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Molecular, morphological and agronomic characterization of the sweet potato (*Ipomoea batatas* L.) germplasm collection from Mozambique: Genotype selection for drought prone regions

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ABSTRACT

Sweet potato (*Ipomoea batatas* (L.) Lam) is one of the most important root crops in Mozambique, ranking in the 3rd position, after cassava and maize. Within the scope of the national and regional strategies/initiatives, we have used a multi-analysis approach to characterize the national sweet potato germplasm collection at two different levels: i) genetic, morphological and agronomic diversity; and ii) agronomic potential (storage root yield, vine weight, biomass, harvest index and dry matter content) toward drought tolerance. This collection, composed by 44 accessions, comprises 28 genotypes cultivated in three different provinces of Mozambique (Gaza, Inhambane and Zambezia), nine from other African countries (Kenya, South Africa, Uganda and Zimbabwe), one from the United States of America, and six from CGIAR research centers (IITA and CIP). According to our results, the Mozambican germplasm bank presents a high level of diversity, comparable to those from the collections of the primary centers of origin and South Africa, therefore constituting of a good source of agronomic traits for breeding. Regarding drought tolerance, six Mozambican genotypes (Admarc, Chingova, Nhacoongo-1, Xihetamakote, Nwanatuyo, and Chissicuana-2), one from Uganda (NASPOT-5), one from Zimbabwe (Moz. white), one from Kenya (SPK 004), and one from the USA (Resisto) seem to have the highest potential to be used in regions with frequent drought seasons and in future breeding programs. The results showed that such integrated analysis can be used to successfully characterize the genetic material in terms of suitability to drought-prone regions, therefore helping sweet potato crop management, with economic and food security impacts.

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1. Introduction

Sweet potato (*Ipomoea batatas* (L.) Lam) is one of the most important root crops in the world, particularly in Sub-Saharan Africa (SSA) where its cultivation area covers around 3 million hectares with an estimated annual production of ca.13 million tons (Low and van Jaarswels, 2008). This commodity is highly productive with a low demand of inputs and labor. Additionally, it tolerates recalcitrant growth conditions, is enriched in vitamins (A, C, D and E) and provides more edible energy than all other food staples. Altogether, these aspects make this crop suitable and attractive to farmers with limited resources (Woolfe, 1992; Elameen et al., 2008; Low et al., 2009; Srekanth et al., 2010). In fact, over the last decade sweet potato has become increasingly important in SSA, where it is expanding faster than all other major food crops (Low et al., 2009; Walker et al., 2011).

In Mozambique, sweet potato is the 3rd most important staple after cassava and maize (Walker et al., 2006; FAOSTAT, 2010), with an

estimate production of 920,000 tons in 2010 (FAOSTAT, 2010). The country appears at the bottom of the Human Development Index list and is one of the most vulnerable to natural disasters and climate changes (MICOA, 2007; UNICEF, 2007). Within this context, and given the potential of sweet potato to alleviate hunger and malnutrition, in 2000 the International Potato Center (CIP) established a partnership with the Agricultural Research Institute of Mozambique (IIAM) to launch a Program aiming the dissemination of the beta-carotene rich Orange Fleshed Sweet Potato (OFSP). Among others, this program included the characterization of the sweet potato germplasm collection from Mozambique, a prerequisite for the rational use and conservation of the available genetic resources (de Vicente et al., 2006; Fraleigh, 2006).

The standard characterization of crop genetic resources includes conventional approaches such as the use of descriptor lists of morphological characters or the evaluation of the agronomic performance, complemented by molecular techniques (Gepts, 2006; Khoury et al., 2010). While morpho-agronomic characterization facilitates the efficient utilization of germplasm collections in a breeding program, providing direct useful information about the genetic relationships and

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specific traits of agronomic importance (Pagnotta et al., 2009; Khoury et al., 2010; Elameen et al., 2011; Laurie et al., 2013), molecular marker-based characterization constitutes a powerful complementary tool, producing more accurate data on genetic distances in a genotype \times environment independent way (Pagnotta et al., 2009; Malviya et al., 2012). Nowadays, molecular markers are an essential component for the devise of ex situ and in situ conservation strategies. Amplified Fragment Length Polymorphism (AFLP), Inter-Simple Sequence Repeats (ISSR), and Random Amplified Polymorphic DNA (RAPD) have been successfully used to monitor and characterize the genetic diversity of sweet potato germplasm collections (Connolly et al., 1994; Zhang et al., 1998, 2000; Hu et al., 2003; Elameen et al., 2008; Prakash et al., 2008; Veasey et al., 2008; Arizio et al., 2009; Lin et al., 2009; Moulin et al., 2012) and can now be employed in routine procedures for DNA fingerprinting and to evaluate genetic diversity in this species.

In this paper we report on the molecular, morphological and agronomic characterization of the sweet potato germplasm collection from Mozambique (deposited at IIAM), including the analysis of the productivity performance of each variety cultivated under irrigation and drought (rainfed) conditions. It should be pointed out that drought is one of the major concerns in the country, building strong restrictions to crop productivity. This way, we provide useful information to assist the management of the core collection, but most importantly, for the selection of the best, less risky, accessions for drought prone areas as well as for breeding toward drought resistance. The work was conducted under the context of the actual scenario of Mozambique (and SSA in general) regarding the vulnerability to natural disasters, food insecurity and malnutrition, and the national program for OFSP dissemination. It is in line with the *Action Plan for the Reduction of Absolute Poverty (PARPA II, 2006)*, the *Strategy and Action Plan for Biological Diversity Conservation in Mozambique (Estratégia e Plano de Acção para a Conservação da Diversidade Biológica de Moçambique, 2003)* and with the *Sweetpotato Action for Security and Health in Africa (SASHA)*, an initiative designed to improve the food security and livelihoods of poor families in SSA by exploiting the untapped potential of sweet potato.

2. Materials and methods

2.1. Plant material and trial location

Forty four accessions (Table 1) introduced in Mozambique with the reasoning of being drought tolerant have been evaluated. These included: i) 28 accessions collected in three provinces of Mozambique: Gaza (17), Inhambane (9), and Zambezia (2); ii) 9 accessions from other African countries: South Africa (4), Zimbabwe (3), Kenya (1) and Uganda (1); iii) one accession from the United States of America; and iv) 6 accessions from CGIAR research centers: International Institute of Tropical Agriculture (IITA) (2) and *Centro Internacional de las Papas* (CIP) (4).

Field trials were conducted during two cropping seasons, 2006/2007 and 2007/2008, at the Umbeluzi Research Station (26° 03' South latitude, 32° 23' longitude East and 12 m above sea level), district of Boane, province of Maputo, South of Mozambique. The site has a semi-arid to dry climate with a mean annual precipitation of 679 mm, average temperature ranging from 23 °C to 26 °C during the rainy season and 17 °C to 23 °C during the dry season, daily evaporation between 2.8 and 7.2 mm, and annual evaporation of 1857 mm (Gomes, 1996). Information on the water status of Umbelúzi (Supplementary Table S1) provides evidence that it is a suitable site for testing drought tolerance.

