Characterization of Ugandan Sweetpotato Germplasm Using Fluorescent Labeled Simple Sequence Repeat Markers

Benard Yada and Phinehas Tukamuhabwa
Department of Crop Science, Makerere University, P.O. Box 7062, Kampala, Uganda

Bramwell Wanjala
Kenya Agricultural Research Institute, Biotechnology Centre, P.O. Box 14733-00800, Westlands, Nairobi, Kenya

Dong-Jin Kim
International Institute of Tropical Agriculture (IITA), P.O. Box 30709, Nairobi 00100, Kenya

Robert A. Skilton
Biosciences eastern and central Africa (BecA), International Livestock Research Institute (ILRI), P.O. Box 30709, Nairobi 00100, Kenya

Agnes Alajo and Robert O.M. Mwanga 1,2
National Agricultural Research Organization (NARO), National Crops Resources Research Institute (NaCRRI), Namulonge, P.O. Box 7084, Kampala, Uganda

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Abstract. The genetic relationships among 192 superior, high–yielding, and disease-resistant sweetpotato [Ipomoea batatas (L.) Lam] accessions from the Ugandan germplasm collection were analyzed using 10 fluorescent labeled simple sequence repeat (SSR) markers. Relatedness among the genotypes was estimated using the Nei and Li genetic distance coefficient, cluster analysis and principle component analysis methods of NTSYS-pc software. The polymorphic information content of the SSR markers used in this study ranged from 0.23 to 0.76 for loci IB-S07 and IB-R12, respectively, with a mean value of 0.62. The number of polymorphic alleles detected per locus ranged from two to six with a mean of four, a confirmation of the effectiveness of microsatellite detection on this automated ABI 3730 sequencer. The mean pairwise genetic distance among the 192 genotypes was 0.57, an indication of moderately high genetic diversity. Cluster analysis divided the accessions into four major groups with no relationship to the district of origin. Two sets of duplicates were identified through SSR genotyping in this study. Up to 190 genotypes was 0.57, an indication of moderately high genetic diversity. Cluster analysis divided the accessions into four major groups with no relationship to the district of origin. Two sets of duplicates were identified through SSR genotyping in this study. Up to 190 genotypes was 0.57, an indication of moderately high genetic diversity. Cluster analysis divided the accessions into four major groups with no relationship to the district of origin. Two sets of duplicates were identified through SSR genotyping in this study. Up to 190 genotypes was 0.57, an indication of moderately high genetic diversity. Cluster analysis divided the accessions into four major groups with no relationship to the district of origin. Two sets of duplicates were identified through SSR genotyping in this study. Up to 190 genotypes was 0.57, an indication of moderately high genetic diversity. Cluster analysis divided the accessions into four major groups with no relationship to the district of origin. Two sets of duplicates were identified through SSR genotyping in this study. Up to 190 genotypes was 0.57, an indication of moderately high genetic diversity. Cluster analysis divided the accessions into four major groups with no relationship to the district of origin. Two sets of duplicates were identified through SSR genotyping in this study. Up to 190 genotypes.
material from the screen house was ground to powder in a prechilled mortar in liquid nitrogen and transferred to 1.5-mL Eppendorf tubes. Thereafter, 700 μL of fresh extraction buffer (2% CTAB buffer and 2% β-mercaptoethanol) was added to the powder, vortexed, and the homogenate was incubated at 4°C for 30 min. The tubes were spun at 14,000 rpm. The aqueous phases were removed and carefully transferred into new labeled Eppendorf tubes. Each tube was added 400 to 500 μL of isopropanol. The tubes were inverted several times and allowed to sit at 4°C for 30 min. The tubes were spun at 14,000 rpm for 20 min, and the supernatants in each tube were poured off and the tubes were air-dried. The pellets were washed in 1.0 mL of 90% ethanol and centrifuged at 14,000 rpm for 20 min, and the pellets were dried overnight. The DNA samples were dissolved in 150 μL of 1.0 mM MgCl2, and a tracking and stabilization dye (Bioneer, Daejeon, North Korea). To realize UTOPO RTaq DNA polymerase, 250 ng of DNA sample, 2.5 μL of primers, 5.0 μL of dNTPs, 10 mM Tris-HCl (pH 9.0), 30 mM KCl, 1.5 mM MgCl2, and NED (yellow) [International Patent (CIP), Lima, Peru] (Table 2) were used in this study. The PCR was performed in a total reaction volume of 10 μL using the Accupower PCR premix tube containing lypsyphosphorylated 1 U top Taq DNA polymerase, 250 μM dNTPs, 10 mM Tris-HCl (pH 9.0), 30 mM KCl, 1.5 mM MgCl2, and a tracking and stabilizing dye (Bioneer, Daejeon, North Korea). To the premix was added 2.5 μL of 1.0 pmol of primers, 5.0 μL of 1.0 ng DNA template, and 2.5 μL of double-distilled water. The PCR program consisted of an initial denaturation at 94°C for 4 min followed by 35 cycles of 94°C for 1 min, 1 min annealing at 58°C, and 72°C for 1 min. This was followed by

