	9	0.80	−0.02	−6
	Dev.R.G	54	1.85	0.40*	125
	Het.R.E	7	1.39	−0.02	−6
	Dev.R.E	56	1.74	0.34*	106
RCA	*E*	7	998,000.7	42,052.2**	199
	G	9	513,529.3	21,172.6**	100
	G × *E*	63	174,768.2	45,481.9**	215
	SUB Het.R.G	9	179,795.9	366.6	1
	Dev.R.G	54	173,930.2	45,062.9**	99
	Het.R.E	7	284,778.1	6188.1	14
	Dev.R.E	56	161,016.9	38,606.3**	85
RMG	*E*	7	640,903.5	31,666.6**	5,094
	G	9	41,294.1	621.7	100
	G × *E*	63	31,346.3	8,512.1**	1,369
	SUB Het.R.G	9	82,102.3	3,701.0**	44
	Dev.R.G	54	22,886.9	4,282.4**	50
	Het.R.E	7	47,066.3	884.3	10
	Dev.R.E	56	29,381.3	7,529.6**	89

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

† TYLD, Total root yield, t ha^{-1}; HI, harvest index (%); RDM, root dry matter content (%); RST, root starch content (% DM); RSU, root sucrose content (% DM); RBC, root β-carotene content (μg g^{-1} DM); RFE, root Fe content (μg g^{-1} DM); RZN, root Zn content (μg g^{-1} DM); RCA, root Ca content (μg g^{-1} DM); RMG, root Mg content (μg g^{-1} DM).

‡ Het.R., heterogeneity due to regression; Dev.R., deviation from regression lines.

the zero PC1 and PC2 values than the environments of Serere and Mobuku. The Kachwekano environments were in between. Varieties with lower RFE content across environments showed small differences to the zero PC1 and PC2 values (Kakamega, Zambezi, Ejumula, and Resisto) or large differences to the zero PC1 and PC2 values (KMI61). Cultivars with elevated RFE content across environments displayed larger differences to the zero PC1 and PC2 values (Naspot_5/50, Abuket_1, Carrot_C, and SPK004/6/6). For RZN, the PC1 and PC2 components of the AMMI analysis explained 52.0 and 16.7% of *G* × *E* interaction, respectively (Fig. 2c). The seasons of each location were associated with Namulonge, Kachwekano, and Mobuku but were less pronounced for Serere. Again, the environments of Namulonge showed smaller differences to the zero PC1 and PC2 values than all environments except Mobuku Season 2. No cultivars with higher RZN content (>10 μg g^{-1}) showed lower differences to the zero PC1 and PC2 values, while others (SPK004/6 and Abuket_1) showed large differences to the zero PC1 and PC2 values. For RCA, PC1 and PC2 components of the AMMI analysis explained 44.4 and 30.8% of the *G* × *E* interaction, respectively (Fig. 2d). The seasons of the locations Namulonge and Mobuku were associated. Conversely, the seasons for locations Kachwekano and Serere were not associated and large differences in PC2 values were observed. Again, the environments of Namulonge had small differences to the zero PC1 and PC2 values, but both environments were among environments with low Ca mean values across genotypes. Varieties with higher RCA content across environments (>1850 μg g^{-1}) showed low differences to the zero PC1 and PC2 values (Zambezi, Abuket_1, and Resisto) as well as large differences to the zero PC1 and PC2 values (SPK004/6/6 and Carrot_C). For RMG, PC1 and PC2 components of the AMMI analysis explained 45.8 and 20.5%, respectively (Fig. 2e). The seasons were associated for the locations Namulonge and Mobuku and not associated for locations Kachwekano and Serere. Between Kachwekano Season 1 and Season 2, extreme differences to zero in PC1 and PC2 values were observed. Among cultivars with elevated RMG levels across environments (>500 μg g^{-1}), cultivars with larger differences to the zero PC1 and PC2 values (Ejumula, Carrot_C, and Abuket_1) were observed as well as one cultivar with smaller differences to the zero PC1 and PC2 values (Zambezi).

