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Genetic Diversity in White- and Orange-Fleshed Sweetpotato Farmer Varieties from East Africa Evaluated by Simple Sequence Repeat Markers

S. Tumwegamire,* P. R. Rubaihayo, D.R. LaBonte, F. Diaz, R. Kapinga, R. O. M. Mwanga, and W. J. Grüneberg

ABSTRACT

Sweetpotato [*Ipomoea batatas* (L.) Lam] farmer varieties are still the backbone of production and breeding programs in Sub-Sahara Africa. Usually, farmer varieties in Sub-Sahara Africa are white- or cream-fleshed sweetpotato (WFSP), but recently orange-fleshed sweetpotato (OFSP) were found in East Africa. The objective of the study was to characterize WFSP and OFSP germplasm from East Africa. Eighty-five East African farmer varieties (29 OFSPs and 56 WFSPs) and seven varieties of non-African origin as check clones were analyzed for diversity using 26 simple sequence repeat (SSR) markers. A total of 158 alleles were scored with an average of 6.1 alleles per SSR loci. The mean of Jaccard's similarity coefficients was 0.54. The unweighted pair group method analysis (UPGMA) revealed a main cluster for East Africa germplasm at a similarity coefficient of 0.52. At a similarity coefficient of about 0.55 subclusters within the East African germplasm were observed, but these were neither country nor flesh color specific. Analysis of molecular variance (AMOVA) found a significant difference between East African and non-African germplasm and a nonsignificant difference between OFSP and WFSP germplasm. In conclusion, the East African germplasm appears to be distinct from non-African germplasm, and OFSP and WFSP farmer varieties from East Africa are closely related. Orange-fleshed sweetpotato farmer varieties from East Africa might show similar adaptation to Sub-Sahara African environments as WFSP and a big potential in alleviating vitamin A deficiency.

S. Tumwegamire, W.J. Grüneberg, R. Kapinga, and F. Diaz, International Potato Center (CIP), P.B. 22274, Kampala, Uganda or P.B. 1556 Lima 12, Peru; P.R. Rubaihayo, Crop Science Department, Makerere University, P.B. 7062 Kampala, Uganda; D.R. LaBonte, Louisiana State University, AgCenter; 104B M.B. Sturgis Hall, LSU Campus, Baton Rouge, LA 70803, USA; R.O.M. Mwanga, National Crops Resources Research Institute (NaCRRI), P. B. 7084, Kampala, Uganda. Received 13 July 2010. *Corresponding author (s.tumwegamire@cgiar.org).

Abbreviations: AMOVA, analysis of molecular variance; DM, dry matter; *j*, Jaccard's similarity coefficient; OFSP, orange-fleshed sweetpotato; PCR, polymerase chain reaction; SPVD, sweetpotato virus disease; SSR, simple sequence repeat; UPGMA, unweighted pair group method analysis; WFSP, white- or cream-fleshed sweetpotato.

Sweetpotato [*Ipomoea batatas* (L.) Lam] is a hexaploid crop, usually clonally propagated by stem cuttings, but true seed production easily occurs by open pollination (Martin and Jones, 1986). It is of neotropical origin and crossed the Pacific via Polynesia before the discovery of the New World (Huaman et al., 1999; Zhang et al., 2000). In Africa it was introduced by explorers from Spain and Portugal during the 16th century (O'Brien, 1972; Zhang et al., 2000, 2004). To date sweetpotato has become a staple food crop in some countries of Eastern and Central Africa (Scott et al., 2000; Ewell, 2002), particularly in Uganda where daily per capita intake is about 240 g (FAO, 2007). This reliance in Sub-Sahara Africa and elsewhere underscores the importance of a crop as third in importance after potato (*Solanum tuberosum* L.) and cassava (*Manihot esculenta* Crantz) (FAO, 2007). In Sub-Sahara Africa, farmer varieties are still the backbone of sweetpotato production and breeding (Abidin, 2004; Grüneberg et al., 2009).

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The awareness of sweetpotato as a healthy food crop is increasing, especially the orange-fleshed sweetpotato (OFSP) that is very rich in provitamin A carotenoids (Woolfe, 1992). Vitamin A deficiency presents severe public health problems in Sub-Sahara Africa and Asia (Pfeiffer and McClafferty, 2007) but can be alleviated by consuming OFSP (Low et al., 2007). However, the germplasm in Sub-Sahara Africa is nearly exclusively white fleshed and characterized by high storage root dry matter (DM) contents (around 30%). Most of introduced OFSP germplasm from the Americas, which has low DM contents (approximately 22 to 26%), has collapsed (Grüneberg et al., 2009) due to extreme high pressure of sweetpotato virus disease (SPVD) in Sub-Sahara Africa, especially in East Africa (Gibson et al., 1998). Sweetpotato virus disease often causes yield losses of up to 90% in high virus pressure zones of Sub-Sahara Africa (Gibson et al., 1998; Karyeija et al., 2000). Recently, germplasm collection exercises have found about 25 and 10 OFSP farmer varieties in Uganda and Tanzania, respectively (CIP, 2005), with elevated DM contents (about 30% DM).

Molecular markers have been used for phylogenetics and germplasm evaluation to study the origin of sweetpotato and its dissemination into the Pacific and Asia (He et al., 1995; Hu et al., 2003; Prakash et al., 1996; Zhang et al., 2004). African germplasm has been studied by Gichuki et al. (2003), on basis of random amplified polymorphic DNA (RAPD) markers using 74 accessions from different regions of the world (including 17 East African accessions), and Gichuru et al. (2006), on basis of four simple sequence repeat (SSR) primers using 57 African accessions. A large genetic diversity in African germplasm was observed and the possibility was suggested that sweetpotato has an additional secondary diversity center around the East Africa region. This is evidenced by a large number of farmer varieties adapted to East Africa, which meet environmental challenges and consumer preference in Sub-Sahara Africa much better than introduced germplasm (Mwanga et al., 2007, 2009).