| No. | Code   | District | No. | Code   | District | No. | Code   | District |
|-----|--------|----------|-----|--------|----------|-----|--------|----------|
| 1   | MLE191 | Mbale    | 49  | RAK791 | Rakai    | 97  | MSK1020| Masaka   |
| 2   | PAL102 | Pallisa  | 50  | RAK829 | Rakai    | 98  | MSK1040| Masaka   |
| 3   | LIR279 | Lira     | 51  | RAK831 | Rakai    | 99  | MPG1118| Mpiji    |
| 4   | MLE183 | Mbale    | 52  | RAK835 | Rakai    | 100 | MKN1173| Mukono   |
| 5   | PAL133 | Pallisa  | 53  | RAK1303| Pallisa  | 101 | MKN1200| Mukono   |
| 6   | PAL148 | Pallisa  | 54  | KBL648 | Kabale   | 102 | MKN1180| Mukono   |
| 7   | PAL56  | Pallisa  | 55  | KML932 | Kamuli   | 103 | MPG1151| Mpiji    |
| 8   | PAL134 | Pallisa  | 56  | KML940 | Kamuli   | 104 | MKN1186| Mukono   |
| 9   | SRT45  | Soroti   | 57  | KML924 | Kamuli   | 105 | LUI2128| Luweero  |
| 10  | SRT1   | Soroti   | 58  | RAK846 | Rakai    | 106 | MKN1210| Mukono   |
| 11  | BSHT76 | Bushenyi | 59  | KML915 | Kamuli   | 107 | MKN1212| Mukono   |
| 12  | MLE171 | Mbale    | 60  | APA354 | Apac     | 108 | MKN1224| Mukono   |
| 13  | PAL115 | Pallisa  | 61  | MBR535 | Mbarara  | 109 | LUI2125| Luweero  |
| 14  | KM183  | Kumi     | 62  | HMA490 | Homia    | 110 | LUI2128| Luweero  |
| 15  | KM176  | Kumi     | 63  | HMA496 | Homia    | 111 | LUI2128| Luweero  |
| 16  | BSHT40 | Bushenyi | 64  | MBR530 | Mbarara  | 112 | LUI2125| Luweero  |
| 17  | BSHT48 | Bushenyi | 65  | KSR659 | Kisoro   | 113 | LUI3102| Luweero  |
| 18  | LIR276 | Lira     | 66  | KSR650 | Kamuli   | 114 | KBL650 | Kabale   |
| 19  | SRT24  | Soroti   | 67  | LUI1300| Luweero  | 115 | KSR663 | Kisoro   |
| 20  | SRT47  | Soroti   | 68  | LUI1257| Luweero  | 116 | KRE713 | Kabarole |
| 21  | SRT32  | Soroti   | 69  | LUI1230| Luweero  | 117 | KRE724 | Kabarole |
| 22  | ARAR22 | Arua     | 70  | MKN1188| Mukono   | 118 | KRE734 | Kabarole |
| 23  | ARAR17 | Arua     | 71  | MKP1120| Mpiji    | 119 | BSHT77 | Bushenyi |
| 24  | ARAR28 | Arua     | 72  | KML915 | Kamuli   | 120 | KML912 | Mukono   |
| 25  | ARAR29 | Arua     | 73  | APA354 | Apac     | 121 | KML924 | Kumi    |
| 26  | ARAR30 | Arua     | 74  | MBR535 | Mbarara  | 122 | KML915 | Kamuli   |
| 27  | ARAR31 | Arua     | 75  | KML940 | Kamuli   | 123 | KML877 | Kamuli   |
| 28  | ARAR32 | Arua     | 76  | IGA972 | Iganga   | 124 | KML865 | Kamuli   |
| 29  | ARAR33 | Arua     | 77  | IGA995 | Iganga   | 125 | KML823 | Kamuli   |
| 30  | ARAR34 | Arua     | 78  | KML915 | Kamuli   | 126 | KML850 | Kamuli   |
| 31  | ARAR35 | Arua     | 79  | MBR600 | Mbarara  | 127 | KML850 | Kamuli   |
| 32  | ARAR36 | Arua     | 80  | MBR531 | Mbarara  | 128 | KML850 | Kamuli   |
| 33  | ARAR37 | Arua     | 81  | MBR531 | Mbarara  | 129 | KML850 | Kamuli   |
| 34  | KML900 | Kamuli   | 82  | LUI1237| Luweero  | 130 | MDS432 | Mpiji    |
| 35  | KML882 | Kamuli   | 83  | MKP1168| Mukono   | 131 | MDS432 | Mpiji    |
| 36  | KML876 | Kamuli   | 84  | MBR605 | Mbarara  | 132 | MDS432 | Mpiji    |
| 37  | KML882 | Kamuli   | 85  | IGA975 | Iganga   | 133 | MBR605 | Mbarara  |
| 38  | KML876 | Kamuli   | 86  | KML956 | Kamuli   | 134 | KML850 | Kamuli   |
| 39  | KML878 | Kamuli   | 87  | KML941 | Kamuli   | 135 | KML850 | Kamuli   |
| 40  | KML878 | Kamuli   | 88  | IGA978 | Iganga   | 136 | KML850 | Kamuli   |
| 41  | KML878 | Kamuli   | 89  | KML961 | Kamuli   | 137 | KML850 | Kamuli   |
| 42  | KML878 | Kamuli   | 90  | KML942 | Kamuli   | 138 | PAL159 | Palisa   |
| 43  | KML878 | Kamuli   | 91  | IGA963 | Iganga   | 139 | PAL150 | Palisa   |
| 44  | KML878 | Kamuli   | 92  | IGA998 | Iganga   | 140 | PAL151 | Palisa   |
| 45  | KML878 | Kamuli   | 93  | MPG1112| Mpiji    | 141 | PAL98  | Palisa   |
| 46  | KML878 | Kamuli   | 94  | HMA490 | Homia    | 142 | SRT234 | Soroti   |
| 47  | KML878 | Kamuli   | 95  | MPG1199| Mpiji    | 143 | KMI86  | Kumi     |
| 48  | KSR676 | Kisoro   | 96  | MPG1117| Mpiji    | 144 | SRT35  | Soroti   |