DISCUSSION

The significant ($p > 0.05$) environment effects on TYLD and HI, the two yield parameters in the present study, are consistent with previous studies (Grüneberg et al., 2005; Mwanga et al., 2007; Tumwegamire et al., 2011a). The best-yielding environments, Namulonge Season 1 and Mobuku Season 2, are likely a result of favorable rain conditions characteristic of the environments. Unlike Mobuku Season 1, where the crop grew on irrigation only, the crop at Mobuku Season 2 benefited from both irrigation and natural rainfall. The low yields obtained at Namulonge Season 2 are probably a result of poor rains at the beginning of the season. Enough soil moisture is critical for sweetpotato vine establishment and initiation of storage root forming roots (Gajanayaka et al., 2013). Overall, except for Mobuku, rains were normal and

Table 9. Estimates obtained using the dynamic concept of genotype × environment interaction for storage root yield, Fe, Zn, Ca, and Mg content of storage roots.

	Parameter†	Storage root yield	Fe	Zn	Ca	Mg
Genotypes						
Resisto	*b*	1.366	1.355	1.307	1.133	0.785
	MS Dev.R.	16.62	0.68	1.13	37,302.9	5,297.2
Kakamega	*b*	1.397	1.051	1.022	−0.037	0.854
	MS Dev.R.	15.82	3.57	1.22	85,220.6	11,146.9
Ejumula	*b*	1.592	0.886	0.840	0.639	1.045
	MS Dev.R.	44.48	1.13	0.24	88,829.0	15,960.4
SPK004/6/6	*b*	0.753	0.809	1.069	1.180	0.737
	MS Dev.R.	14.20	4.58	1.14	104,577.5	8,591.4
Naspot_5/50	*b*	0.595	1.314	0.926	1.286	1.557
	MS Dev.R.	8.29	2.78	0.21	77,864.9	15,111.1
Zam*b*ezi	*b*	0.567	0.820	0.815	1.175	0.848
	MS Dev.R.	42.98	1.38	0.39	30,655.1	3,878.6
KMI61	*b*	0.834	0.767	1.080	0.658	0.537
	MS Dev.R.	27.33	6.46	0.86	29,415.8	4,848.4
Carrot_C	*b*	0.671	1.377	1.130	1.838	1.720
	MS Dev.R.	91.75	2.99	0.67	144,282.8	16,754.4
Abuket_1	*b*	1.133	1.183	1.059	1.310	1.427
	MS Dev.R.	68.86	2.45	1.41	49,978.8	8,032.3
SPK004/6	*b*	1.093	0.438	0.752	0.819	0.491
	MS Dev.R.	67.28	2.86	1.05	134,558.5	13,370.6
LSD regression (0.05)		0.81	0.99	0.73	1.40	0.63
B-test mean square deviation from regression line		+	ns‡	ns	ns	ns
Environments§						
MBK1	*b*	0.949	1.472	1.562	1.115	0.928
	MS Dev.R.	69.71	4.00	0.85	104,331.3	15,597.1
MBK2	*b*	2.027	0.056	1.003	0.896	0.299
	MS Dev.R.	74.79	1.97	0.32	35,601.9	5,746.8
NM1	*b*	2.098	2.043	1.135	0.313	1.135
	MS Dev.R.	86.53	0.93	0.49	34,672.7	7,589.8
NM2	*b*	0.322	0.774	−0.112	0.102	0.496
	MS Dev.R.	25.09	2.75	0.26	48,093.2	5,244.0
SR1	*b*	0.697	1.724	1.504	2.101	1.232
	MS Dev.R.	40.04	2.70	0.71	60,106.2	12,584.7
SR2	*b*	0.842	−0.371	1.374	0.699	1.031
	MS Dev.R.	18.79	2.67	1.45	42,777.7	14,098.5
KA1	*b*	0.743	1.211	0.547	1.910	3.154
	MS Dev.R.	20.31	4.68	1.14	93,960.7	21,820.9
KA2	*b*	0.322	1.092	0.987	0.863	−0.275
	MS Dev.R.	14.95	1.83	0.88	144,015.7	20,152.7
LSD regression (0.05)		2.04	2.28	1.85	1.54	1.96
B-test mean square deviation from regression line		Ns	Ns	Ns	Ns	Ns

† MS Dev.R., mean square deviation from regression line.

