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RESEARCH ARTICLE

REVISED Continuous Storage Root Formation and Bulking in Sweetpotato [version 2; peer review: 1 approved, 1 approved with reservations, 1 not approved]

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v2 **First published:** 11 Feb 2019, **3**:83
https://doi.org/10.12688/gatesopenres.12895.1
Second version: 14 Oct 2019, **3**:83
https://doi.org/10.12688/gatesopenres.12895.2
Latest published: 08 Apr 2020, **3**:83
https://doi.org/10.12688/gatesopenres.12895.3

Abstract

This study investigated the phenotypic variation of continuous storage root formation and bulking (CSRFAB) growth patterns underlying the development of sweetpotato genotypes for identification of potential varieties adapted to piecemeal harvesting for small scale farmers. The research was conducted between September 2016 and August 2017 in Uganda. Genotypes from two distinct sweetpotato genepool populations (Population Uganda A and Population Uganda B) comprising 130 genotypes, previously separated using 31 simple sequence repeat (SSR) markers were used. Measurements (4 harvest times with 4 plants each) were repeated on genotypes in a randomized complete block design with 2 replications in 2 locations for 2 seasons. We developed a scoring scale of 1 to 9 and used it to compare growth changes between consecutive harvests. Data analysis was done using residual or restricted maximum likelihood (REML) in GenStat 18th Edition. There were strong linear and quadratic trends over time (P<0.001) indicating a non-linear growth pattern within and between locations, seasons, and genotypes for most traits. Some genotypes displayed early initiation and a determinate linear increase of bulking, while others showed late initiation following a quadratic growth pattern. Broad sense heritability of CSRFAB would be low due to large GxE interactions, however, it was relatively high (50.5%) compared to other yield related traits indicating high genetic influence and accuracy of the developed method to quantify yield overtime. A high level of reproducibility (89%) was observed comparing 2017A and 2017B seasons (A and B are

Open Peer Review

Reviewer Status ✗ ✓ ?

	Invited Reviewers		
	1	**2**	**3**
version 3 (revision) 08 Apr 2020			
version 2 (revision) 14 Oct 2019			? report
version 1 11 Feb 2019	✗ report	✓ report	

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first and second season, respectively) at the National Crops Resources Research Institute (NaCRRI), Namulonge, Uganda. Choosing CSRFAB genotypes can more than double the sweetpotato production (average maximum yield of 13.1 t/ha for discontinuous storage root formation and bulking (DSRFAB) versus 28.6 t/ha for CSRFAB demonstrating the importance of this underresearched component of storage root yield.

Keywords
Sweetpotato, yield, continuous storage root formation and bulking, growth pattern, phenotypic variation

Any reports and responses or comments on the article can be found at the end of the article.

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Competing interests: No competing interests were disclosed.

Grant information: This work was supported by the Bill and Melinda Gates Foundation [OPP1019987] as part of the SASHA II project, and the CGIAR Research Program on Roots, Tubers and Bananas (RTB) under the CGIAR Fund Donors (http://www.cgiar.org/about-us/our-funders/).
The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

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How to cite this article: Bararyenya A, Tukamuhabwa P, Gibson P *et al.* **Continuous Storage Root Formation and Bulking in Sweetpotato [version 2; peer review: 1 approved, 1 approved with reservations, 1 not approved]** Gates Open Research 2019, **3**:83 https://doi.org/10.12688/gatesopenres.12895.2

First published: 11 Feb 2019, **3**:83 https://doi.org/10.12688/gatesopenres.12895.1

REVISED **Amendments from Version 1**

We would like to thank the reviewers for their thorough review of our manuscript. They raised concerns and their input has been very helpful for improving the manuscript. We generally agree with their comments and we have revised the manuscript as recommended and indicated exceptions giving reasons. We addressed the concerns raised by Professor Arthur Villordon and Professor Hussein Shimelis and a detailed report of responses is provided.

Main differences between this version and the previous version are:

1) We have revised the last sentence on page 4, paragraph 2 that was confusing the two different processes, "storage root formation" and "continuous storage root formation and bulking". We included most of the references suggested by reviewer 1 and also provided original references as requested.

2) We have revised the scale to address the queries raised by Prof. Villordon and the revision does not affect the data.