Table 1. List of 192 superior sweetpotato landrace accessions selected and genotyped.
Polishing the polymerase chain reaction products and simple sequence repeat fragment analysis. PCR products were pooled by combining 5.0 µL of each amplified product diluted with 2% TBE agarose gel and the relative fluorescence unit on the ABI 3730 sequencer. The capillary electrophoresis runs were post-PCR-coloured in three sets on the basis of dye color and fragment size (Table 2). A standard cocktail mix for fragment analysis was prepared by thoroughly mixing 12.0 µL of 500 LIZ size standard and 1000 µL Hi-Di Formamide. Then 1.0 µL of each pooled PCR product was mixed with 9.0 µL of the cocktail mix in a 96-well PCR plate, gently vortexed, and spun down at 3000 rpm for 2 min. The mix was denatured at 95 °C for 3 min and quickly chilled on ice for 5 min and then loaded into the ABI 3730 sequencer for fragment analysis. SSR fragment sizing was done using the Genemapper v3.7 software (Applied Biosystems), which performed peak detection and fragment size matching from the reference data. Allele calls were automatically made when a peak from a data sample matched the location of a bin. Completed results were run in AlleloBin software (Prasanth et al., 1997) to correct any errors in the scored alleles resulting from slippage of DNA polymerase during PCR resulting into stutter peaks (Schlotterer and Tautz, 1992). The allele calls were then converted to binary data using ALS-Binary software (Prasanth and Chandra, 1997) for the subsequent analyses.