‡ ns, not significant.

§ KA1, Kachwekano Season 1; KA2 Kachwekano Season 2; MBK1 Mobuku Season 1; MBK2 Mobuku Season 2; NM1 Namulonge Season 1; NM2 Namulonge Season 2; SR1 Serere Season 1; and SR2 Serere Season 2.

higher during the first season than the second season for all the sites. In the second season, the rains started late and were erratic, which possibly accounts for the lower yields during the second than first season. It is important to note that the environmental effects were significant for all the studied nutritional traits except RDM (Table 3). However, this should not be misunderstood to mean significant *G* × *E* interactions (Tumwegamire et al., 2011a). The non-significant environmental effects on RDM indicate that selection and characterization in one environment can be extrapolated to other environments.

Table 10. Estimates obtained using the static concept of genotype × environment interaction for storage root yield, Fe, Zn, Ca, and Mg content of storage roots.

	Parameter	Storage root yield	Fe	Zn	Ca	Mg
Genotypes						
Resisto	σ^2_j	175.1	7.38	4.48	96,058.4	24,274.9
	Ecovalence	25.7	1.05	1.17	32,859.9	6,025.2
Kakamega	σ^2_j	181.7	7.15	3.20	73,114.2	32,916.9
	Ecovalence	27.1	3.07	1.05	126,698.7	10,239.0
Ejumula	σ^2_j	256.0	3.88	1.66	96,490.5	48,667.5
	Ecovalence	68.3	1.02	0.26	82,655.8	13,744.9
SPK004/6/6	σ^2_j	61.0	6.35	3.33	159,110.0	24,764.9
	Ecovalence	17.4	4.06	0.99	91,253.3	9,582.4
Naspot_5/50	σ^2_j	37.6	8.78	1.95	149,248.4	90,653.9
	Ecovalence	21.2	2.75	0.19	70,819.1	22,900.1
Zambezi	σ^2_j	64.5	3.67	1.70	95,124.3	26,353.4
	Ecovalence	53.0	1.30	0.40	27,797.4	4,067.6
KMI61	σ^2_j	83.4	7.71	3.14	46,820.4	13,399.6
	Ecovalence	25.7	5.74	0.75	31,049.0	11,022.6
Carrot_C	σ^2_j	117.5	9.57	3.20	292,285.1	109,188.5
	Ecovalence	87.9	3.08	0.61	158,731.1	30,983.7
Abuket_1	σ^2_j	169.7	7.28	3.51	128,409.7	72,114.0
	Ecovalence	60.5	2.22	1.22	47,619.5	12,720.0
SPK004/6	σ^2_j	160.6	3.16	2.06	148,796.1	19,176.3
	Ecovalence	58.4	3.62	1.02	116,973.1	19,772.8
Environments†						
MBK1	σ^2_j	71.4	4.74	1.36	132,657.2	16,084.7
	Ecovalence	61.9	3.68	0.83	93,165.0	13,877.6
MBK2	σ^2_j	109.7	1.76	0.54	57,427.2	5,338.8
	Ecovalence	77.5	2.24	0.29	31,991.6	6,377.0
NM1	σ^2_j	123.2	3.10	0.76	33,965.8	10,073.0
	Ecovalence	89.5	1.42	0.44	45,965.6	6,793.8
NM2	σ^2_j	23.3	2.77	0.23	43,086.6	5,296.5
	Ecovalence	27.1	2.47	0.54	68,603.5	5,316.7
SR1	σ^2_j	40.7	4.02	1.19	195,042.4	15,106.5
	Ecovalence	36.5	2.68	0.69	92,301.7	11,325.8
SR2	σ^2_j	24.1	2.45	1.09	53,701.41	15,274.7
	Ecovalence	16.9	3.40	1.32	40,934.7	12,534.5
KA1	σ^2_j	23.8	4.96	1.76	200,637.7	45,075.5
	Ecovalence	18.7	4.19	1.07	110,112.9	31,374.5
KA2	σ^2_j	14.3	2.45	1.02	151,934.9	18,109.5
	Ecovalence	18.1	1.63	0.78	128,613.6	22,112.2

† KA1 Kachwekano Season 1; KA2 Kachwekano Season 2; MBK1 Mobuku Season 1; MBK2 Mobuku Season 2; NM1 Namulonge Season 1; NM2 Namulonge Season 2; SR1 Serere Season 1; and SR2 Serere Season 2.