2.2. Morphological and agronomic characterization

Morphological characterization was performed in three replicates of each genotype, in a randomized split plot design and comprised a total of 16 characters, including 6 quantitative and 10 qualitative traits

Table 1

Identification of the variety and geographical origin corresponding to each of the 44 sweet potato accessions from the germplasm collection characterized in this study.

Variety name	Origin	Accession ID
Nhacutse 5	Gaza (Xai-Xai)	3
Nwaracu	Gaza (Xai-Xai)	4
Nwazambane	Gaza (Xai-Xai)	5
Nwamanhiça	Gaza (Xai-Xai)	11
Nhacutse 3	Gaza (Xai-Xai)	13
Tuang-Thuang	Gaza (Xai-Xai)	18
Nhacutse 2	Gaza (Xai-Xai)	25
Xiadla xa kau	Gaza (Chókwé)	28
Nhacutse 4	Gaza (Xai-Xai)	31
Nwamazambe	Gaza (Chókwé)	34
Nwamonguane	Gaza (Xai-Xai)	36
Chulamete	Gaza (Macia)	37
Nwaxitsimbwane	Gaza (Chókwé)	40
Cacilda	Gaza (Chókwé)	41
Nwanatuyo	Gaza (Chókwé)	42
Xihetamakote	Gaza (Chókwé)	44
Ximitakwatse	Gaza (Macia)	46
Chissicuaana 2	Inhambane (Morrumbene)	2
Nhacoongo 1	Inhambane (Nhacoongo)	8
Chissicuaana 3	Inhambane (Morrumbene)	21
Jogó	Inhambane (Morrumbene)	27
Xitsekele	Inhambane (Homoine)	29
Chissicuaana 1	Inhambane (Morrumbene)	30
Jogó 2	Inhambane (Morrumbene)	32
Mafambane	Inhambane (Homoine)	35
Xiphone	Inhambane (Morrumbene)	39
Admarc	Zambezia	14
UNK-Malawe	Zambezia	24
Tacna	South Africa	1
Mafutha	South Africa	10
ST 87-030	South Africa	16
Atacana	South Africa	19
Cordner	Zimbabwe	52
Chingova	Zimbabwe	53
Moz white	Zimbabwe	56
SPK 004	Kenya	58
NASPOT 5	Uganda	6
Resisto	USA	47
TIS 9265	IITA	45
TIS 2534	IITA	54
440203	CIP	17
Jonathan	CIP	48
CN 1448-49	CIP	50
Lo 323	CIP	57

CIP – International Potato Center; IITA – International Institute of Tropical Agriculture.

(Table 2), selected from the sweet potato descriptors (Huamán, 1991). All qualitative traits were assessed using a continuous scale, thus being suitable to be collectively used with the quantitative traits in the multivariate analysis.

The agronomic characterization was conducted in a split plot design with two water regimes, namely irrigation and rainfed (dry) conditions and three replications. The genotypes were assigned randomly to different plots and non-randomized irrigations levels were allocated. Five main attributes were measured, namely the total storage root yield, weight of the vines, biomass, harvest index (HI) and dry matter content (DM).

2.3. RAPD analysis

Total genomic DNA was extracted from leaves as described in Taura et al. (2001). Average yield was calculated spectrophotometrically (SmartSpec™ 3000, Biorad) and DNA samples were stored at –20 °C until use. RAPD assays (Williams et al., 1990) were performed as described in Taura et al. (2001). PCR reactions were carried out in a final volume of 25 μ l containing 50 ng of genomic DNA, 1 \times PCR buffer (20 mM Tris-HCl pH 8.4, 50 mM KCl), 1.5 mM MgCl₂, 0.2 mM dNTPs, 0.1 pmol primer and 0.5 U of *Taq* DNA polymerase (Invitrogen). PCR amplifications were done in a thermal cycler (iCycler, Biorad),

Table 2

List of the morphological descriptors used to characterize the 44 sweet potato accessions from the Mozambican germplasm collection.

Characters	Code
<i>Vine characters</i>	
Length of the main vine	LMV
Length of the internode	LI
Diameter of the internode	DI
Predominant color of the main vine	PCV
Secondary color of the vine	SCV
Type of vine pubescence	TVP
<i>Leaf characters</i>	
General leaf outline	GLO
Type of leaf lobes	TLL
Number of leaf lobes	NLL
Shape of the central leaf lobe	SCL
Vein pigmentation	VP
Size of the mature leaf	SML
Color of the immature leaf	CIL
Color of the mature leaf	CML
Length of the petiole	LP
Pigmentation of the petiole	PP

programmed as follows: pre-denaturation for 2 min at 94 °C; 35 cycles of 1 min at 94 °C, 1 min at 35 °C and 2 min at 72 °C and a final extension of 3 min at 72 °C to complete elongation. Fifty one decamer primers (Invitrogen) were initially tested in 6 random samples, from which 8 primers were selected for further analysis (Table 3). For each reaction, a negative control, in which DNA was replaced by water, was included. Duplicate reactions of at least two different DNA extractions were performed for all samples to assess the consistency of the amplification profile. PCR products were resolved by electrophoresis in 1.2% agarose gels, stained with ethidium bromide in 1× TAE buffer and photographed under ultraviolet light using the Gel Doc System (Biorad).

2.4. Data analysis

For multivariate analyses, the unweight pair group method using arithmetic averages (UPGMA) and sequential agglomerative hierarchical nested (SAHN) routines were performed for cluster analysis. The Jaccard similarity coefficient and the Euclidian distance were used for molecular and morphological characterization based on non-redundant characters, respectively. In each case, goodness of fit was determined by computing a cophenetic value matrix for the dendrograms and comparing with the original similarity matrix. For analysis of molecular data, RAPD amplicons were transformed into a binary matrix consisting of “0” and “1” (absence and presence of bands across samples, respectively). Data from agronomic performance was standardized and a pair-wised correlation matrix was calculated and subjected to eigenvalue decomposition to identify orthogonal components of the original matrix and generate a Principal Component Analysis (PCA) plot. Cluster and PCA analyses were performed using the software NTSYSpc version 2.20e (Rohlf, 2005).

Table 3

Primer sequence, total number of bands (TNB), number of polymorphic bands (NPB), percentage of polymorphic bands (P%), average number of bands, average number of polymorphic bands and resolving power (Rp) generated by RAPD primers.

PRIMER	SEQUENCE (5'-3')	TNB	NPB	P%	Rp
OPA 4	AATCGGGCTG	7	6	85.7	8.5
OPH 20	GGGAGACATC	8	5	62.5	11.6
OPH 15	AATGCGCAC	14	14	100	12.9
OPH 19	CTGACCAGCC	18	17	94.4	21.5
OPA 18	AGGTGACCGT	11	11	100	8.7
OPH 9	AGTCGTCCCC	9	9	100	12.7
S21	CAGGCCCTTC	13	13	100	11.8
S31	CAATCGCCGT	13	13	100	18.9
TOTAL		93	88		
AVERAGE		11.6	11	92.8	13.3

RAPD resolving power (Rp) was calculated as described by Prevost and Wilkinson (1999).

Pearson correlations were calculated using Microsoft Excel 2010 and box-plots were built using the “Box Plot template for Excel” software (Vertex42, LLC).