### Results and Discussion

Polymorphic information content. The PIC value reflecting genetic diversity of the 10 microsatellite loci ranged from 0.23 for locus IB-S07 to 0.76 for locus IB-R12 with an average of 0.62 (Table 3). Except for primers IB-S07 and IB-R08, the other primers were highly polymorphic with PIC values higher than 0.50. IB-R12 was the most polymorphic primer. The high average PIC value observed in this study is an indication of the use of more informative sweetpotato SSR markers.

Polymerase chain reaction amplifications and number of alleles detected. Initial analysis by gel electrophoresis revealed high yield for most of the PCR reactions. The number of alleles detected per locus ranged from two for locus IB-R08 to six for IBCIP-13 with an average of four and the allele sizes ranged from 39 to 373 bp (Table 3). Because sweetpotato might be an autoploidy crop with a large genome (Cervantes-Flores et al., 2008), the number of alleles per locus is expected to range from one to six, although no single genotype showed up to six alleles at a particular locus. However, as a result of the polyploid and highly outcrossing nature of sweetpotato, allele dose effects such as simplex, duplex, and triplex could not be differentiated in this study. There was no relationship between the number of repeats and polymorphism. The 192 genotypes were clearly distinguished by the 10 SSR primer pairs suggesting that SSR markers have good discriminatory power for genotyping sweetpotato germplasm. For example, only six SSR primer pairs generated scorable allelic information for typing 113 Latin American sweetpotato cultivars (Zhang et al., 2000a). Four SSR primer pairs also discriminated among 57 East African sweetpotato genotypes (Gichuru et al., 2006). The level of polymorphism detected by SSRs in this study was higher than that detected by other SSR techniques used by Gichuru et al. (2006) and Zhang et al. (2000a). This could be because of a good choice of highly polymorphic SSR markers used in the study. Tseng et al. (2002), however, obtained greater polymorphism in sweetpotato using SAMPL as a remedy to the limitation of dosage effect detection in SSRs as previously proposed by Butler et al. (1999).

Genetic distances among sweetpotato genotypes. The frequency of pairwise genetic distance coefficients for the SSR analysis is shown in Figure 1. The SSR-based genetic distance coefficients ranged from 0.0 to 1.0 with a mean of 0.57. The relatively high mean genetic distance and wide range of genetic diversity demonstrated the high variability among the 192 sweetpotato accessions. Statistical analysis of the polymorphic information content (PIC), the measure of the usefulness of each marker in distinguishing one individual from another, was determined (Weir, 1996) as:

$$\text{PIC} = 1 - \sum \text{Pi}^2$$

where Pi is the frequency of the ith allele.

To investigate the diversity among the accessions, the number of alleles per locus was computed, and genetic distances among all pairs of individuals were calculated using the Nei and Li coefficient (Nei and Li, 1979). The distance matrix was then subjected to cluster analysis using the unweighted pair group method using arithmetic averages (UPGMA) algorithm of NTSYS-pc software version 2.2 (Rohlf, 1993) to generate a dendrogram (Sneath and Sokal, 1973). Principal component analysis (PCA) was used to graphically display genetic relationships (Gower, 1966).

### Table 2. Simple sequence repeat primer sequences, dyes, loading sets, and polymerase chain reaction product dilutions.

| Primer | Forward | Reverse | Dye | Coload set | Product dilution |
|--------|---------|---------|-----|------------|-----------------|
| IB-R16 | GACTCTTCTGGTTGTAGTTGC | AGGGTTAAGGGGAGACT | VIC | 1 | 1:100 |
| IB-R19 | GGCTAGTGGAGAAGGCTCACA | AAGAAGTAGACTCCTGCCAC | PET | 1 | 1:60 |
| IB-R03 | GCTGCTTCTGGTTGTAGTTGC | AGGGTTAAGGGGAGACT | VIC | 1 | 1:100 |
| IB-R00 | GATAGGTTAGAGAGGCAAG | CCATAGACCATTTTGAGAAG | NED | 2 | 1:75 |
| IB-R09 | AGACTGCTAGGGTTATCTCTTTCAA | GGAGTACGTAACCTCCACG | VIC | 1 | 1:50 |
| IB-S00 | GCTGCTAATCCTGCTCTCTT | GGAATCTGATACGGGAG | VIC | 1 | 1:50 |
| IB-R10 | GATCAGACACTTTAGATGT | GGGGTTATCTCCACGAGC | VIC | 1 | 1:50 |
| IB-R12 | GATCGAGGAGAAGGCCTACA | GAGACTGCTAGGGTTATCTCT | VIC | 1 | 1:50 |
| IB-S07 | GCTGCTTCTGGTTGTAGTTGC | AGGGTTAAGGGGAGACT | VIC | 1 | 1:50 |