Genotypes were not significantly ($p > 0.05$) different for yield (except for Naspot_5/50), RFE, and RMG content (Table 4). However, other studies have reported significant differences among genotypes for TYLD (Collins et al., 1987; Grüneberg et al., 2005), RFE, and RMG (Grüneberg et al., 2009a; Laurie et al., 2012). The contrast observed in the present study is likely due to the limited number and a more narrow set of cultivars used compared with previous studies. The high TYLD observed for cultivars Ejumula, SPK004/6, and SPK004/6/6 confirm previous results with the same cultivars (Mwanga et al., 2007, 2009). All the three cultivars were released in Uganda and represent the potential gains in breeding for OFSP cultivars with high TYLD, RDM, and RBC (Mwanga et al., 2009). These cultivars of the category DS OFSP clearly have higher RDM and RST content than the cultivar Resisto, which belongs to the traditional moist or medium dry and sweet OFSP category. However, in this study, the check Resisto had significantly higher RBC content (~350 μg g^{-1} dry wt. basis) than DS OFSP cultivars. In the previous study with 2 environments (Tumwegamire et al., 2011a), this was not clearly observed. However, the present estimates are consistent with those reported elsewhere (Laurie et al., 2012; Grüneberg et al., 2009a) for Resisto.

For RBC, the associated percentage RDA of all the cultivars were high (220.7–518.8%) assuming as high as 250 g of daily serving for a 5- to 8-yr-old child (Table 5). This intake is comparable to the 240-g daily per capita intake of sweetpotato in Uganda (FAOSTAT, 2007). Even at as low as 50 to 100 g daily ration, the cultivars (except Naspot_5/50) can meet 100% RDA of a 5- to 8-yr-old child, suggesting that the cultivars could be useful in alleviating VAD in many areas across the world including southern and eastern Asia and the northeastern states of Brazil where VAD prevalence is high but with low per capita consumption of sweetpotato. High percentage RDA for Ejumula, Carrot_C, Resisto, Zambezi, and KMI61 have been reported in a previous study (Tumwegamire et al., 2011a). The potential to alleviate VAD using OFSP has been demonstrated (Low et al., 2001, 2007; van Jaarsveld et al., 2005; Laurie et al., 2012).

As expected, the $\sigma^2_{G\times E}$ component for RBC and RST were nonsignificant ($p > 0.05$), suggesting the possibility of improving the traits with high selection efficiency in the early stages of the sweetpotato breeding program. Grüneberg et al. (2005) reported similar findings for RBC and RST. In the present study, the $\sigma^2_{G\times E}$ component for RDM were highly significant ($p < 0.01$) but fractional (0.4) compared with the corresponding σ^2_G component (1), again, consistent with the observation of Grüneberg et al. (2005). Furthermore, the proportion of $\sigma^2_{G\times E}$ compared with the corresponding σ^2_G component was close to 1 for HI and RSU content. The observation for HI is similar to what Grüneberg et al. (2005) observed. These favorable variance component ratios for selection are reflected in heritability estimates of >0.7 for HI, RDM, RST, RSU, and RBC, which reach the highest value of 0.96 for RBC. On the basis of this observation, as well as previous $G \times E$ studies (Grüneberg et al., 2005), there is negligible $G \times E$ interactions for RBC, and stability analysis reveals no information. However, significant environmental main effects on RBC, which are much less pronounced than genotypic main effects on RBC, were observed in this study as well as in previous studies (Grüneberg et al., 2005). In this study, the significant σ^2_E was about three

Table 11. Pearson correlation coefficients among observed traits.† Estimates based on all clones (*N* = 10).