The main objectives of this study were to characterize genetic relationships among and between East African OFSP and white- or cream-fleshed sweetpotato (WFSP) farmer varieties and how these two phenotypic groups compare with non-African OFSP and WFSP accessions.

MATERIALS AND METHODS

Plant Material

A total of 92 sweetpotato accessions were used for the study (Table 1). Eighty-five cultivars were collections from East Africa. Seven accessions were of non-African origin, namely 'Jewel' and 'Resisto' from the United States, 'Xushu 18' and 'Yanshu 1' from China, 'Naveto' from Papua New Guinea, and 'Zapallo' and 'Jonathan' from Peru. Fifty-five accessions were collected from Uganda, 23 from Kenya, six from Tanzania, and one from Zambia. Twenty-six of the accessions were East African OFSP farmer varieties from Uganda (14), Kenya (seven), Tanzania (four), and Zambia (one). Moreover, two modern varieties developed in Uganda were used in this study, namely 'SPK004/1' ('NASPOT 7') and 'SPK004/6' ('NASPOT 9 0'). The accessions or clones, with a CIP Identification Code or with a CIP Identification Code in process (Table 1), are held in trust at CIP's gene bank as in vitro plantlets.

DNA Extraction

Total DNA was isolated from 200 mg of fresh leaf tissue using a modified protocol by Dellaporta et al., (1983). The leaves were obtained from an individual plant for each accession or clone. The leaf tissue was ground in 600 μL of Dellaporta buffer (containing β-mercapto ethanol) using a mortar and pestle. The contents were transferred to labeled tubes (1.5 mL) to which 42 μL of 20% sodium dodecyl sulfate (SDS) was added and mixed well. The mixture was incubated at 65°C for 10 min before adding 160 μL of 5 M potassium acetate and mixing the contents again. The new mixture was then incubated on ice for 10 min. The tubes were centrifuged at 15115 *g* (13000 rpm) for 10 min. About 650 μL of the supernatant were transferred into new 1.5 ml tubes. An equal amount of cold isopropanol was added to the supernatant and centrifuged at 15115 *g* (13000 rpm) for 10 min to precipitate the DNA as a pellet. Isopropanol was discarded and DNA pellet was washed by adding 500 μL of 70% ethanol and centrifuged at 15115 *g* (13000 rpm) for 5 min before discarding the ethanol. The DNA pellets were air dried for 35 min and suspended in about 200 μL of autoclaved Tris-ethylenediaminetetraacetic acid (EDTA) (TE) buffer (pH 8). Finally 2 μL of DNase-free RNase A were added to the DNA and the test tubes incubated at 37°C for 30 min. The DNA was preserved at –20°C until it was used.

Simple Sequence Repeat Amplification

DNA samples were quantified and a total of 3 ng of total genomic DNA from each of the samples was used for polymerase chain reactions (PCRs). Twenty-six pairs of SSR primers (Table 2) confirmed for sweetpotato DNA amplification (Buteler et al., 1999; Diaz and Grüneberg, 2008) were used for the reactions. A final volume of reaction mixture was 10 μL containing 25 mM $MgCl_2$, 10x buffer, 10 mM deoxyribonucleotide triphosphate (dNTPS), 1 μM M13 FORWARD 700/800, 1 μM forward primer, 1 μM reverse primer, 5 U μL^{-1} *Taq* polymerase, 10 ng μL^{-1} DNA, and double distilled H_2O was used for the PCR. The amplification conditions were set up thus: 94°C for 4 min and denaturation at 94°C for 1 min; annealing at between 56.0 and 62.0°C (depending on the annealing temperature of the primer); polymerization at 72°C for 1 min; step 2 (annealing at between 56.0 and 62.0°C (depending on the annealing temperature of the primer) repeated 30 times, and a final extension at 72°C for 7 min. Amplification products were analyzed and read on a computer automated Licor (4300) DNA Analyzer (Licor Biosciences, Lincoln, NE) for 26 pairs of SSR primers.

Simple Requence Repeat Data Scoring and Analysis

Genotypes were scored for the presence (1) or absence (0) of each fragment. Only those with medium or high intensity were taken into account. Fragments with the same mobility on the gel

Table 1. Description of clones used for the genetic diversity study in farmer varieties from East Africa and as checks.