Consensus ranks of the accessions ordered according to their agronomic performance were established by means of a non-weighted unsupervised rank aggregation method: RankAggreg v. 0.4-1 (Pihur et al., 2009) for R (v. 2.9.2; <http://www.R-project.org>). The merged rank list was obtained from calculated Spearman footrule distances and the Cross-Entropy Monte Carlo algorithm, to compare the relationship of the relative ordering by different methods of analysis.

3. Results

3.1. Molecular diversity

The 8 RAPD primers selected for the analysis of the 44 sweet potato accessions generated a total of 93 scorable fragments, 88 of which (94.6%) polymorphic (Table 3). A dendrogram based on UPGMA analysis was generated using the Jaccard coefficient and shows the clustering pattern between the accessions (Fig. 1). The cophenetic coefficient computed against the original data matrix was $r = 0.86$ ($t = 9.26$; $p = 1.00$). Forty one out of 44 accessions, with similarity coefficient ranging from 0.24 to 0.79, were grouped into 6 clusters (Fig. 1). The first cluster was the most heterogeneous regarding the geographical origin and

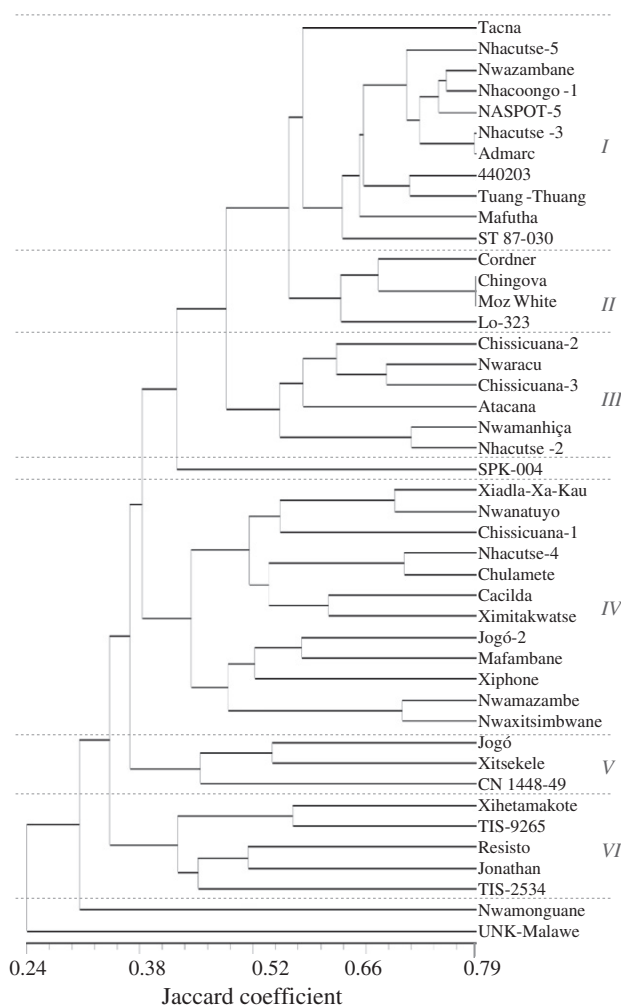


Fig. 1. Dendrogram based on UPGMA analysis generated using the Jaccard coefficient representing the phenetic relationships among the 44 sweet potato accessions.

included 6 individuals from Mozambique, three from South Africa, one from CIP and the genotype from Uganda. The second cluster included the three accessions from Zimbabwe and one from CIP. The third cluster grouped five genotypes from Mozambique and one from South Africa. The fourth and major cluster was exclusively composed by genotypes from Mozambique (8 from Gaza and 6 from Inhambane). The fifth cluster included only three individuals, two from Mozambique and one from CIP. The sixth cluster was mainly composed by international accessions (two from IITA, one from CIP and one from the USA), added with genotype Xihetamakote from Gaza (Mozambique). Three accessions, SPK 004 (Kenya), Nwamanguane (Gaza, Mozambique) and UNK-Malawe (Zambezia, Mozambique) did not fit in any particular cluster.

3.2. Morphological diversity

Table 4 provides the Pearson coefficient correlation among the scored morphological traits accessed in the 44 sweet potato accessions. Characters with $r > 0.90$ on the same organ were observed between the *Type of leaf lobes* (TLL) and *Shape of the central leaf lobe* (SCL) ($r = 0.95$) and between *General leaf outline* (GLO) and TLL ($r = 0.90$). Hence, due to redundancy, TLL was excluded from the cluster analysis to avoid overweighting and biasing the results. A dendrogram generated from the Euclidian distances based on the remaining morphological data is showed in Fig. 2. Goodness of fit was proved after Mantel test using the cophenetic matrix and the original data ($r = 0.79$; $t = 7.87$; $p = 1.00$). The 44 accessions were clustered into 4 main clusters: cluster I with 21-, cluster II with 10-, cluster III with seven-, and cluster IV with three accessions, respectively. The remaining genotypes (Chingova, Nhacutse-3, 440203) presented higher genetic distances and did not fit in any particular cluster.

3.3. Agronomic performance

Among the agronomic traits investigated, a high positive significant Pearson correlation ($r = 0.98$) was observed between biomass and vine weight (Table 5). As stated above, these two attributes were considered redundant. To evaluate differences in crop productivity under irrigated and rainfed conditions, a Principal Component Analysis (PCA) was applied to the agronomic data using a correlation coefficient to assess simultaneously the pattern of variation between samples. Considering the redundancy between biomass and vine weight, the former trait was not included in the PCA. The dispersion of the accessions, distributed outside the center of the plot, points to substantial agronomic diversity among the material analyzed (Fig. 3). The first three principal

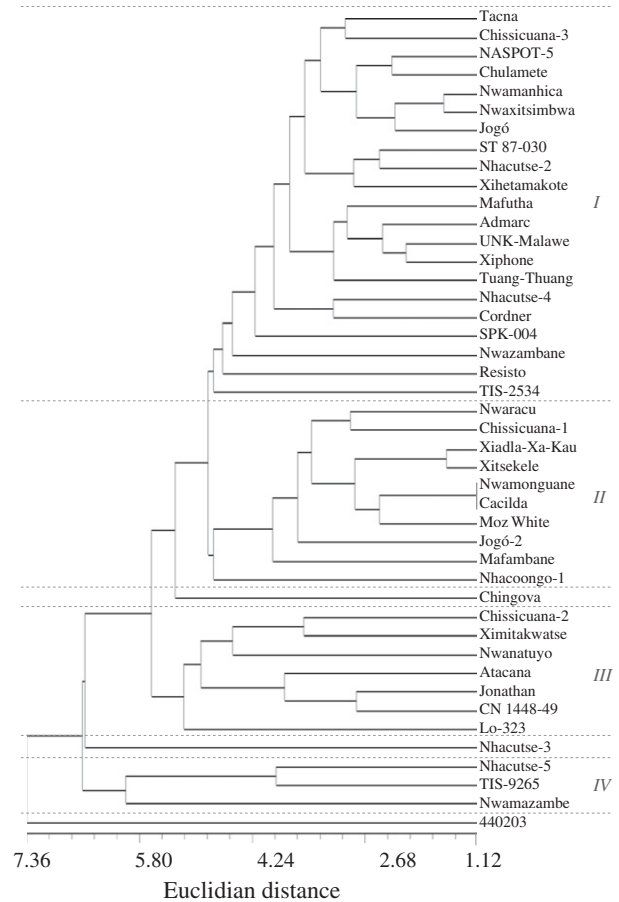


Fig. 2. Dendrogram based on UPGMA analysis generated using the Euclidean distances representing the phenotypic distances between the 44 sweet potato accessions.