3) We added the missing original reference and a missing acronym on page 4 and the sentence was corrected to read: It is reported that the onset of storage root initiation can be observed to occur as early as 7 to 13 days after planting (DAP) (Du Plooy, 1989) and the total storage root numbers vary from 30 to 112 DAP depending on the genotype and the environmental conditions under which they are grown (Belehu *et al.*, 2004; Wilson & Lowe, 1973; Yanfu *et al.*, 1989).

4) We included cumulative data in relevant figures and we discussed their implication and reflected them in the text. In the conclusion, we included a text to highlight the advantage of CSRFAB over the DSCRAB ones.

We hope that the changes we have made as suggested by the reviewers have improved the quality of the manuscript, and any further suggestions that the reviewers may have are welcome.

Any further responses from the reviewers can be found at the end of the article

Introduction

Sweetpotato (*Ipomoea batatas* (L.) Lam, family Convolvulaceae.) is one of the most important food crops worldwide, with approximately 106 million tons produced in almost 120 countries from an area of about 8 million ha and an average global yield of 11.1 tons/ha (FAO, 2016). Asia is the world's largest sweetpotato producing continent, with 79 million tons, followed by Africa (FAOstat, 2016). About 75% of this global production is from China alone. A total of 21.3 million tons is produced in Africa, with 48% from the Great Lakes region. In East Africa, the crop is the second most important root crop after cassava and has played an important role as a famine-relief crop during its long history and has recently been reevaluated as a health-promoting food (Low *et al.*, 2017). Uganda ranks as the fourth largest sweetpotato producer in the world after China, Nigeria and Tanzania, with a production of 2.1 million t. In Africa, Uganda is ranked third after Nigeria and Tanzania. Sweetpotato is one of the main staple crops in the food systems of Uganda, Rwanda, and Burundi with a per capita consumption of 50.9, 80.1 and 57.0 kg, respectively (Table 1).

On average and across the 30-year period, the population across East Africa increased by two-and-half-fold while sweetpotato production increased by two-fold. This trend resulted in a decrease in per capita production from 86 to 56 kg per person. Statistics in general underestimate production in most annual plants since not all crop production is recorded. Usually, only the main planting season is recorded even though crops are grown over two to three growing seasons per year (Bararyenya *et al.*, 2018a)). The most noticeable production increase took place in Tanzania with more than ten-fold increase of tonnage following an almost two-fold increase in growing area and almost four-fold increase in yields. The highest productivity is recorded in Kenya, with more than 17 t/ha/yr, followed by Tanzania (12.5 t/ha/yr). In other East African countries, productivity has more or less stagnated. The yield increase in the region over the 30-year period

Table 1. Increase in sweetpotato production in East and Central African countries, production data for 1985 and 30 years later for 2015.

Country	Area		Yield		Production per year		Population		Per annum	
	x 1000 ha		tons per ha		x 1000 tons		millions		kg per capita	
	1985	2015	1985	2015	1985	2015	1985	2015	1985	2015
Burundi	87.0	58.6	6.4	9.9	555.0	580.9	4.7	10.2	118.0	57.0
Kenya	50.0	72.2	9.9	17.1	488.0	1232.3	19.7	47.2	24.8	26.1
Rwanda	135.9	139.7	7.1	6.7	979.5	931.0	6.1	11.6	160.1	80.1
Uganda	358.7	454.5	4.6	4.5	1664.0	2045.2	14.7	40.1	113.6	50.9
Tanzania	290.0	746.6	4.6	12.5	303.0	3454.5	21.8	53.9	13.9	64.1
Average	921.6	1471.6	8.1	8.6	3989.5	8243.9	13.4	32.6	86.1	55.6
Increase		**1.60**		**1.06**		**2.07**		**2.44**		**30.45**

Source: FAOstat, 2016

can be attributed to breeding and release of improved varieties by national breeding programs, and to the introduction of new varieties mainly, by the International Potato Center (CIP). The increase in yield can also be explained by the importance and recent interest in sweetpotato as a food and nutritious crop compared to the early 1990s when it was hardly known.