### Table 3. Primer, repeat motifs, annealing temperature (Tm), size range, alleles per locus, total number of alleles, and polymorphic information content (PIC) of 10 primers.

| Primer | Repeat motif | Tm (°C) | Size range | Alleles per locus | Total alleles | PIC |
|--------|--------------|---------|------------|------------------|--------------|-----|
| IB-R16 | (GATA)4 | 60      | 201–213    | 3                | 428          | 0.65 |
| IB-R19 | (CAG)5b    | 60      | 190–208    | 4                | 392          | 0.68 |
| IB-R13 | (ACC)3+(CGG)2+(TGC)2 | 60 | 196–373    | 6                | 477          | 0.68 |
| IB-R03 | (GCC)5     | 60      | 243–258    | 4                | 463          | 0.71 |
| IB-R09 | (AT)11I10 | 50      | 193–203    | 4                | 318          | 0.72 |
| IB-R08 | (T3A)4     | 50      | 204–216    | 2                | 230          | 0.36 |
| IB-R12 | (CAG)5A    | 60      | 303–342    | 5                | 496          | 0.76 |
| IB-S07 | (TGC)7     | 60      | 162–178    | 4                | 193          | 0.23 |
| IB-CIP-7 | (CCA)2+3+(CGG)2+13+(CCA)3+(CG)4 | 50 | 39–99      | 6                | 492          | 0.74 |

**Mean** | | | | 4 | 395 | 0.62 |
distances among landraces indicates moderately high genetic diversity. Most distance coefficients were in the range of 0.5 to 0.6, accounting for 60.7% of the pairwise distance coefficients in this study. Genotypes MLE191 and KML942 collected from the neighboring districts of Mbale and Kamuli, respectively, were identified as duplicates, although they differed significantly in their vine and leaf coloration but had similar storage skin and flesh color. MLE191, a popular accession from Mbale, could have been brought to Kamuli for cultivation by a farmer who could not name it or vice versa (McGregor et al., 2001). Likewise, genotypes ARA237 from the Arua district and KSR663 from the Kisoro

Fig. 1. Frequency distribution of pairwise genetic distance estimates among 192 sweetpotato genotypes.

Fig. 2. Dendrogram showing genetic relationships among 192 Ugandan sweetpotato genotypes.
district also had a distance coefficient of 0.0 (duplicates). These districts are both bordered by the Democratic Republic of Congo from where the farmers could have brought this accession. This environment could have affected the pigmentation traits leading to differential scoring of these traits on the accessions. The highest pairwise genetic distance was observed between genotypes BSH748 and MLE163 from Bushenyi and Mbale districts, respectively. A high mean genetic distance of 0.58 was also found among sweetpotato genotypes from China, the world’s leading producer (He et al., 2006). In contrast, Gichuru et al. (2006) observed low diversity among some East African sweetpotato genotypes probably because of the small number of accessions collected from few districts and also fewer number of SSR primers (four primer pairs) used in the study. Similar low diversities have been observed among the sweetpotato genotypes from Tanzania (Elameen et al., 2008), Papua New Guinea (Zhang et al., 1998), and the United States (He et al., 1995). The relatively high genetic diversity of sweetpotato in Uganda can be attributed to the self-incompatibility leading to chance seedlings in farmers’ fields and vegetative propagation of the crop and directed selection in the crop for various uses such as human food, livestock feed, and poultry feed coupled with new introductions and mutations. High levels of polymorphism among sweetpotato plants are maintained through vegetative propagation and self-incompatibility in the crop (He et al., 1995).