components accounted for 70.4% of the whole variation. From the agronomic features quantified, global vine weight and yield and the differences observed in harvest index (HI) under the different water regimes were the most significantly discriminant (Table 6). In fact, the first principal component (PC1), explaining 30.9% of the total variation, showed a high positive coefficient with vine weight (irrigation and rainfed) and dry mater (rainfed), and a negative coefficient with HI (irrigation). The second principal component, which explained an

Table 4

Pearson coefficient of correlation among the 16 morphological traits measured on the 44 sweet potato accessions. Bold values are significant at 99% of probability.

Descriptors	LMV	LI	DI	PCV	SCV	TVP	GLO	TLL	NLL	FCL	SML	VP	CML	CIL	LP	PP
LMV	1.00															
LI	0.37	1.00														
DI	0.25	0.37	1.00													
PCV	0.02	-0.04	0.08	1.00												
SCV	0.24	0.02	-0.16	-0.27	1.00											
TVP	0.14	0.18	0.39	0.08	-0.29	1.00										
GLO	-0.53	-0.26	-0.35	0.17	-0.171	-0.17	1.00									
TLL	-0.55	-0.32	-0.25	0.28	-0.24	-0.05	0.90	1.00								
NLL	-0.49	-0.33	-0.26	0.18	-0.21	-0.06	0.90	0.88	1.00							
SCL	-0.49	-0.26	-0.22	0.33	-0.23	-0.03	0.83	0.95	0.79	1.00						
SML	0.06	-0.00	0.06	0.21	0.22	0.00	-0.06	-0.02	-0.03	0.00	1.00					
VP	0.20	0.03	0.40	0.60	0.03	0.13	-0.21	-0.09	-0.24	-0.03	0.17	1.00				
CML	0.01	-0.11	-0.29	0.02	-0.05	-0.22	-0.05	-0.13	-0.11	-0.12	-0.22	-0.06	1.00			
CIL	0.14	0.14	0.04	0.39	-0.25	0.12	0.09	0.04	-0.01	0.07	-0.08	0.12	0.10	1.00		
LP	-0.18	0.13	0.14	0.04	-0.25	0.14	0.16	0.16	0.13	0.11	0.14	0.02	-0.19	-0.23	1.00	
PP	-0.01	0.04	0.10	0.88	-0.12	0.01	0.14	0.19	0.10	0.27	0.13	0.68	0.00	0.34	0.05	1.00

Values in bold represent significant correlations at 99% of probability. LMV – length of the main vine; LI – length of the internode; DI – diameter of the internode; PCV – predominant color of the main vine; SCV – secondary color of the vine; TVP – type of vine pubescence; GLO – general leaf outline; TLL – type of leaf lobes; NLL – number of leaf lobes; SCL – shape of the central leaf lobe; SML – size of the mature leaf; VP – vein pigmentation; CML – color of the mature leaf; CIL – color of the immature leaf; LP – length of the petiole; PP – pigmentation of the petiole.

Table 5

Pearson's correlation coefficients obtained among five agronomic traits in 44 sweet potato accessions. Bold values are significant at 99% of probability.

	Y	V	B	HI	DM
Y	1.00				
V	0.50	1.00			
B	0.67	0.98	1.00		
HI	0.47	-0.36	-0.20	1.00	
DM	0.14	0.38	0.36	-0.22	1.00

Storage root yield (Y), vine weight (V), harvest index (HI), dry matter (DM).

additional 21.4% of variation, was mainly related to yield (irrigation and rainfed) and HI (rainfed).

Table 7 ranks the different sweet potato accessions under irrigated, rainfed and irrigation + rainfed taking into account the overall agronomic traits. Ranks from individual traits and water regimes are given in Supplementary Table S2. Under irrigation conditions, the best 10 accessions were from Gaza (Ximitakwatse, Nhacutse 2, Nwamongwane, Tuang-Tuang) and Inhambane (Xiphone, Nhacoongo 1, Xitsekele and Chissicuana 2) provinces, USA (Resisto) and South Africa (ST_87-030). Under rainfed conditions, the 10 best performances were obtained with 5 accessions from Mozambique (Xihetamakote and Nwanatuyo from Gaza, Nhacoongo 1 and Chissicuana 2 from Inhambane and Admarc from Zambezia), two from Zimbabwe (Chingova and Moz_white), one from Uganda (NASPOT 5), one from Kenya (SPK-004), and one from the USA (Resisto). When ranking the overall data from the rainfed and irrigation trials, 6 out of the 10 best performing accessions were also from Mozambique (Nhacoongo 1, Admarc, Chissicuana 2, Ximitakwatse, Xitsekele, Nwanatuyo), the other four being from the neighbor country, South Africa (Atacana, Tacna and ST_87-030), and USA (Resisto).

Fig. 4 illustrates the statistical comparison of the global-top10 accessions with the global average of the total sample set (44 accessions) for the 4 non-redundant parameters analyzed under irrigation (I) and rainfed (D) conditions. For both water regimes, most of the accessions (8/10) presented higher yields than the average: Resisto, Admarc, Chissicuana-2, and Tacna (I and D), Ximitakwatse and Atacana (I), and Xitsekele and Nwanatuyo (D). Six out of the top 10 accessions presented above average vine weight: Nhacoongo 1, Chissicuana 2, Ximitakwatse, and Xitsekele (I and D), Admarc (I), and Nwanatuyo (D). HI values were superior to the overall average in Resisto, Atacana, and ST_87-030 (I and D) as well as in Admarc (D). Above average dry matter (DM) values in

Table 6

Eigenvectors for each trait, revealed by Principal Component Analysis. Bold values stand for the most discriminative variables in each PC.

Traits	PC1	PC2	PC3
<i>Irrigation</i>			
Storage root yield	0.149	0.819	0.894
Vine weight	1.149	0.431	0.131
Harvest Index	- 0.851	0.353	0.754
Dry matter	1.073	-0.296	0.382
<i>Rainfed</i>			
Storage root yield	0.220	1.214	- 0.397
Vine weight	0.898	0.533	-0.382
Harvest index	-0.662	0.880	-0.233
Dry matter	0.840	-0.194	0.268

the irrigation and rainfed trials were observed in 4 (Nhacoongo 1, Ximitakwatse, Xitsekele, and ST_87-030) and 6 (Resisto, Nhacoongo 1, Admarc, Ximitakwatse, Tacna, and ST_87-030) accessions, respectively. DM values were similar among accessions and trials (ca. 30–35%).