Clone	Clone type†	Origin		Local Identification Code	Flesh color§	Skin color¶	CIP Identification Code#	Collecting institute††
		Country‡	District					
MSK1025 Bitambi	FV	UG	Masaka	UG01	C	B	i.p.	NaCRRI
SRT40 Mary	FV	UG	Soroti	UG02	C	C	No	NaCRRI
APA365 Anam Anam	FV	UG	Apac	UG03	C	C	i.p.	NaCRRI
MBR539 Kitekamaju	FV	UG	Mbarara	UG04	W	C	i.p.	NaCRRI
Jayalo	FV	KE	Siaya	KE22	Y	PR	i.p.	KARI
KBL172 Magabali	FV	UG	Kabale	UG05	C	C	i.p.	NaCRRI
KMI61	FV	UG	Kumi	UG06	O	C	i.p.	NaCRRI
Sudan	FV	UG	Luwero	UG07	LO	C	No	NaCRRI
MLE165 Namafumbiro	FV	UG	Mbale	UG08	C	C	No	NaCRRI
SRT30 Nyara	FV	UG	Soroti	UG09	LO	C	No	NaCRRI
Nyandere	FV	KE	Siaya	KE01	PY	PR	i.p.	KARI
Obuogo_1	FV	KE	Siaya	KE02	C	C	i.p.	KARI
Kunykubiongo	FV	KE	Siaya	KE03	C	PR	No	KARI
Marooko	FV	KE	Siaya	KE04	C	C	i.p.	KARI
Carrot Dar	FV	TZ	Ilara	TZ01	DO	C	i.p.	SRI Kibaha
KSR652 Mugumire	FV	UG	Kisoro	UG10	C	C	i.p.	NaCRRI
ARA 208 Ombivu	FV	UG	Arua	UG11	C	PR	i.p.	NaCRRI
ARA 214	FV	UG	Arua	UG12	C	C	i.p.	NaCRRI
MLE173 Kijovu	FV	UG	Mbale	UG13	C	PR	i.p.	NaCRRI
LIR 257 Otada	FV	UG	Lira	UG14	C	C	No	NaCRRI
MBR536 Karebe	FV	UG	Mbarara	UG15	C	C	i.p.	NaCRRI
KSR652 Kakoba	FV	UG	Kisoro	UG16	Y	PR	i.p.	NaCRRI
Bunduguza	FV	UG	NA‡‡	UG17	C	PR	i.p.	NaCRRI
KSR675 Nora II	FV	UG	Kisoro	UG18	C	C	i.p.	NaCRRI
KBL618 Kigabali	FV	UG	Kabale	UG19	C	C	i.p.	NaCRRI
MLE163 Kyebandula	FV	UG	Mbale	UG20	C	C	i.p.	NaCRRI
MLE184 Manafayareta	FV	UG	Mbale	UG21	W	PR	No	NaCRRI
Mayai	FV	TZ	Zanzibar	TZ02	DO	C	No	ARI Kizimbani
Carrot_C	FV	TZ	Ilara	TZ03	DO	C	i.p.	SRI Kibaha
ARA244 Shinyanga	FV	UG	Arua	UG22	LO	C	i.p.	NaCRRI
Tororo_3	FV	UG	Tororo	UG23	C	C	i.p.	NaCRRI
KBL632 Nyinakamanzi	FV	UG	Kabale	UG24	C	PR	No	NaCRRI
LIR296	FV	UG	Lira	UG25	LO	PR	i.p.	NaCRRI
SRT52	FV	UG	Soroti	UG26	O	C	No	NaCRRI
KMI83 Ikala2	FV	UG	Kumi	UG27	LO	C	i.p.	NaCRRI
SRT02 Araka white	FV	UG	Soroti	UG28	C	C	i.p.	NaCRRI
SRT01 Osapat	FV	UG	Soroti	UG29	Y	C	i.p.	NaCRRI
MBR521 Nkwasahansi	FV	UG	Mbarara	UG30	C	PR	i.p.	NaCRRI
SRT34 Abuket 2	FV	UG	Soroti	UG31	LO	C	i.p.	NaCRRI
SRT39 Rwanda	FV	UG	Soroti	UG32	O	C	No	NaCRRI
HM A490 Kawogo	FV	UG	Hoima	UG33	C	B	No	NaCRRI
HM A493 Tanzania	FV	UG	Moima	UG34	LO	C	i.p.	NaCRRI
PAL161	FV	UG	Palisa	UG35	LO	C	i.p.	NaCRRI
KML883 Silkempya	FV	UG	Kamuli	UG36	W	C	No	NaCRRI
Zambezi	FV	ZB	NA	ZBO1	DO	PR	i.p.	ZARI
KSR637 Kamabereikumi	FV	UG	Kisoro	UG37	C	C	i.p.	NaCRRI
SPK004/6	MV	UG	NaCRRI	UG38	O	PR	No	NaCRRI
SRT49 Sanyuzameza	FV	UG	Soroti	UG39	Y	PR	No	NaCRRI
Resisto	MV	USA	NA	NA	DO	B	440001	NA
Kala	FV	UG	Soroti	UG40	LO	C	i.p.	NaCRRI
SRT33 Abuket 1	FV	UG	Soroti	UG41	O	P	i.p.	NaCRRI
KBL627 Mukazi	FV	UG	Kabale	UG42	C	C	i.p.	NaCRRI
Ejumula	FV	UG	Katakwi	UG43	DO	C	No	NaCRRI
K-46	FV	KE	Siaya	KE05	O	PR	i.p.	KARI

(cont'd)

Table 1. Continued.

Clone	Clone type†	Origin		Local Identification Code	Flesh color§	Skin color¶	CIP Identification Code#	Collecting institute††
		Country‡	District					
Ukerewe	FV	TZ	Ukerewe	TZ04	Y	PR	i.p.	ARI Ukiruguru
KBL619 Kamamanzi	FV	UG	Kabale	UG44	C	P	i.p.	NaCRRI
K-37	FV	KE	Siaya	KE06	LO	C	i.p.	KARI
APA352 Oketodede	FV	UG	Apac	UG45	C	C	i.p.	NaCRRI
SPK 004/1	MV	UG	NaCRRI	UG46	LO	PR	i.p.	NaCRRI
Wagabolige	FV	UG	Busonga	UG47	C	C	No	NaCRRI
MBR600 Kisakyabikiramaria	FV	UG	Mbarara	UG48	C	C	No	NaCRRI
IGA963 Nyongerabalenzi	FV	UG	Iganga	UG49	C	C	No	NaCRRI
Plot143	FV	KE	Kakamega	KE07	C	NA.	i.p.	KARI
PAL153 Abukoki	FV	UG	Palisa	UG50	C	C	i.p.	NaCRRI
KMI56 Opira	FV	UG	Kumi	UG51	C	B	No	NaCRRI
Cheglina	FV	KE	Homabay	KE08	C	C	i.p.	KARI
K-118	FV	KE	Siaya	KE09	LO	C	i.p.	KARI
K-52	FV	KE	Kakamega	KE10	C	NA	No	KARI
Oguroiwe	FV	KE	Siaya	KE11	C	C	i.p.	KARI
Nyatonge	FV	KE	Siaya	KE12	C	C	i.p.	KARI
Polista	FV	KE	Mwanza	KE13	C	PR	i.p.	KARI
K-566632	MV	KE	KARI	KE14	O	PR	i.p.	KARI
KMI81 Ikala	FV	UG	Kumi	UG52	LO	C	i.p.	NaCRRI
KRE733 Kitambi	FV	UG	Kabalore	UG53	C	PR	i.p.	NaCRRI
Pipi	FV	TZ	Zanzibar	TZ05	LO	C	i.p.	ARI Kizimbani
Kemb10	FV	KE	KARI	KE15	C	C	i.p.	KARI
MSK1047 Bwanjure	FV	UG	Masaka	UG54	W	PR	i.p.	NaCRRI
K-135	FV	KE	Migori	KE16	O	C	i.p.	KARI
Wera	FV	KE	NA	KE17	Y	C	i.p.	KARI
K-134	FV	KE	Migori	KE18	LO	PR	No	KARI
SPK004	FV	KE	Kakamega	KE19	LO	P	441768	KARI
Nyaguta	FV	KE	Siaya	KE20	C	P	i.p.	KARI
Budagala	FV	KE	Mwanza	KE21	C	NA	No	KARI
MBR580 Nylon	FV	UG	Mbarara	UG55	C	C	No	NaCRRI
Jewel	MV	USA	NA	NA	DO	PR	440031	NA
Xushu-18	MV	CH	NA	NA	C	PR	440025	NA
Yanshu-1	MV	CH	NA	NA	C	PR	440024	NA
Naveto	FV	PNG	NA	NA	C	P	440131	NA
Tanzania	FV	TZ	NA	TZ06	Y	C	440166	NA
SPK004 (CIP)	FV	KE	NA	NA	LO	P	No	NA
Zapallo	MV	PE	NA	NA	O	C	420027	NA
Jonathan	FV	PE	NA	NA	O	C	420014	NA