Cluster analysis. The standard distance matrix-generated dendrogram grouped the genotypes into four major clusters (Fig. 2). Within each cluster, the genotypes mainly did not group according to geographic origin. For instance, Cluster 1 has 16 genotypes collected from the districts of Mbale, Kamuli, Kumi, Rakai, Mpigi, Pallisa, Lira, and Kisoro. Similarly, Cluster 2 consisted of genotypes from Kumi, Rakai, and Luweero districts. Cluster 3 had the largest number of genotypes and many subclusters, and Cluster 4, likewise, did not show a geographic pattern. Clustering among some East African cultivars indicated a lack of geographic association as well (Gichuru et al., 2006). However, clear regional patterns of clustering were observed among the sweetpotato genotypes from Latin America (Zhang et al., 2000a, 2004). The lack of geographic associations among the Ugandan genotypes may be a result of gene flow because farmers have routinely shared planting material over the years of sweetpotato cultivation in Uganda. Self-incompatibility and high outcrossing favors gene flow in sweetpotato (He et al., 1995).

Principal component analysis. Principal component analysis was also conducted to analyze the genetic relationships among the individual accessions. The first two principal components accounted for 23.1% and 17.6% of the variance in the PCA plot of the genotypes, respectively. Similar to the cluster analysis results, PCA did not result in a discernible grouping of genotypes by the regions of collection (Fig. 3). Tseng et al. (2002) observed similar results between UPGMA clustering and PCA in the genotyping and assessment of genetic relationships among elite polycross breeding cultivars of sweetpotato in Taiwan using SAMPL polymorphisms.

**Conclusion**

The 10 fluorescent-labeled microsatellites detected on ABI 3730 have distinguished the 192 Ugandan sweetpotato genotypes. The relatively high level of genetic diversity is an indication of the broad genetic base for sweetpotato in Uganda. The identification of 190 diverse genotypes of varying characteristics for use in hybridization schemes in the region will enhance accession development and contribute to sweetpotato productivity in SSA. These East African sweetpotato genotypes have several unique important characteristics like high dry matter content, high resistance to virus diseases, and vigorous foliage cover, although they have low root beta-carotene content (Gichuki et al., 2003). The genotypes are ready for cleaning and in vitro conservation at NaCRRI and CIP, Lima, Peru. Sources of genes for these characteristics have been identified in the distinct genotypes of the Ugandan sweetpotato collection. Two duplicates identified from this morphologically distinct collection confirm the advantage of molecular characterization over morphological characterization. This efficient genotyping will enhance low-cost conservation and use of these superior genotypes. To enhance breeding for orange-fleshed cultivars, genotypes MLE172 from Mbale and KM183, both having high dry matter, are recommended as parental genotypes. Meanwhile, KBL616, KBL648, KSR659, KSR676, and

![Fig. 3. Two-dimension principle component analysis plot of 192 Ugandan sweetpotato genotypes.](image-url)
KRE693 are highly recommended as parental genotypes for breeding *Alternaria* blight resistance in the region. The genotypes SRT27, SRT47, MBL191, MSD382, HMA496, RA8K08, RA8K35, KML875, and MPG1122 are high-yielding and moderately resistant to both SPVD and *Alternaria* blight. These are recommended for breeding high-yielding cultivars of sweetpotato. Finally, to improve SPVd resistance, SRT37, KMI83, MSK1026, MPG1103, MPG1117, and LUW1290 are the recommended parental genotypes to be used in breeding. Passport data and complete description of the germplasm are available at: http://www.viazivitamu.org/ugasp_db/index.php.

**Literature Cited**

Abidin, P.E. and E.E. Carey. 2001. Sweetpotato genetic diversity in North-Eastern Uganda: Germplasm collection, farmer knowledge, and morphological characterization. HorticScience 36:487 (abstr.)

Aritua, V. and R.W. Gibson. 2002. The perspective of sweetpotato chlorotic stunt virus in sweetpotato production in Africa: A review. African Crop Science Journal 10:281–310.

Buteler, M.I., R.L. Jarret, and D.R. LaBonte. 1999. Sequence characterization of microsatellites in diploid and polyploid *Ipomoea*. Theor. Appl. Genet. 99:123–132.