The gain variations of each agronomic trait are shown in **Fig. 5**. Most of the accessions (37 out of 44) presented gains in yield and vine weight under irrigation conditions. The values ranged from 0.59- (Resisto from the USA) to 4.93-fold (Ximitakwatse from Macia, Gaza, Mozambique) for yield (**Fig. 5A**) and 0.55 (Jonathan, from CIP) to 4.22-fold (Nwamongwane from Macia, Gaza, Mozambique) for vine weight (**Fig. 5B**). Regarding yield, considerable statistically significant gains (≥ 2 fold) were obtained with 13 accessions (Group 1): nine from Mozambique (Nhacutse 3, Tuang-Thuang, Chissicuana 3, Nhacutse 2, Chissicuana 1, Jogó 2, Nwamongwane, Xiphone and Ximitakwatse), one from South Africa (ST_87-030), one from Zimbabwe (Cordner), one from CIP (Jonathan), and one from IITA (TIS 9265). Moderate yield gains (1 to 2-fold) were obtained with 20 accessions (Group 2): 13 from Mozambique (Nwaracu, Nwazambane, Nhacoongo 1, Nwamanhiça, Admarc, UNK-Malawe, Jogó, Xiadla xa kau, Xitsekele, Mafambane, Chulamete, Cacilda and Xihetamakote), three from South Africa (Tacna, Atacana and Mafutha), one from Zimbabwe (Moz white) and three from CIP (440203, CN 1448-49 and Lo 323). Low yield gains (≤ 1 -fold) were observed in four accessions (Group 3): three from Mozambique (Chissicuana 2, Nhacutse 5, Nwamazambe) and one from the USA (Resisto).

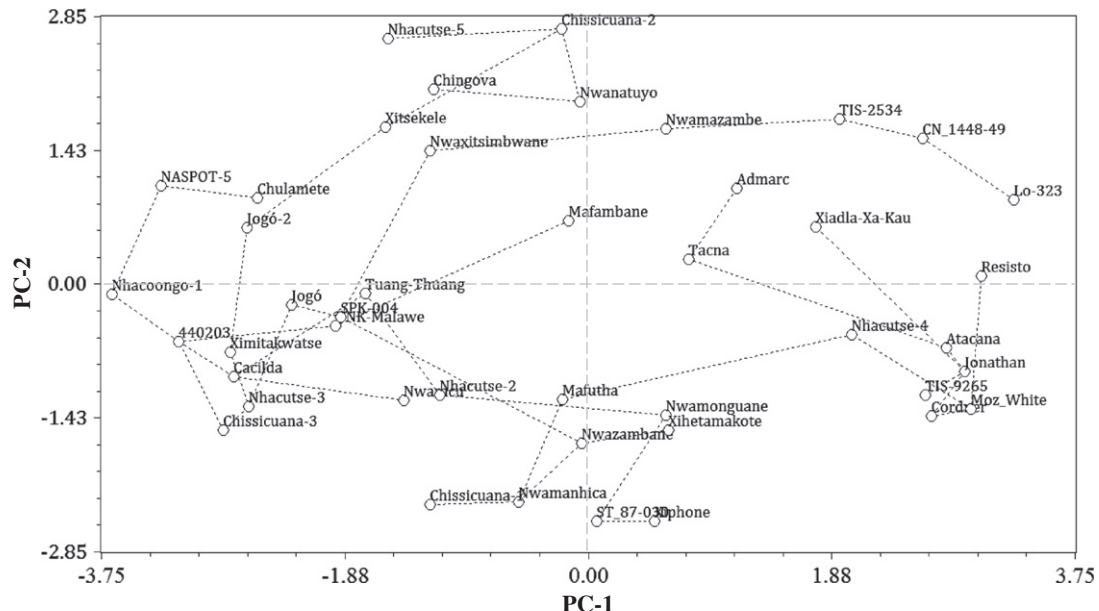


Fig. 3. Principal Component Analysis (PCA) plot of patterns of relationship among the 44 accessions, based on 4 agronomic traits, measured under irrigation and under rainfed conditions.

Table 7

Ranking of the 44 sweet potato accessions according to their global agronomic performance in the two trials (irrigation and rainfed) and globally (irrigation + rainfed).

Rank	Irrigation (global)	Rainfed (global)	Both conditions (global)
1	Ximitakwatse	Admarc	Resisto
2	Nhacutse-2	Resisto	Nhacoongo-1
3	Nwamonguane	Chingova	Admarc
4	Tuang-Thuang	NASPOT-5	Chissicuana-2
5	Xiphone	Nhacoongo-1	Ximitakwatse
6	Resisto	Moz_White	Atacana
7	Nhacoongo-1	SPK-004	Xitsekele
8	ST_87-030	Xihetamakote	Nwanatuyo
9	Xitsekele	Nwanatuyo	Tacna
10	Chissicuana-2	Chissicuana-2	ST_87-030
11	Tacna	Atacana	Xiadla-Xa-Kau
12	Atacana	Nhacutse-5	Nhacutse-5
13	Jogo-2	Nwamazambe	NASPOT-5
14	Xiadla-Xa-Kau	Xiadla-Xa-Kau	Xihetamakote
15	Nwaracu	Tacna	Xiphone
16	Admarc	Xitsekele	Moz_White
17	Nwanatuyo	Mafambane	Chingova
18	Nhacutse-5	Nwaxitsimbwane	Jogo-2
19	Jonathan	ST_87-030	Nhacutse-2
20	Nwazambane	Lo-323	Tuang-Thuang
21	Chissicuana-3	Ximitakwatse	Chissicuana-3
22	Cordner	Chissicuana-1	Nhacutse-4
23	Nhacutse-4	Chulamete	Nwaxitsimbwane
24	440203	Nhacutse-4	Nwamonguane
25	Nhacutse-3	Chissicuana-3	Nwazambane
26	Xihetamakote	Jogo	Nwamazambe
27	UNK-Malawe	UNK-Malawe	SPK-004
28	NASPOT-5	Jogo-2	Nwaracu
29	Nwaxitsimbwane	Nwazambane	Lo-323
30	TIS-9265	TIS-2534	Chissicuana-1
31	Cacilda	Xiphone	UNK-Malawe
32	Chissicuana-1	Nhacutse-3	Jonathan
33	Moz_White	Nwamanhica	Nhacutse-3
34	Lo-323	440203	440203
35	Chulamete	Mafutha	Chulamete
36	Nwamazambe	Cacilda	Mafambane
37	Jogo	Jonathan	Jogo
38	Chingova	Nwaracu	Cordner
39	TIS-2534	TIS-9265	Cacilda
40	Nwamanhica	CN_1448-49	TIS-2534
41	Mafambane	Cordner	TIS-9265
42	CN_1448-49	Tuang-Thuang	Nwamanhica
43	Mafutha	Nhacutse-2	Mafutha
44	SPK-004	Nwamonguane	CN_1448-49

About half of the accessions from Group 1 (ST 87-030, 440203, Tuang-Thuang, Chissicuana 3, Nhacutse 2, Nwamonguane, Cacilda, TIS 9265) presented also considerable gains (≥ 2 -fold) in vine weight, while accessions Nhacutse 3, Jogo 2, Ximitakwatse, and Cordner and Chissicuana 1, respectively, presented moderate (1 to 2-fold), low (≤ 1 -fold), and no gains. Four (Nwaracu, Admarc, 220203 and Cacilda), nine (Tacna, Nhacoongo 1, Atacana, UNK-Malawe, Xitsekele, Mafambane, Chulamete, CN 1448-49 and Lo 323) accessions from Group 2 presented respectively, high and moderate increments in vine weight. Within this group, Xihetamakote presented a moderate gain under rainfed conditions. With the exception of Resisto, showing a low increase in vine weight, all the other accessions from Group 3 (Chissicuana 2, Nhacutse 5 and Nwamazambe; all from Mozambique) have shown moderate increments in this parameter.