†FV, farmer variety; MV, modern variety.

‡UG, Uganda; KE, Kenya; TZ, Tanzania; ZB, Zambia; USA, the United States; CH, China; PGN, Papua New Guinea; PE, Peru.

§C, cream; W, white; Y, yellow; O, orange; LO, light orange; PY, pale yellow; DO, deep orange.

¶B, brown; C, cream PR, purple red; P, pink.

#i.p., designation of CIP code in process; No, no acquisition from CIP.

††NaCRRI, National Crops Resources Research Institute (Namulonge, Uganda); KARI, Kenya Agricultural Research Institute (Nairobi, Kenya); SRI Kibaha, Sugarcane Research Institute Kibaha (Kibaha, Dar es Salaam, Tanzania); ARI Kizimbani, Agricultural Research Institute Kizimbani (Kizimbani, Zanzibar, Tanzania); ZARI, Zambia Agricultural Research Institute (Mansa, Zambia); ARI Ukiruguru, Agricultural Research Institute Ukiruguru (Ukiruguru, Mwanza, Tanzania).

‡‡NA, no available information.

but with different intensities were not distinguished from each other when genotypes were being compared. Using NTSYS-pc software version 2.2 (Rohlf, 1993), similarity matrices were constructed from the binary data with Jacard's coefficients (Jaccard, 1908). Jaccard's similarity = $Nab/(Na + Nb)$, in which Nab represents the number of fragments shared by accessions a and b, Na the amplified fragments in sample a, and Nb the amplified fragments in sample b. A dendogram was constructed from the genetic similarity matrix by weighted paired group method analysis (UPGMA) (Sneath and Sokal, 1973). Analysis of molecular variance (AMOVA) was performed using Arlequin 3.1 version computer software (Excoffier et al., 2006) to quantify the genetic variation and relationship levels between and within East African and non-African germplasm on one hand and OFSP and WFSP on the other. For the two levels of AMOVA, four populations, namely East African OFSP germplasm, East African WFSP germplasm, non-African OFSP germplasm, and non-African WFSP germplasm, were used. A

Table 2. Description of simple sequence repeat (SSR) markers used to characterize sweetpotato genotypes by currently used names, motifs, forward and reverse primers, and annealing temperature.

Name	Forward primers	Reverse primers	Motif	Temperature (°C)	Reference
IB242	5-gcggaacggacgagaaaa-3	5-atggcagagtgaaaatggaaca-3	(ct)3ca(ct)11	58	Buteler et al., 1999
IB297	gcaatttcacacacaaacacg	cccttcttccaccactttca	(ct)13	58	Buteler et al., 1999
IB316	caaacgcacaacgctgtc	cgcgtcccgcttatttaac	(ct)3c(ct)8	58	Buteler et al., 1999
IB324	tttggcatgggcctgtatt	gttcttctgcactgcctgattc	–	56	Tseng et al., 2002
IBCIP-1	cccacccttcattccattact	gaacaacaacaaaaggtagagcag	(acc)7a	63	Yañez, 2002
IB-R03	gtagagttgaagagcgagca	ccatagacccattgatgaag	(gcg)5	58	Benavides (unp.)†
IB-S07	gcttgcttgtggttcgat	caagtgaagtgatggcgttt	(tgtc)7	60	Benavides (unp.)
IB-S10	ctacgatctctcggtgacg	cagcttctccactccctac	(ct)12	60	Benavides (unp.)
IB-S11	ccctgcgaaatcgaaatct	ggacttcctctgccttgttg	(ttc)10	58	Benavides (unp.)
IB-R12	gatcgaggagaagctccaca	gccggcaaattaagtccatc	(cag)5a	60	Benavides (unp.)
IB-R13	gtaccgagccagacaggatg	cctttgggattggaacacac	(ttc)6	58	Benavides (unp.)
IB-R16	gacttccttggtgtagttgc	agggttaagcgggagact	(gata)4	60	Benavides (unp.)
IB-S17	cagaagagtacgttgctcag	gcacagttctccatcctt	(gga)4	58	Benavides (unp.)
1B-S18	ctgaacccgacagcacaag	gggaagtgaccggacaaga	(tagc)4	58	Benavides (unp.)
IB-R20	cttcactctgctcgccatta	gtacttggacgggaggatga	(ggc)5	54	Benavides (unp.)
IB-R21	gacagtctccttctcccata	ctgaagctcgtcgtcaac	(gac)5	58	Benavides (unp.)
IBC12	tctgagcttctcaaacatgaaa	tgagaattcctggcaaccat	(ttc)6	56	Solis et al. (unp.)‡
J175	atctatgaaatccatcactctcg	actcaattgtaagccaaccctc	(aatc)4	58	Solis et al. (unp.)
J10A	tcaaccactttcattcactcc	gtaattccaccttgcgaagc	(aag)6	58	Solis et al. (unp.)
J67	cacccatttgatcatctcaacc	ggctctgagcttccattgttag	(gaa)5	58	Solis et al. (unp.)
J116A	tcttttgcatcaaagaaatcca	cctcagcttctgggaaacag	(cct)6	58	Solis et al. (unp.)
JB1809	cttctcttgctcgcctgttc	gatagtcggaggcatctcca	(cct)6(ccg)6	60	Solis et al. (unp.)
IBJ522a	acccgcatagacactcacct	tgaccgaagtgtatctagtgg	(cac)6–7	57	Solis et al. (unp.)
IBC5	ccacaaaaatcccagtcaaca	agtggtcgtcgacgtaggtt	(aag)8	62	Solis et al. (unp.)
IBJ544b	agcagttgaggaaagcaagg	caggatttacagccccagaa	(tct)5	61–62	Solis et al. (unp.)
IB-S01	tcctccaccagctctgattc	ccattgcagagccatacttg	(aga)10	56	Benavides (unp.)