Despite the giant strides made through breeding and release of 27 high yielding and disease resistant varieties (Mwanga *et al*., 2016), Uganda has over the last 30 years consistently reported extremely low yields of 4 t/ha (Table 1) compared to the achievable yields of over 40 t/ha under improved conditions. The low yield could be attributed partly to the growing of low yielding and highly disease susceptible landraces by small-scale farmers. Abidin (2004) reported high farmer preference for their landraces, while Sseruwu (2012) associated this preference with lack of farmer desired attributes in the newly released varieties. In Uganda and other East African countries, piecemeal harvesting, characterized by repeated harvesting from the same sweetpotato plants on a mound, ridge or other seedbed over time, is the predominant mode of harvesting among subsistence and commercial sweetpotato farmers. Importantly, this practice is also known in other root and tuber crops including potato, cassava and yam. Recently, Tadesse *et al*. (2017) reported that piecemeal harvesting was the dominant practice among poor potato farmers (60% of respondents) in Ethiopia, whereas the majority of the wealthy and medium-wealthy farmers combined piecemeal harvesting with harvesting all at once. Farmers harvest enough for one or few meal(s), or enough for one market. This is because these crops are very difficult to store, and storage for fresh sweetpotato produce is virtually non-existent. Therefore, the practice allows for in-ground storability and market partitioning during the cropping season. It also creates room for new storage roots to initiate and enlarge for the next harvest. However, breeding and selection have been based on a single harvest and no breeding research has tried to understand the genetics underlying traits associated with these common practices in sweetpotato farming systems. CSRFAB in sweetpotato is associated with the perennial nature of the crop and allows for longer photosynthetic activity resulting from persistent canopy development leading to increased plant productivity. This is supported in the case of practices in Uganda by the fact that more than 90% (n = 350) of the farmers have no knowledge of the maturity periods of the local sweetpotato varieties they grow (Bashaasha *et al*., 1995).

Maturity periods in sweetpotato vary with genotype and the environmental conditions under which they are grown. Common external signs of maturity such as senescing and yellowing of leaves do not apply to all varieties. In addition, storage roots do not all mature at the same time, while the storage root formation period is highly variable among genotypes (Belehu, 2003; Belehu *et al*. 2004; Lowe & Wilson, 1974; Wilson & Low, 1973; Yanfu *et al*., 1989). It is reported that the onset of storage root initiation can occur as early as 7 to 13 days after planting (DAP) (Du Plooy, 1989), and the total storage root number to form varies from 30 to 112 DAP depending on the genotype and the environmental conditions under which they are grown (Yanfu *et al*., 1989). Furthermore, sweetpotato storage roots can undergo periods of arrested growth during unfavorable conditions and then continue active growth upon favorable conditions (Ravi *et al*., 2009). There are many reported studies on the effects of storage root formation and bulking under controlled conditions on sweetpotato yields (Gajanayake & Reddy, 2016; Meyers *et al*., 2013; Solis *et al*., 2014; Villordon, 2015) and under field experiments (Agata, 1982; Belehu *et al*., 2004; Du Plooy, 1989; Enyi, 1977; Gajanayake *et al*., 2014; Lowe & Wilson, 1974; Wilson & Lowe, 1973; Wilson, 1982; Yanfu *et al*., 1989). However, most of the studies were undertaken on single season harvest basis, and no study attempted to understand the continuous storage root formation and bulking (CSRFAB) patterns overtime under field conditions to focus on improving the trait through breeding.