Gains in HI under irrigation were observed in 18 accessions, the values ranging from ca. 0.40- (ST_8730, South Africa) to ca. 3.22-fold (Xihetamakote, Chokwe, Gaza) (Fig. 5C). In most of the accessions (15 out of 18), the increments were in line with those obtained for yield and vine weight. Residual DM gains (≤ 0.25 -fold; Fig. 5D) were observed in 21 accessions, with the higher values (ca. 0.30) obtained in two genotypes, Nhacutse-2 and Nwamongwane both from Xai-Xai. Like in the case of HI, most of the accessions presented concomitant increments in yield and vine weight.

Under rainfed conditions, only one accession, NASPOT-5 from Uganda, presented a gain in yield (< 1 -fold) and HI (> 1.5) (Fig. 5). Regarding vine weight, gains were observed in two accessions (Nwanatuyo, Xihetamakote). Nine accessions (Chissicuana 2, Nhacutse 5, Admarc, Nwamazambe, Nwaxitsimbwane, NASPOT 5, Chingova, CN 1448-49, TIS 2534) presented HI gains ranging from ca. 0.5- to 2-fold (Fig. 5C). DM gains under rainfed conditions were observed in 13 accessions and, like in the case of irrigation, with less than 0.3-fold gains (Fig. 5D). Six genotypes (Nhacutse 4, Nwaxitsimbwane, Nwanatuyo, Chingova, TIS 2534, and SPK 004) presented similar root storage yield under irrigation and rainfed conditions. From this group, two accessions (Nhacutse 4 from Gaza, Mozambique, and SPK 004 from Kenya), maintained the trend (no gain/loss) in vine weight, three presented higher values in the irrigation trial, and one (Nwanatuyo) presented a slight gain (less than 0.5-fold) under rainfed conditions. HI and DM of 16 and 13 genotypes, respectively, were not influenced by the water regime. Nhacutse 4 had consistent results (no gains/losses) in all parameters analyzed and SPK 004 in all parameters but DM.

A Pearson correspondence analysis was also conducted between morphological and agronomic characters and two significant correlations were found: i) length of main vine (LMV), showing positive correlations with vine ($r = 0.36$) and biomass ($r = 0.33$) and a negative correlation with the harvest index (HI) ($r = -0.37$); ii) color of the mature and immature leaf (CML and CIL, respectively), exhibiting a significant positive correlation ($r = 0.30$) and negative correlation ($r = -0.34$) with DM, respectively. The results are given in Table 8.

4. Discussion

The rational management of plant genetic resources for conservation and breeding purposes involves necessarily the characterization of germplasm collections. In this study, we have analyzed the genetic and morpho-agronomic diversity as well as the agronomic performance under irrigation and rainfed conditions of the sweet potato collection from Mozambique.

Reliable and reproducible RAPD amplification patterns were obtained, disclosing high levels of polymorphism (94.6%) and displaying a convenient resolving power (average 13.3). The mean genetic similarity was around 0.52 (Fig. 1). This value is close to those found among sweet potato germplasm collections from the primary centers of origin (Sagredo et al., 1998; Zhang et al., 1998, 2000; Veasey et al., 2008) and China (He et al., 2006), being in line with the observations of Gichuki et al. (2003) regarding the high levels of variation within different geographical regions. Thus, RAPD analysis suggests that the core selection for the establishment of the Mozambican sweet potato collection was successful in what concerns the levels of genetic diversity. This is also reflected in the cluster analysis, where the Mozambican accessions are distributed over 5 out of the 6 clusters, with two out grouping genotypes. This pattern of distribution is extensible to the different geographic regions within the country. Although half of the accessions were grouped in cluster IV, the maximal genetic similarity within this cluster was around 0.70, a value quite similar to the mean genetic similarity of the Tanzanian regional collection (Elameen et al., 2008). Only two pairs of accessions, Nhacutse-3 and Admarc (respectively from Gaza and Zambezia, Mozambique) and Chingova and Moz white (both from Zimbabwe) were closely related, the latter pair possibly representing duplicates.

The Mantel test revealed no significant, but an unusually high correlation between matrices built using morphological and molecular ($p = 0.75$) data (Table 9). In fact, the results of the cluster analysis based on the phenotypic diversity (Fig. 2), partially corroborate the molecular data: i) 8 out of the 12 accessions from RAPD-derived cluster I remain together in cluster I from morphological traits (Admarc, Tuang-Thuang and Nwazambane from Mozambique, Tacna, ST 87-30 and Mafutha from South Africa, NASPOT 5 from Uganda, and Cordner from Zimbabwe); ii) 9 out of the 12 Mozambican cultivars composing cluster II in the RAPD dendrogram were distributed over cluster I (Chulamete,