†unp., unpublished data; developed from 2002 to 2003 at CIP.

‡unp., unpublished data; developed from 2005 to 2006 at CIP.

matrix of genetic distances between different populations of germplasm was also generated by AMOVA.

RESULTS

A total of 158 polymorphic bands were scored for the 26 SSR primers and used to differentiate 85 local plus seven introduced sweetpotato cultivars (Table 3). All markers were polymorphic, and the number of bands or alleles ranged from 2 to 11 per SSR marker loci, with an average of 6.1 alleles. The PCR products ranged between 110 bp and 395 bp in size.

The frequencies of pair-wise similarity coefficients for SSR analysis of 92 sweetpotato accessions is shown in Fig. 1. The SSR based Jaccard's similarity coefficients ranged between 0.30 and 1.00 with a mean of 0.54. Most similarity coefficients were observed between 0.50 and 0.59, accounting for 54.0% of the total frequency of pair-wise similarity coefficients. Additional 25.0 and 17.0% of the coefficients, respectively, ranged from 0.40 to 0.49 and from 0.60 to 0.69.

The genetic variability and relationships among the studied sweetpotato accessions are presented in a dendogram (Fig. 2). A number of accessions with a similarity coefficient of 1.00 were identified. These include (i) UG15 and UG17, (ii) UG04 and UG23, and (iii) KE07 and KE01 among the WFSP farmer varieties and (i) UG31, UG07, and UG12 and (ii) Zapallo and UG32 among the OFSP farmer varieties. Our results also identified some accessions (mostly East African) that clustered closely at the early fusion steps of the cluster analysis. These include KE17 and KE09 (Jaccard's similarity coefficient [j] = 0.98), KE15 and UG40 (j = 0.98), UG52 and UG27 (j = 0.97), KE12 and UG50 (j = 0.98), UG18 and UG02 (j = 0.97), UG48 and UG55 (j = 0.95), UG54 and SPK004 (CIP) (j = 0.98), UG05 and UG19 (j = 0.82), TZ04 and KE06 (j = 0.97), TZ02 and TZ03 (j = 0.97), and KE14 and Jewel (j = 0.96). This result is interesting in that, unlike the duplicate accessions, some of the closely clustered accessions differ in countries of origin (e.g., KE12 and UG50) and root flesh color (e.g., TZ04 and KE06), which may suggest common ancestry.

The majority of East African farmer varieties were clustered at final fusion steps with the non-African germplasm. At about 0.52 similarity coefficient, most East African farmer varieties, except UG47, ZB01, KE22, and KE14, formed a main cluster (A), which is clearly separate from other clusters B, C, and D that comprise mostly non-African accessions. The exceptional accessions, namely ZB01 and KE14, closely clustered with OFSP varieties Jewel and Resisto from the United States, while KE22 closely clustered with the modern Chinese varieties Xushu

Table 3. Number of polymorphic alleles and their bp range generated by simple sequence repeat (SSR) markers in farmer varieties from East Africa and check.

Name	No. alleles	bp range
IB S17	8	182–204
J116a	9	207–251
IB 242	6	136–155
IB-S11	9	254–305
IB-S01	7	233–268
IB-R13	9	225–298
IB-R12	5	356–395
IBCIP-1	4	155–167
IB-S07	4	193–211
IB-S10	11	307–337
J67	7	191–217
IB-S18	2	296–298
J10A	8	191–225
J175	5	133–149
IB316	5	151–167
IBC5	9	108–130
IBJ544b	7	191–214
IBJ522a	5	235–305
IB-R03	5	302–312
IB-R16	5	215–243
IB324	4	136–152
IB-R20	3	206–223
IB-R21	3	181–207
JB1809	5	144–155
IBC12	9	110–134
IB297	4	150–182

18 and Yanshu 1. UG47 closely clustered with neither East African nor non-African accessions.

In spite of a distinct cluster (A) by East African sweetpotato farmer varieties, at about 0.55 similarity coefficient, clear subclusters A1 through A5 were identified. The subclusters A1 and A2 contained the well-known farmer varieties TZ06 and KE19, respectively. However, none of the subclusters contained accessions originating from one country or with similar root flesh color.

The AMOVA was used to distinguish between the East African sweetpotato germplasm and non-African germplasm (Table 4). A second analysis examined differences between OFSP germplasm and WFSP germplasm (Table 5). The difference between East African and non-African accessions was significant and accounted for 11.61% of the molecular variance. Contrastingly, the difference between OFSP and WFSP accessions was not significant and was explained by –14.16% of the molecular variance. In both scenarios, the variation due to individual accessions in different populations was significant ($p > 0.001$) and accounted for the majority, 82.9 and 91.9%, respectively, of the observed molecular variance.