Cervantes-Flores, J.C., G.C. Yencho, A. Kriegner, B. Buteler, M.I., R.L. Jarret, and D.R. LaBonte. 1999. Sequence characterization of microsatellites in diploid and polyploid *Ipomoea*. Theor. Appl. Genet. 99:123–132.

Connolly, A.G., I.D. Godwin, M. Cooper, and I.H. Delacy. 1994. Interpretation of random amplified polymorphic DNA marker data for fingerprinting sweetpotato (*Ipomoea batatas*) genotypes. Theor. Appl. Genet. 88:332–336.

Diaz, J., P. Schmiediche, and D.F. Austin. 1996. Polygon of crossability between eleven species of *Ipomoea*: Section Batatas (Convolvulaceae). Euphytica 88:189–200.

Doyle, J.J. and J.L. Doyle. 1990. Isolation of plant DNA from fresh tissue. Focus 12:13–15.

Elameen, A., S. Fjellheim, A. Larsen, O.A. Rognli, L. Sundheim, S. Mosla, E. Masumba, K. Mtunda, and S.S. Klemisdal. 2008. Analysis of genetic diversity in a sweet potato (*Ipomoea batatas*) germplasm collection from Tanzania as revealed by AFLP. Genet. Resources Crop Evol. 55:397–408.

FAOSTAT. 2007. June 2009. <http://faostat.fao.org/>.

Gichuki, S.T., M. Berenyi, D. Zhang, M. Herman, J. Schmidt, J. Glossl, and K. Burgh. 2003. Genetic diversity in sweetpotato (*Ipomoea batatas*) in relationship to geographic sources as assessed with RAPD markers. Genet. Resources Crop Evol. 50:429–437.

Gichuru, V., V. Aritua, G.W. Lubega, R. Edema, E. Adipala, and P.R. Rubaihayo. 2006. A preliminary analysis of diversity among East African sweetpotato landraces using morphological and simple sequence repeat (SSR) markers. Acta Hort. 703:159–164.

Gower, J.C. 1966. Some distance properties of multivariate analysis. Biometrika 53:325–338.

He, G., C.S. Prakash, and R.L. Jarret. 1995. Analysis of genetic diversity in a sweetpotato (*Ipomoea batatas*) germplasm collection using DNA amplification fingerprinting. Genome 36:25–29.

He, X., Q. Liu, K. Ishiki, H. Zhai, and Y. Wang. 2006. Genetic diversity and genetic relationships among Chinese sweetpotato landraces revealed by RAPD and AFLP markers. Breed. Sci. 56:201–207.

Hu, J., M. Nakatani, A.G. Lalusin, T. Kuranouchi, and T. Fujimura. 2003. Genetic analysis of sweetpotato and its wild relatives using inter-simple sequence repeat (ISSR)s. Breed. Sci. 53:297–304.

Hu, J., M. Nakatani, K. Mizuno, and T. Fujimura. 2004. Development and characterization of microsatellite markers in sweetpotato. Breed. Sci. 54:177–188.

Huamán, Z. 1992. Morphological identification of duplicates in collections of *Ipomoea batatas*. CIP Research Guide 36, Lima, Peru.

Huamán, Z., C. Aguilar, and R. Ortiz. 1999. Selecting a Peruvian sweetpotato core collection on the basis of morphological, eco-geographical, and disease and pest reaction data. Theor. Appl. Genet. 98:840–845.

Huamán, Z. and D.P. Zhang. 1997. Sweetpotato, p. 29–38. In: Fuccillo, D., L. Sears, and P. Stapleton (eds.). Biodiversity in trust. Cambridge Univ Press, Cambridge, UK.

Hwang, S.Y., Y.T. Tseng, and H.F. Lo. 2002. Application of simple sequence repeats in determining the genetic relationships of cultivars used in sweetpotato polycross breeding in Taiwan. Sci. Hort. 93:215–224.

Huama´n, Z. and R.J. Hijmans. 1998. RAPD variation in *Ipomoea batatas* landraces of the Vale do Ribeira. Sci. Agr. 64:416–427.

Hu, J., M. Nakatani, A.G Lalusin, T. Kuranouchi, and T. Fujimura. 2003. Genetic analysis of sweetpotato and its wild relatives using inter-simple sequence repeat (ISSRs). Breed. Sci. 53:297–304.