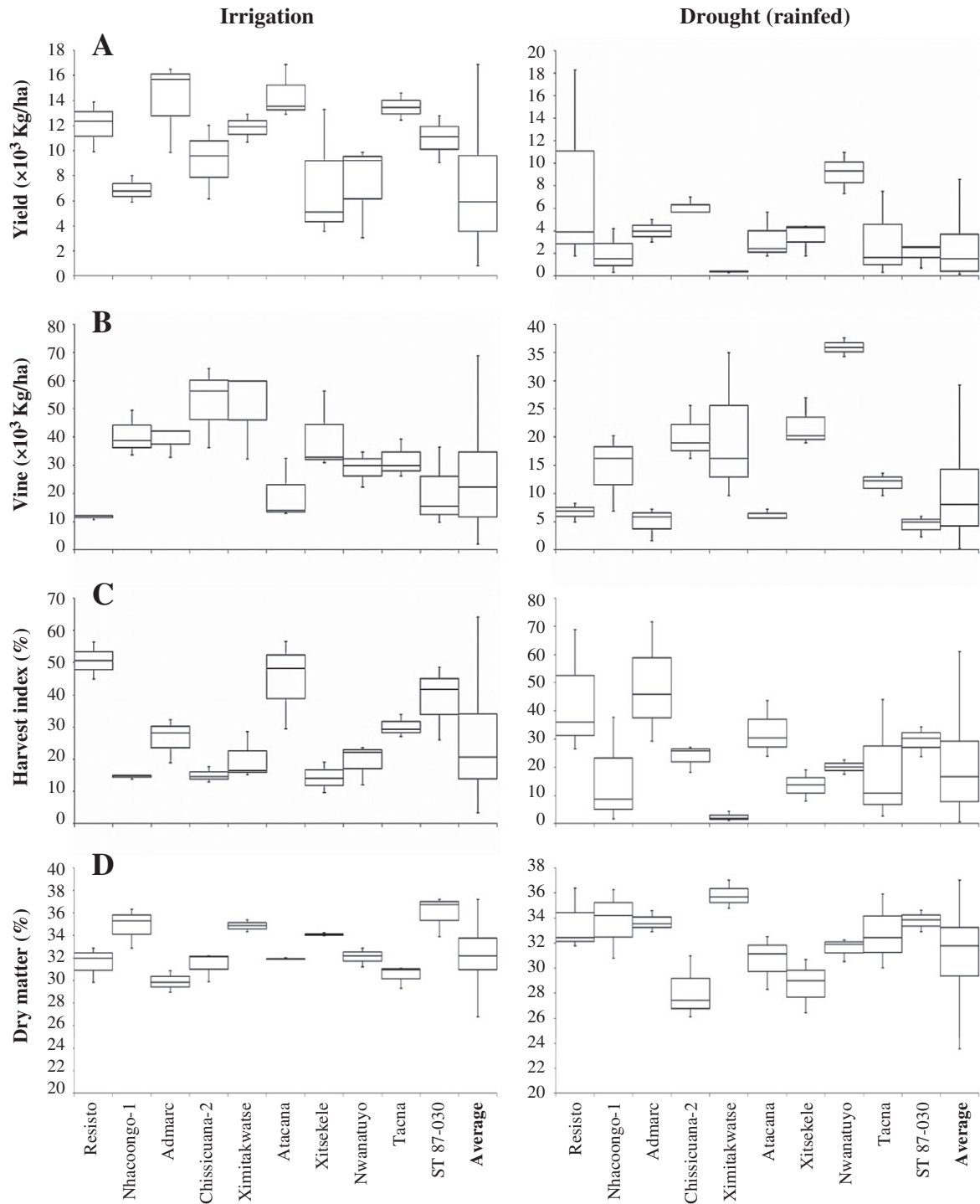


Fig. 4. Box-whisker plot of agronomic performance, storage root yield (A), vine weight (B), harvest index (C) and dry matter (D), comparing the statistics of the global-top10 ranked accessions with the main average observed for all 44 accessions analyzed, measured under irrigation (left panel) and rainfed (right panel) conditions.

Nwaxitsimbwa, Xiphone and Nhacutse 4) and II (Chissicuana 1, Xiadlaxa-kau, Cacilda, Jogó 2, and Mafambane) in the tree constructed based on morphological data. Additionally, like in the case of RAPD, the morphological analysis did not reflect the geographical origin of the genotypes, except for three accessions from CIP (Jonathan, CN 1448-49, and Lo-323). Similar results were obtained with the sweet potato collections from Brazil (Veasey et al., 2007), South Africa (Laurie et al., 2013), Tanzania (Tairo et al., 2008; Elameen et al., 2011), and Uganda (Yada et al., 2010).

The agronomic diversity of the 44 accessions was also high, as revealed by the substantial dispersion observed outside the center of

the PCA plot (Fig. 3). This result contrasts with the low agronomic diversity of the Tanzanian collections from the Mikocheni Agricultural Research Institute (Tairo et al., 2008), from the Sokoine University of Agriculture, Morogoro and from the Sugarcane Research Institute (Elameen et al., 2008, 2011) and is most likely due to the fact that a national germplasm bank is not available in Tanzania, with most of the collections located regionally (Tairo et al., 2008; Elameen et al., 2011). Agronomic cluster analysis did not significantly correlate to the molecular and morphological analyses, but the correlation with the later was considerably high, i.e. $p = 0.86$ (Table 9). Even so, it should be highlighted that 6 cultivars (Tacna, ST 87-30, Mafutha, Admarc,