	TYLD	HI	RDM	RST	RSU	RBC	RFE	RZN	RCA
Estimates based on all clones (*N* = 10)									
HI	0.670								
RDM	0.066	−0.057							
RST	−0.042	−0.162	0.342						
RSU	0.11	0.171	−0.207	−0.762					
RBC	0.122	0.253	−0.2	−0.477	0.368				
RFE	−0.042	−0.091	0.018	−0.401	0.225	0.067			
RZN	−0.098	−0.039	0.004	−0.211	0.129	0.053	0.747		
RCA	0.101	0.175	0.140	−0.293	0.317	0.228	0.376	0.346	
RMG	0.064	0.086	0.082	−0.242	0.196	0.036	0.545	0.416	0.735
Estimated based on all clones without check clone Resisto (*N* = 9)									
HI	0.660								
RDM	0.144	0.087							
RST	−0.048	−0.102	−0.061						
RSU	0.117	0.108	0.067	−0.741					
RBC	0.164	0.219	0.217	−0.211	0.186				
RFE	−0.066	−0.106	0.052	−0.521	0.234	0.079			
RZN	−0.116	−0.052	−0.078	−0.375	0.160	0.113	0.759		
RCA	0.119	0.210	0.171	−0.405	0.392	0.249	0.390	0.358	
RMG	0.103	0.145	0.088	−0.338	0.274	0.095	0.563	0.452	0.764

† TYLD, total root yield (t ha^{-1}); HI, harvest index (%); RDM, root dry matter content (%); RST, root starch content (% dry matter [DM]); RSU, root sucrose content (% DM); RBC, root β-carotene content (μg g^{-1} DM); RFE, root Fe content (μg g^{-1} DM); RZN, root Zn content (μg g^{-1} DM); RCA, root Ca content (μg g^{-1} DM); RMG, root Mg content (μg g^{-1} DM).

times smaller than σ^2_G, which clearly shows that the environment affects RBC levels in sweetpotato but without important interactions with genotypes. Hence, we suggest that the trait complex HI, RDM, RST, RSU, and RBC can be selected with high efficiency in the early breeding stages. However, for a final proof of this concept for breeding in early breeding stages variance component estimates in early breeding stages on the basis of applied breeding material of early breeding stages with thousands of clones should be made, because it can be expected that σ^2_G is larger at these stages. This might not result in higher operational broad-sense heritability because breeding is operating with much less environments (usually 1 or 2, rarely 3) in early breeding stages.

Traits with significant ($p < 0.05$) or highly significant ($p < 0.01$) $\sigma^2_{G\times E}$ components (Table 7) and ratios of $\sigma^2_{G\times E}/\sigma^2_G > 2$ included TYLD and all root mineral content. Very high $\sigma^2_{G\times E}/\sigma^2_G$ ratios for TYLD were also reported by Grüneberg et al., (2005). It is well known that breeding for yield is complex and requires more environments (Ngeve and Bouwkamp, 1993; Collins et al., 1987; Manrique and Hermann, 2001; Grüneberg et al., 2005). However, HI, a major yield component, might be very useful to select for yield and yield stability in sweetpotato (Grüneberg et al., 2005). The significant $G \times E$ interactions for minerals in the present study differ from preliminary findings reported by Grüneberg et al. (2009a) and suggest that breeding for RFE, RZN, RCA, and RMG content in sweetpotato (low σ^2_G and relatively high $\sigma^2_{G\times E}$) is complex and requires information about the causes of these $G \times E$ interactions before the breeder embarks on enhancing these minerals. However, breeding for enhanced mineral content in sweetpotato would be desirable as part of the sweetpotato biofortification program at CIP and with the partners.

For TYLD, the current study demonstrated that the dynamic concept of using slope of regression lines is useful for selection among genotypes. However, only about one-fifth of the $G \times E$ interaction for TYLD was explainable by the heterogeneity of regression as a result of genotypes. This corresponds nearly exactly to the findings of Grüneberg et al. (2005). The reason that only one-fifth of the $G \times E$ interaction for TYLD was explainable by the heterogeneity of regression lines in both studies might be due to the fact that different agroecological zones were used as test environments. Within a single agroecological zone, it is expected that the dynamic concept using slope of regression lines is more applicable vs. multiple environments. For example, in an extended $G \times E$ analysis for TYLD by AMMI, locations in different seasons showed associated PC1 and PC2 values (Fig. 2a). Although the heterogeneity of regression lines with respect to environments was not significant, it was observed that Namulonge Season 1 and Mobuku Season 2 had steep slopes of regression lines (Table 9), indicating the usefulness by these locations to differentiate among accessions for TYLD. Such environments are also useful for preliminary yield tests in early breeding stages. However, unusual weather changes during crop growth can make these locations also nearly useless for yield selection such as we experienced at Namulonge in Season 2. Namulonge changed in the slope of