The genetic distances matrix is presented in Table 6. A significantly short genetic distance (0.045) was observed between OFSP and WFSP East African farmer varieties. In contrast, a significantly ($p < 0.05$) large genetic distance (0.289) was observed between OFSP and WFSP non-African accessions. Furthermore, both OFSP (0.195 and 0.231) and WFSP (0.212 and 0.193) East African farmer varieties showed significant ($p < 0.01$) long genetic distances in comparison to OFSP and WFSP non-African accessions, respectively.

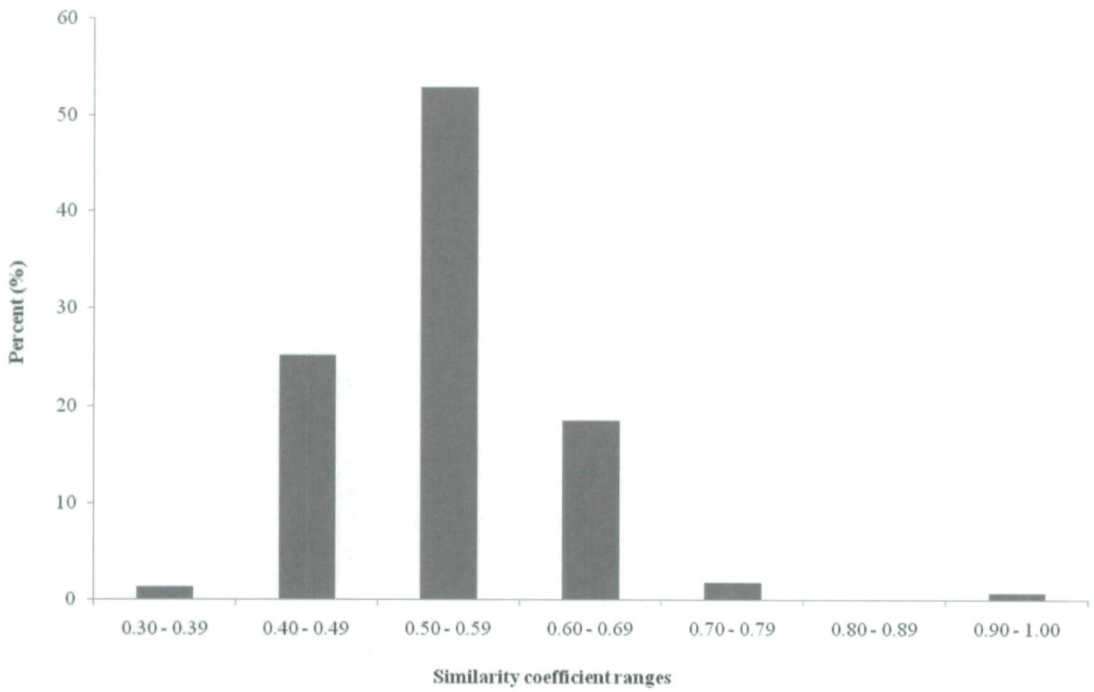

Figure 1. Frequency distribution of pairwise simple sequence repeat (SSR) similarity coefficients among 85 East African farmer varieties and seven non-African varieties.

DISCUSSION

With a total of 158 loci, all polymorphic and ranging between 2 and 11 loci per primer (Table 3), the present study showed high levels of polymorphism with the SSR markers. This result confirms the extraordinary discriminatory capacity of the SSR markers reported in previous studies (Gichuru et al., 2006). Buteler et al. (1999) also obtained high polymorphism, ranging between 3 and 10 alleles per SSR in sweetpotato. Yada et al. (2010) obtained two to six alleles per primer. However, Hwang et al. (2002) obtained a lower level of polymorphism, ranging between one and four alleles per SSR locus using mostly different SSR primers and annealing temperatures. Hwang et al. (2002) attributed high level of polymorphism to large genome size and heterozygosity of sweetpotato. It should be noted that genetic diversity due to heterozygosity in sweetpotato is driven by both the mating system (outcrossing in combination with self incompatibility) and the high ploidy level of sweetpotato (autohexaploid)