Knowledge of the growth patterns of storage root formation and bulking traits is critical for crop yield improvement, crop management, and specifically for timing fertilizer application and irrigation. Sweetpotato has been for centuries selected for its starchy roots on seasonal basis and may have been progressively losing its perennial feature. It is well known in other root and tuber crops that yields are a result of the rate and duration of the period of tuberization, which in turn depends on longevity of the leaves, the beginning of storage root formation, and duration of the growth cycle. In almost all experiments, the end time of storage root formation was not defined or properly assessed; number of storage roots was infrequently recorded and maximum number of storage roots was never established. The effect of longer vegetative maintenance periods of green leaves observed in some genotypes has never been investigated in sweetpotato, but it is reported to influence greater productivity in potato (Çalişkan *et al*., 2007). Despite these deficiencies, the storage root formation and bulking patterns are widely regarded as a key developmental stage in the crop's life, having profound implications for subsequent growth and development. It was therefore hypothesized that longevity of green foliage due to genetic properties in CSRFAB sweetpotato genotypes is greater than in discontinuous storage formation and bulking (DSRFAB) genotypes. Consequently, the extended period of green leaves for CSRFAB genotypes will impact storage root formation and bulking leading to a significant increase in yield. This expected variation in yield and yield components is mainly due to longer duration of photosynthetic activity and the great availability of photo-synthesizing material, mostly its green leaves (Paltridge *et al*., 1984). Thus, the amount of change in the mean value of expected responses associated with a unit increase in growth time, holding all other variables constant, varies with increased growth time periods of some sweetpotato cultivars and produces higher amounts of storage root number and weight. To really understand the evolution of a trait, we need to know whether any variability in that trait can be assigned to genetic effects. If so, and if there is fitness variation associated with the trait; it will be subject to natural selection (Croston *et al*., 2015). This study investigated genetic variability of CSRFAB and, characterized growth patterns at different development stages to identify possible CSRFAB sweetpotato genotypes in the germplasm collection in Uganda for use as parents in improvement of the trait.

Methods

Plant materials and experimental sites

Plant materials. This study utilized 130 genotypes currently used for population improvement in Uganda for various breeding purposes and were screened for CSRFAB traits (Table 2). The 130 cultivars included two distinct sweetpotato gene pool populations (Uganda A and Uganda B) that were formed to reflect similarity within and divergence between the populations based on 31 simple sequence repeat (SSR) markers (David *et al.*, 2018). The genotypes are maintained by the International Potato Center (CIP) at the National Crops Resources Research Institute (NaCRRI) at Namulonge in Uganda.

Experimental sites and duration of the study. Grüneberg *et al.* (2005) identified Uganda as a mega-environment for sweetpotato selection for East African countries, and a breeding platform where crossings and selection in early and later breeding stages were conducted. The results from such environments are extended to all East African countries with one or two more season evaluations for confirmation. Two locations, NaCRRI-Namulonge and National Semi-Arid Resources Research Institute (NaSARRI-Serere) were therefore selected to host the trials for screening potential CSRFAB genotypes adapted to the East African agroecologies. The trials were planted on September 22, 2016 and September 29, 2016, respectively at Namulonge and Serere and harvested from January through April 2017 for the first season (2016B). In the second season (2017A), trials were planted on March 10, 2017 and March 29, 2017, respectively, at Namulonge and Serere and harvested from June to September 2017. The altitude of the sites was around 1,150 meters above sea level with an average day temperature of 22.2°C. Crops were not irrigated and often suffered from low rainfall 4 months after

Table 2. List of genotypes screened for continuous storage root formation and bulking in Uganda, 2016 to 2017.