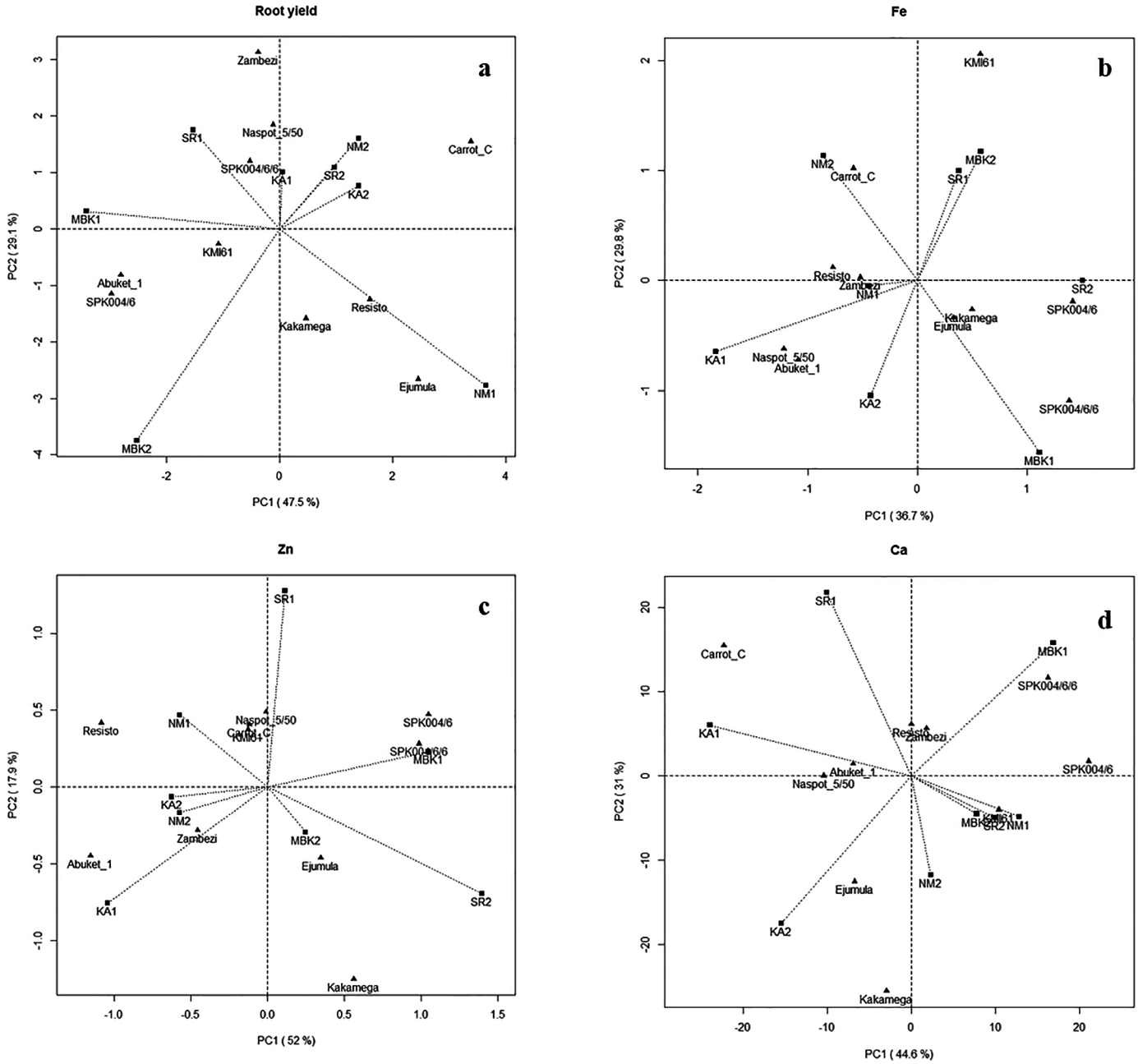

Fig. 2 (continued on next page). The additive main effects and multiplicative interaction biplot of 10 sweetpotato clones evaluated for (a) storage root yield, (b) Fe storage root content, (c) Zn storage root content, (d) Ca storage root content, and (e) Mg storage root content in eight environments in Uganda. KA1, Kachwekano Season 1; KA2, Kachwekano Season 2; MBK1, Mobuku Season 1; MBK2, Mobuku Season 2; NM1, Namulonge Season 1; NM2, Namulonge Season 2; SR1, Serere Season 1; SR2, Serere Season 2.

regression line from nearly 2.0 in Season 1 to nearly 0.3 in Season 2. To monitor the suitability of selection environments in early breeding stages, experienced breeders often include at least five check clones in trials (Grüneberg et al., 2009a). The AMMI analysis for TYLD revealed the possibility of finding as widely adapted cultivars (Kakamega and SPK004/6/6) among DS OFSP cultivars as Resisto a medium dry and sweet OFSP variety.

For RFE, RZN, and RCA, regression analysis for either genotypes or environments did not result in a significant fit of the regression model and explained nearly 0% of the total $G \times E$ interaction. However, for RMG, the variance