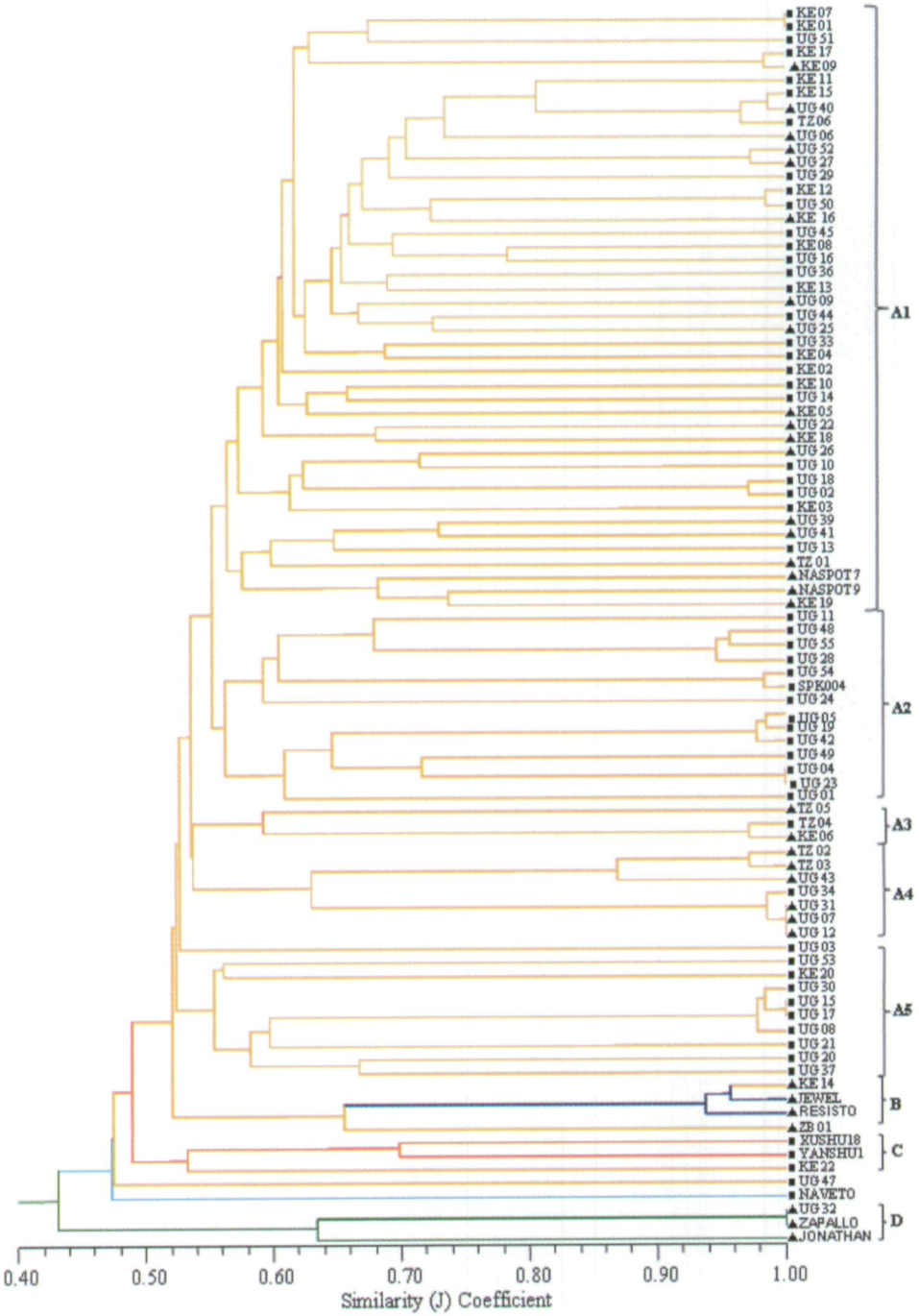

Figure 2. Dendrogam of the unweighted pair group method analysis (UPGMA) cluster analysis on the basis of Jaccard's simple sequence repeat (SSR) based genetic similarities among 85 East African farmer varieties and seven varieties of non-African origin used as check clones (origin of clones: orange = Africa, green lines = South American germplasm, light blue = Pacific, deep blue = North America, and red = China; origin of East Africa farmer varieties: UG = Ugandan, cultivars, KE = Kenya, TZ = Tanzania, ZB = Zambia; ■ = white-fleshed clones, ▲ = orange-fleshed clones).

Table 4. Analysis of molecular variance (AMOVA) of 92 sweetpotato accessions grouped into East African versus non-African germplasm.

Source of variation	df	Sum of squares	Variance components	Percentage variation
Among groups†	1	60.34	2.60***	11.61
Among populations‡ within groups	2	85.44	1.22***	5.44
Within populations	85	1,551.31	18.56***	82.95
Total	88	1,697.09	22.38	

***Significant at the 0.001 probability level.

†Groups are East African germplasm and non-African germplasm.

‡Populations are East African orange-fleshed sweetpotato (OFSP) cultivars, East African white- or cream-fleshed sweetpotato (WFSP) accessions, non-African OFSP accessions, and non-African WFSP accessions.

Table 5. Analysis of molecular variance (AMOVA) of 92 sweetpotato accessions grouped into orange-fleshed sweetpotato (OFSP) versus white- or cream-fleshed sweetpotato (WFSP) germplasm.

Source of variation	df	Sum of squares	Variance components	Percentage variation
Among groups†	1	47.571	–2.85 NS‡	–14.16
Among populations§ within groups	2	79.724	4.41***	21.91
Within populations	85	1551.31	18.56***	92.25
Total	88	1697.09	20.12	

*** Significant at the p = 0.001 level.

†Groups are OFSP germplasm and WFSP germplasm.

‡NS, none significant.

§Populations are East African OFSP cultivars, East African WFSP accessions, non-African OFSP accessions, and non-African WFSP accessions.

Table 6. The average genetic distances among sweetpotato accessions.

	East African OFSP† germplasm	East African WFSP‡ germplasm	Non-African OFSP germplasm
African WFSP germplasm	0.045***		
Non-African OFSP germplasm	0.195***	0.212***	
Non-African WFSP germplasm	0.231***	0.193***	0.289*

*Significant at $p \leq 0.05$ level.

***Significant at $p \leq 0.001$ level.

†OFSP, orange-fleshed sweetpotato.

‡WFSP, white- or cream-fleshed sweetpotato.

(Zhang et al., 2000). This heterozygosity and genetic diversity can be easily maintained by vegetative propagation (Grüneberg et al., 2009). Our analysis did not estimate heterozygosity; hence, we possibly never fully detected variability within accessions assayed.

The mean genetic similarity coefficient of 0.54 obtained in our study is low, suggesting large diversity among the studied accessions. Yada et al. (2010) obtained a nearly equal coefficient (0.57) while assessing the genetic diversity of Ugandan core germplasm. Comparably, Zhang et al. (2000) reported a low similarity coefficient (0.588) among sweetpotato accessions from South America. It should be noted that South America is known to be a center of diversity and our observed similarity coefficient in predominately African material is only slightly lower. Higher mean similarity coefficient value of 0.64 was reported by Hwang et al. (2002) and concluded a low diversity of the studied germplasm. In our study, about 25% of the similarity coefficients were observed between 0.40 and 0.49 (Fig. 1). This is likely accounted for by the presence of non-African accessions in the studied germplasm.