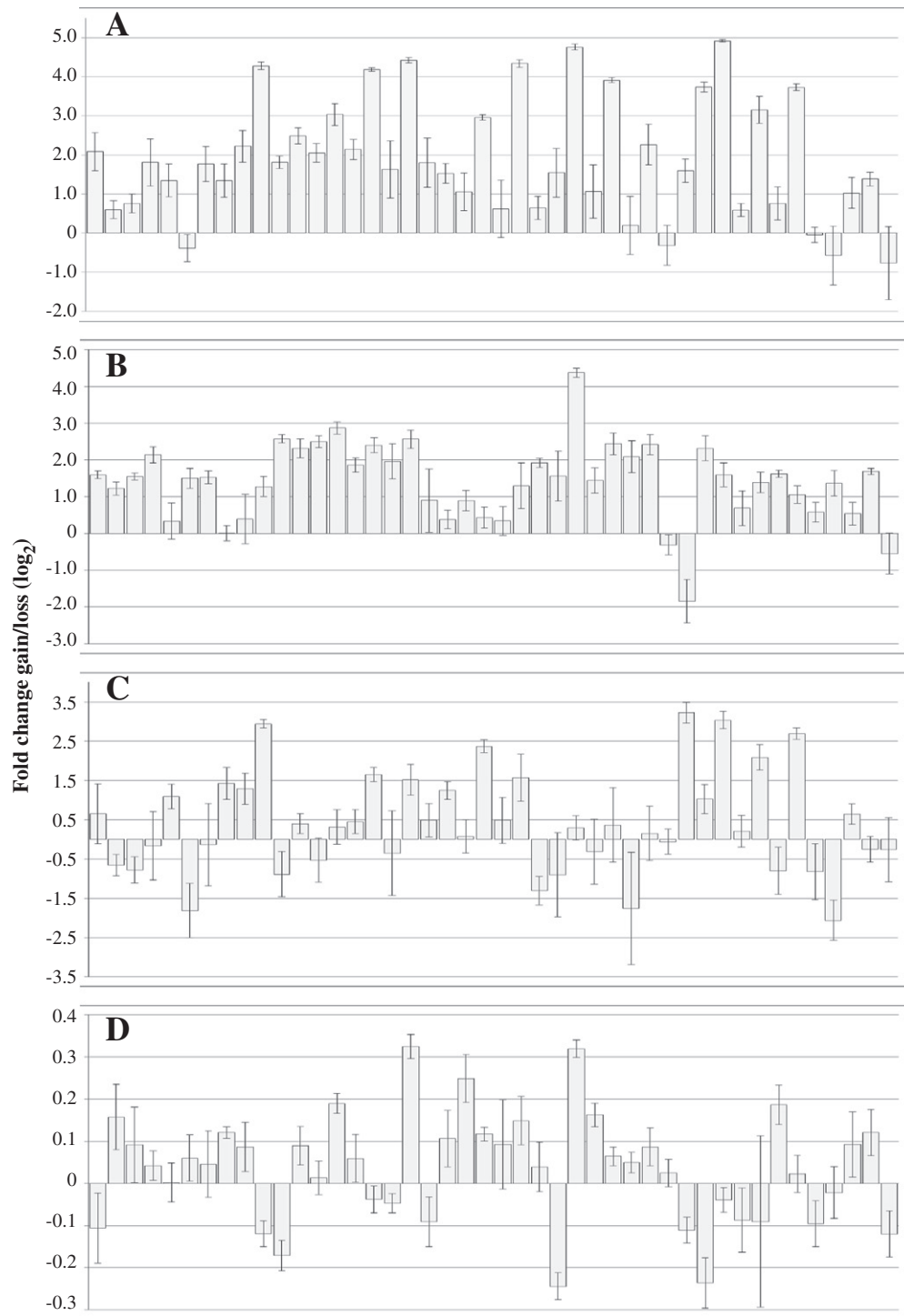


Fig. 5. Fold-change (\log_2) of the ratio between the measured values of storage root yield (A), vine weight (B), harvest index (C) and dry matter (D), under irrigation and under rainfed conditions. From left to right: Tacna, Chissicuana-2, Nhacutse-5, Nwaracu, Nwazambane, NASPOT-5, Nhacoongo-1, Mafutha, Nwamanhica, Nhacutse-3, Admarc, ST_87-030, 440203, Tuang-Thuang, Atacana, Chissicuana-3, UNK-Malawe, Nhacutse-2, Jogó, Xiadla-Xa-Kau, Xitsekele, Chissicuana-1, Nhacutse-4, Jogó-2, Nwamazambe, Mafambane, Nwamonguane, Chulamete, Xiphone, Nwaxitsimbwane, Cacilda, Nwanatuyo, Xihetamakote, TIS-9265, Ximitakwatse, Resisto, Jonathan, CN_1448-49, Cordner, Chingova, TIS-2534, Moz_white, Lo-323, SPK-004.

Cordner and Nwazambane) maintain low dissimilarity distances in the three different approaches used to analyze the sweet potato collection from Mozambique. The statistically significant correlation between the morphological character LMV with the agronomic features vine weight and harvest index (HI), and between the morphological characters CML and CIL with DM (Table 8), make these phenotypic attributes strong candidates to be used as early morphological markers of productivity, when analyzing a new genotype set.

In general, the top 10 accessions presented agronomic performances above average for all parameters analyzed: storage root yield (Y), vine weight (V), HI and dry matter content (DM) (Fig. 4), independently of the water regime. Among them, the Mozambican genotypes were well represented: 8 in the irrigation trial (I) and 5 in the rainfed trial (D), with a regular distribution in what concerns their geographical origin: (I) 4 accessions from Gaza and 4 from Inhambane; and (D) two accessions from Gaza, two from Inhambane and one from Zambezia. This

Table 8

Pearson's correlation coefficients obtained between the morphological and agronomic characters quantified. Bold values are significant at 99% of probability.

	Yield	Vine	Biomass	HI	DM
LMV	-0.03	0.36	0.33	-0.37	0.09
LI	-0.13	0.04	0.01	-0.12	-0.15
DI	0.15	0.21	0.23	-0.04	-0.26
PCV	0.22	-0.08	-0.02	0.24	-0.26
SCV	-0.01	0.03	0.02	-0.05	0.15
TVP	-0.01	-0.12	-0.11	0.15	-0.23
GLO	0.01	-0.15	-0.13	0.09	-0.19
TLL	-0.01	-0.17	-0.16	0.08	-0.27
NLL	0.11	-0.05	-0.02	0.08	-0.05
SCL	-0.04	-0.21	-0.20	0.10	-0.30
SML	-0.03	-0.03	-0.03	-0.00	-0.03
VP	0.14	0.15	0.17	-0.03	-0.27
CML	-0.13	0.12	0.08	-0.22	0.30
CIL	0.00	-0.10	-0.09	0.12	-0.34
LP	-0.10	-0.00	-0.03	0.03	-0.19
PP	0.18	-0.01	0.03	0.17	-0.28

LMV – length of the main vine; LI – length of the internode; DI – diameter of the internode; PCV – predominant color of the main vine; SCV – secondary color of the vine; TVP – type of vine pubescence; GLO – general leaf outline; TLL – type of leaf lobes; NLL – number of leaf lobes; SCL – shape of the central lobe; SML – size of the mature leaf; VP – vein pigmentation; CML – color of the mature leaf; CIL – color of the immature leaf; LP – length of the petiole; PP – pigmentation of the petiole.

result is supported by the PCA analysis based on agronomic performance (Fig. 3). In fact, these accessions are plotted in the most distant positions with respect to the center or at the end of the minimum spanning tree, particularly striking for the top 4 genotypes. This observation is in line with the diversity analysis, supporting the hypothesis of a rigorous and successful establishment of the Mozambican sweet potato collection. Among the regional (African) genotypes, ST_87-030 from South African was one of the top 10 genotypes in (I), while 4 genotypes from Zimbabwe (Chingova and Moz_white), Uganda (NASPOT 5), and Kenya (SPK-004) ranked among the top 10 in the rainfed trial. Resisto, from the USA, was the only international (outside Africa) genotype within the top 10 group, with outstanding results in both (I) and (D) trials. These observations indicate that the national and regional genotypes are better adapted to the local agro-climatic conditions, calling up for their importance in future breeding programs.

As expected, the majority of the genotypes achieved the best performances under irrigation conditions, but independently of their rank, some genotypes behave differently, presenting no gains in both water regimes or even showing gains regarding some parameters under rainfed conditions. Three genotypes from Gaza (Nhacutse 4, Nwaxitsimbwane, Nwanatuyo), one from Zimbabwe (Chingova), one from Kenya (SPK 004) and one from IITA (TIS 2534), presented no gains in storage root yield. The fact that Nhacutse 4 and SPK 004 have shown consistent results (no gains/losses) in all parameters analyzed might be an indicative of drought tolerance and suitability to be used as low risk material under the scope of production stability. Nevertheless, a higher gain/loss value under a particular condition doesn't mean better overall agronomic production. For example, Nhacutse 4 is not in the top 10 list (Tables 7 and S2), so, even though it is not affected by water deficit, its production is not high. The number of accessions with gains under rainfed conditions was limited to one

(NASPOT 5, Uganda), two ((Nwanatuyo and Xihetamakote, Mozambique) and nine (Chissicuana 2, Nhacutse 5, Admarc, Nwamazambe and Nwaxitsimbwane, Mozambique; NASPOT 5, Uganda; Chingova, Zimbabwe; CN 1448-49, CIP; TIS 2534, IITA) in the case of Y, V and HI, respectively. From these, five (NASPOT-5, Nwanatuyo, Xihetamakote, Chissicuana 2 and Admarc) ranked in the top 10 set of samples from the rainfed trial and might be very useful for breeding toward drought tolerance.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.sajb.2013.07.008>.

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Table 9

Correlations and Mantel test among similarity matrices based on morphological, agronomic and molecular data.

	Molecular	Morphological
Morphological	Matrix correlation: $r = 0.05942$ (= normalized Mantel statistic Z) Approximate Mantel t -test: $t = 0.6734$; Prob. random $Z < \text{obs. } Z$: $p = 0.7497$	–
Agronomic	Matrix correlation: $r = -0.06740$ (= normalized Mantel statistic Z) Approximate Mantel t -test: $t = -0.7547$; Prob. random $Z < \text{obs. } Z$: $p = 0.2252$	Matrix correlation: $r = 0.10140$ (= normalized Mantel statistic Z) Approximate Mantel t -test: $t = 1.0697$; Prob. random $Z < \text{obs. } Z$: $p = 0.8576$

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