component from the heterogeneity of regression lines explained nearly two-fifths of the $G \times E$ interaction. This suggests that genotypes in environments with elevated RMG performance, measured on the basis of the average RGM content across genotypes, have different uptake capacities in these environments. Since Namulonge, demonstrated a slope of region of $b = 1.135$ associated with relative low deviations from the regression line (7589.8) in Season 1 it appears that this environment was suitable to differentiate among genotypes for RMG

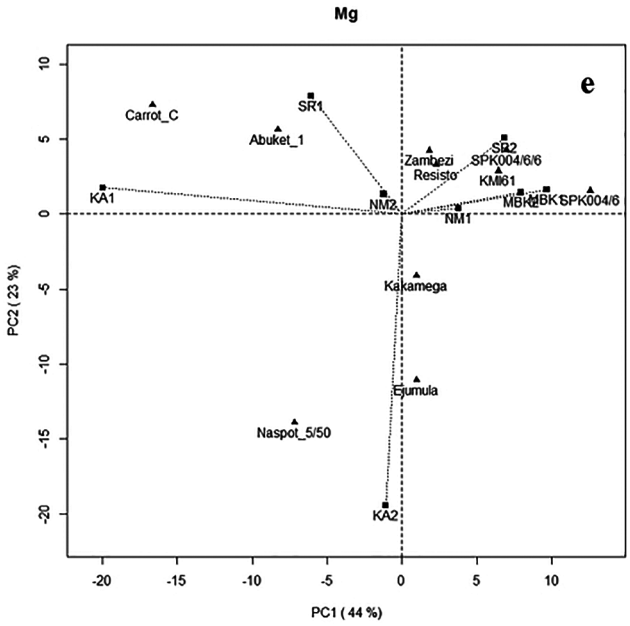

Fig. 2. Continued.

content. However, this suitability for selection can easily change in the event of unfavorable weather conditions (see Namulonge Season 2 in Table 9). On the basis of this study, it appears that the dynamic concept of stability is unsuitable to select and improve selection strategies for RFE, RZN, and RCA content in sweetpotato. Also, the static concept of stability appears unsuitable to select for RFE, RZN, and RCA content of storage roots (Table 10) because stability (low variance of accessions across environments and low ecovalence) is simply associated with undesired low RFE, RZN, and RCA content.