All cultivars with a similarity coefficient of 1.00 are considered duplicate cultivars by the present study. These include (i) UG15 and UG17, (ii) UG04 and UG23, and (iii) KE07 and KE01 among the WFSP farmer varieties and (i) UG31, UG07, and UG12 and (ii) Zapallo and UG32 among the OFSP farmer varieties. All duplicates were of either similar flesh color or country of origin, which improves confidence in our results. The presence of duplicates among the studied accessions is possibly due to farmers' practice of adopting different variety names in different locations (Abidin, 2004). It should be noted that for the past two decades, repeated introductions of foreign germplasm into East Africa have been made as part of CIP's efforts to promote OFSP to combat vitamin A deficiency in the region. Although most of the introduced germplasm have failed due to susceptibility to SPVD and lower acceptability a few of these might have been adopted on a small scale. The cultivar UG32 is identical in its genetic profile to Zapallo. It is probable that Zapallo was locally named Rwanda by farmers in Soroti in Uganda and collected and named UG32 as a putative local African OFSP clone.

These results also identified some closely clustered accessions suggesting close relationship between the accessions. These include KE17 and KE09, KE15 and UG40, UG52 and UG27, KE12 and UG50, UG18 and UG02, UG48 and UG55, UG54 and SPK004 (CIP), UG05 and UG19, TZ04 and KE06, TZ02 and TZ03, and KE14 and Jewel. The presence of closely related accessions originating

from different East African countries is possibly due to free exchange of germplasm between the countries. Equally, the presence of closely related cultivars that differ in flesh color (orange and non-orange) suggest a possibility that OFSP cultivars have evolved from sister WFSP accessions as opposed to only introduced OFSP accessions. However, one exception, in which KE14 and Jewel are closely related, suggests a possibility that some of the OFSP cultivars are interbreeds with introduced germplasm. It should be mentioned that the recently established regional breeding programs are working nearly exclusively with polycross seed nurseries, often in a farmer participatory approach, and orange-fleshed storage root color is one of the breeding objectives. Jewel and Resisto have been heavily used as OFSP parents in East African breeding programs.

In this study, East African farmer varieties except UG47, KE14, KE22, and ZB01 cluster independently from non-African accessions at a similarity coefficient value of 0.52 (Fig. 2), suggesting a clear distant relationship between the two germplasm pools. Our genetic data reinforces our findings that UG32 is actually Zapallo and KE14 is related to Jewel. These were collected in error as farmer varieties in Uganda and Kenya, respectively. Gichuki et al. (2003) made similar observations while comparing white-fleshed varieties collected from East Africa with germplasm from other geographical regions. Nevertheless, the positions of UG47 and KE22 within the non-African germplasm are difficult to explain. Abdelhameed et al. (2007) using amplified fragment length polymorphism (AFLP) analysis clustered UG47 with Tanzanian accessions. The most striking result of our study is that all East African OFSP farmer varieties except ZB01 and KE14 clustered neither with accessions from other regions of the world nor independently from other East African accessions.

The subclusters A1 through A5 identified within the main East African A cluster suggested high genetic diversity within the population. Moreover it is interesting to observe that like the closely clustered accessions, the subclusters are neither country nor flesh color specific. Whereas absence of non-country-specific subclustering of East African sweetpotato cultivars has been reported before (Gichuru et al., 2006) our study is the first to report absence of non-flesh-color specific subclusters within the East African sweetpotato germplasm. This result further enhances the suggestion that East Africa OFSP farmer varieties have evolved from sister WFSP accessions as opposed to being introduced OFSP accessions. This might be important information for local breeding programs and merits the application of molecular markers to characterize local OFSPs before they are used in a breeding program. It has been noted (Gichuki et al., 2003) that East African farmer varieties are unique in several important characteristics such as high dry matter content, high resistance to viruses, and vigorous foliage growth while low in β-carotene and earliness to harvest.

The AMOVA results (Table 4) showed that East African sweetpotato farmer varieties are distinct from non-African sweetpotato accessions. Previous studies have suggested this (Gichuki et al., 2003; Abdelhameed et al., 2007), but had few if any OFSP farmer varieties in their data set to demonstrate this distinction. Abdelhameed et al. (2007) included only Carrot_C (coded TZ03 in this study) while Gichuki et al. (2003) and Gichuru et al. (2006) had none. Furthermore, our AMOVA results (Table 5) found no genetic difference between the OFSP and WFSP accessions. No previous work has made this comparison. As expected, between-individual variations were most significant and accounted for the majority of the molecular variance. Similar findings have been reported by several previous studies on genetic diversity of sweetpotato germplasm (Zhang et al., 2000, 2001; Gichuki et al., 2003; Gichuru et al., 2006; and Abdelhameed et al., 2007). Moreover, it is a clear indication that breeders can form in breeding programs different populations with significant levels of genetic difference, which is a prerequisite to exploit heterosis and improvement of populations.

The genetic distances (Table 6) are consistent with population differences identified by the AMOVA. The significant short genetic distance observed between East African OFSP and WFSP farmer varieties confirm their close genetic relatedness. Also the significant distances between either East African OFSP or East African WFSP and non-African OFSP or non-African WFSP accessions confirm their genetic distinctiveness. The larger and significant genetic distance between non-African OFSP accessions and non-African WFSP accessions is a likely a function of origin. Orange-fleshed sweetpotatos are mostly from the Americas and WFSP mostly from China.

In conclusion, it is very clear from this study that East African farmer varieties, irrespective of flesh color, are distinct from non-African germplasm. It is further clear that majority of the East African OFSP farmer varieties are closely related with their sister East African WFSP farmer varieties. However, there are a few exceptions of OFSP accessions that appeared to have non-African lineage and might be introduced accessions or improved clones related to the introduced accessions. Our results underscore the importance of including East African OFSP farmer varieties in OFSP breeding program targeting East Africa. Storage root quality attributes of most of the accessions have been described by Tumwegamire et al. (2011).

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