He, G., C.S. Prakash, and R.L. Jarret. 1995. Analysis of genetic diversity in a sweetpotato (*Ipomoea batatas*) germplasm collection using DNA amplification fingerprinting. Genome 36:25–29.

He, X., Q. Liu, K. Ishiki, H. Zhai, and Y. Wang. 2006. Genetic diversity and genetic relationships among Chinese sweetpotato landraces revealed by RAPD and AFLP markers. Breed. Sci. 56:201–207.

Hu, J., M. Nakatani, A.G. Lalusin, T. Kuranouchi, and T. Fujimura. 2003. Genetic analysis of sweetpotato and its wild relatives using inter-simple sequence repeat (ISSRs). Breed. Sci. 53:297–304.

Hu, J., M. Nakatani, K. Mizuno, and T. Fujimura. 2004. Development and characterization of microsatellite markers in sweetpotato. Breed. Sci. 54:177–188.

Huamán, Z. 1992. Morphological identification of duplicates in collections of *Ipomoea batatas*. CIP Research Guide 36, Lima, Peru.

Huamán, Z., C. Aguilar, and R. Ortiz. 1999. Selecting a Peruvian sweetpotato core collection on the basis of morphological, eco-geographical, and disease and pest reaction data. Theor. Appl. Genet. 98:840–845.

Hoisington. 1997. AlleloBin. A software for allele binning of microsatellite markers into 0-1 (binary) data. ICRI-SAT, Hyderabad, India.

Price, T.D., A. Qvarnström, and D.E. Irwin. 2003. The role of phenotypic plasticity in driving genetic evolution. Proc. Biol. Sci. 270:1433–1440.

Rohlf, J.F. 1993. NTSYS-pc Numerical Taxonomy and Multivariate Analysis System. Version 1.80. Department of Ecology and Evolution, State University of New York, Stony Brook, NY.

Schlotterer, C. and D. Tautz. 1992. Slippage synthesis of simple sequence DNA. Nucleic Acids Res. 20:211–215.

Sneath, P.H.A. and R.R. Sokal. 1973. Numerical taxonomy. Freeman, San Francisco, CA.

Tseng, Y.T., H.F. Lo and S.Y. Hwang. 2002. Genotyping and assessment of genetic relationships in elite polycross breeding cultivars of sweetpotato in Taiwan based on SAMPL polymorphisms. Bot. Bull. Acad. Sin. 43:99–105.

Veasey, E.A., J.R.Q. Silva, M.S. Rosa, A. Borges, E.A. Bressan, and S. Peroni. 2007. Phenology and morphological diversity of sweetpotato (*Ipomoea batatas*) landraces of the Vale do Ribeira. Sci. Agr. 64:416–427.

Weir, B.S. 1996. Genetic data analysis. II. Methods for discrete population genetic data. Sinauer Associates, Inc., Sunderland, MA.

Yada, B., P. Tukamuhaba, A. Villordon, A. Alajo, and R.O.M. Mwanga. 2010. An on-line database of sweetpotato germplasm collection in Uganda. HorticScience 45:153.

Zhang, D.P., D. Carabucajal, G. Rossell, S. Milla, C. Herrera, and M. Ghislain. 2000a. Microsatellite analysis of genetic diversity in sweetpotato cultivars from Latin America. CIP Program Report 1999–2000.

Zhang, D.P., J. Cervantes, Z. Huamán, and M. Ghislain. 2000b. Assessing genetic diversity of sweetpotato (*Ipomoea batatas*) landraces from tropical America using AFLP. Genet. Resources Crop Evol. 47:659–665.

Zhang, D.P., M. Ghislain, Z. Huamán, A. Golmirzaie, and R.J. Hijmans. 1998. RAPD variation in sweetpotato (*Ipomoea batatas*) landraces from South America and Papua New Guinea. Genet. Resources Crop Evol. 45:271–277.

Zhang, D.P., G. Rossell, A. Kriegner, and R. Hijmans. 2004. AFLP assessment of diversity in sweetpotato from Latin America and the Pacific region: Its implications on the dispersal of the crop. Genet. Resources Crop Evol. 51:115–120.