The trend that accessions with elevated RFE, RZN, and RCA content (Table 10) show larger $G \times E$ interactions is clearly reflected by the AMMI analysis for Fe content (Fig. 2b) and AMMI biplots clearly showed that all clones with elevated RFE content across environments (Naspot_5/50, Abuket_1, Carrot_C, and SPK004/6/6) displayed larger differences to the zero PC1 and PC2 values. Hence, breeding for elevated RFE content and stability of the Fe content across environments appears to be problematic. However, the AMMI analysis for RZN content (Fig. 2c) showed that accessions such as Carrot_C exist with higher RZN content (>10 μg g^{-1}) and lower differences to the zero PC1 and PC2 values. It appears that at Namulonge, both seasons with elevated RZN mean values across genotypes is an interesting selection environment to differentiate among genotypes because of its relatively small differences to the zero PC1 and PC2 values than other environments. The same elevated high mineral content and low contribution to $G \times E$ interactions was also observed for RCA in Zambezi and Ejumula (Fig. 2d) and for RMG in Zambezi (Fig. 2e), indicating that simply associating desired high RFE, RZN, RCA, and RMG content generally with higher contribution to $G \times E$ interactions is an insufficient cause and description of $G \times E$ interactions for mineral content in sweetpotato storage roots. However, the number of accessions used in this study is not large enough to conclusively show that elevated mineral content and low $G \times E$ exists in sweetpotato. This might merit further studies aiming at the heritability of elevated mineral content combined with low contribution to $G \times E$ interaction.

The present study cannot provide any recommendations for selection strategies to elevate storage root mineral content at the current stage. The study only demonstrates that improving mineral content in sweetpotato is much more complicated and complex. However, it appears that it is possible to select and to design breeding strategies to enhance these traits in sweetpotato. Medium to high positive correlations among mineral traits (Table 11) are clearly in favor for selection aimed at elevated mineral content in sweetpotato. In addition to studies aiming at the heritability of elevated mineral content combined with low contribution to $G \times E$, it merits to investigate if selection can be made efficient through an index comprising mineral content. It should be noted that an improvement of RMG content, also not a priority trait for biofortification, indirectly should affect positively RFE, RZN, and RCA content because of the correlation structure among these traits.

The positive correlation between TYLD and HI has been previously reported by Grüneberg et al. (2005, 2009a). The previous study (Tumwegamire et al., 2011a) did not estimate this correlation. However, other positive correlations (Table 11) observed in this study for trait pairs RFE and RZN, RFE and RMG, and RCA and RMG are consistent with the previous study (Tumwegamire et al., 2011a) and genetic correlations reported by Grüneberg et al. (2009b). This is also true for the negative correlations observed in this study between RST and RSU content, as well as RST and RBC content. Unlike in this study, the previous study (Tumwegamire et al., 2011a) and Grüneberg et al. (2009b) found moderate to high negative correlation between RBC and RDM, but it appears from the present study that the negative correlation disappears or is much less pronounced within the DS OFSP category. It is of high interest to develop DS OFSP on a large scale for African farmers and consumers, and this is much easier in breeding populations with less pronounced negative correlation between RBC and RDM than the breeding populations with a high negative correlation between RBC and RDM. This is also a strong argument to reduce crosses between moist or medium dry and sweet OFSP and African high dry matter white-fleshed sweetpotatoes. However, it also appears that within DS OFSP, the positive correlations between RBC and minerals, overall, is less pronounced, so that by means of selecting for more RBC, or intense color, there is an indirect selection for elevated mineral content.

In conclusion, the environment affects β-carotene levels in sweetpotato but without important interactions with genotypes. This is also true for starch and dry-matter content. It is nearly certain that for HI and RSU, $G \times E$ interactions exist in sweetpotato, but the magnitude of these interactions is not large. We suggest that the trait complex, HI, storage root dry matter, RST, RSU, and β-carotene can be selected in early breeding stages with high selection efficiency. For minerals, significant $G \times E$ interactions must be expected, and their magnitude appears to be in between the $G \times E$ interactions of the trait complex, HI, storage root dry matter, RST, RSU, and β-carotene, and the $G \times E$ interactions of the trait and storage root yield. The study demonstrates that improving mineral content in sweetpotato is much more complicated and complex, as expected, and at the current stage, recommendations for selection strategies to elevate storage root mineral content cannot be made. To enhance mineral content in sweetpotato, further studies on the heritability of low contribution to $G \times E$ interactions among clones with elevated mineral content are needed. Medium to high positive correlations among mineral traits clearly favor selection aimed at elevated mineral content in sweetpotato. It is possible to meet the RDA for β-carotene of a 5- to 8-yr-old child using most cultivars in this study with only 50 to 100 g of daily intake.

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