Code	Name	Code	Name	Code	Name	Code	Name	Code	Name
A1	Carrot C	A27	Apa352	B3	Hma496	B29	Mkn1210	B55	K-566632
A2	Ejumula	A28	Luw1274	B4	Msd380	B30	NASPOT 5	B56	New Kawogo
A3	Mayai	A29	Sponge	B5	Luw1230	B31	Kre723	B57	Bitambi
A4	Naspot5/58	A30	NASPOT 7	B6	Srt43	B32	Ara236	B58	Kbl611
A5	Kbl619	A31	NASPOT 10 O	B7	Srt28	B33	SPK004(CIP)	B59	Mkn171
A6	Kmi61	A32	Kml872	B8	Mle199	B34	Mpg1158	B60	Mle191
A7	Kbl631	A33	Msk1040	B9	Mary	B35	Jonathan	B61	Iga998
A8	Pal133	A34	Dimbuka-Bukulula	B10	Kml942	B36	Kml960	B62	Pal134
A9	Pal94 silk	A35	Oguroilwe	B11	Lir302	B37	Bsh741	B63	Wt-237
A10	Rak786	A36	Kmi159	B12	Kbl650	B38	Bnd145l	B64	Iga994
A11	Mpg1128	A37	Mkn1168	B13	Mpg1151	B39	Srt41	B65	Naveto
A12	Tanzania	A38	Apa335	B14	Mkn1180	B40	Srt01	B66	Xushu18
A13	Kala	A39	Apa323	B15	Luw1257	B41	Wagabolige	B67	Yanshu1
A14	Kbl648	A40	Otada	B16	Kre691	B42	Lir258	B68	Zambezi
A15	Kml956	A41	Ukerewe	B17	Mbr536	B43	Pal148	B69	Jewel
A16	Bsh740	A42	Kmi88	B18	Ksr662	B44	Rak865	B70	Caromex
A17	Silk(1254)	A43	Mpg1148	B19	Mle179	B45	Mpg1122	B71	Resisto cip
A18	Rak819	A44	Iga983	B20	Msd431	B46	Msk1079	B72	Baeuregard
A19	SPK004	A45	Pal108	B21	Mle163	B47	Rak848	B73	Kyabafuruki
A20	Nk259l	A46	Rak835	B22	Magabali	B48	Mugande	B74	Tainung 64
A21	Kml881	A47	Msd384	B23	Kbl618	B49	Ara224	B75	Kre696
A22	NASPOT 9 O	A48	Srt27	B24	Mbr552	B50	Dlp3163	B76	Raihna
A23	Tororo 3	A49	Nk318l	B25	Iga978	B51	Msk1094	B77	Tis9265
A24	NASPOT 1	A50	Mle194	B26	Sowola	B52	Tis9101	B78	199062.1
A25	Rak808	B1	Resisto	B27	Hma490	B53	NASPOT 3	B79	Santa amaro
A26	Mpg1146	B2	Ara209	B28	Apa356	B54	NK1081L	B80	Huarmeyano

planting. Namulonge is characterized by a tropical rain forest zone with a bimodal rainfall average of 1,270 mm annually and high sweetpotato virus disease (SPVD) pressure, while Serere is in the tall grassland savanna zone with low rainfall and high weevil population (Table 3).

Experimental design

We used repeated measurements (Hesser, 2015) on genotypes in a randomized complete block design in 2 locations (Namulonge and Serere) for 2 seasons. The experimental plots consisted of two rows of 20 plants (4 replications of five plants, but for ease of data collection and analysis, the samples were collected as two replications). Plant density was 1 m between rows and 0.3 m between plants within rows. Four measurement points (Causton, 1994) were used for flexibility and precision of analysis. The genotypes were sequentially and destructively harvested at 3, 4, 5 and 6 months after planting (MAP) to allow identification of storage root formation and bulking patterns. During each harvest period, four plants were uprooted for above and below ground part data collection. Each row was bordered by two sweetpotato plants at the extreme ends. The plots were kept weed free and no fertilizer or other agro-chemicals were applied.

Data collection methods

Growth and development measurements. Traits that are known to characterize growth in sweetpotato storage roots were selected. These included: (i) number of harvested plants (NPH), allowing calculation of average values, (ii) total storage root number (SRN), (iii) Total root weight (TRW) measured with a round spring balance scale (Hanson, 8 in x 8 in x 3 in), was used to calculate yield as tons per hectare, (iv) commercial and non-commercial storage root number (CRN & NCRN, respectively) and commercial and noncommercial storage root weights (CRW & NCRW, respectively), allowing the estimation of storage root formation, bulking rate, (v) vine weight (VW), (vi) root system weight (RSW) used to calculate biomass yield (BMY), and (vii) harvest index (HI). Senescence (SEN) was estimated using a scale of 1 to 9, where 1 = no senescence, 9 = severe senescence marked by death/drying (CIP/AVRDC/IPGR, 1991).

Development of a scale for continuous storage root formation and bulking (CSRFAB). To capture the possible overtime initiation and bulking in sweetpotato, we developed a rating scale of 1 to 9. The scale rates the expression of CSRFAB trait for an individual genotype. CSRFAB scores were therefore developed throughout the 2016B growing season. Detailed observation of storage root formation and bulking over 6 months provided comprehensive knowledge of the development of a scale for measuring changes in the CSRFAB trait. The scale was set to measure the changes in root formation and bulking of a given individual genotype. The change in scores would reflect the potential of roots to bulk into storage roots (fleshy or lignified), newly initiated storage roots, their status of bulking and their maturity levels. Paired numbers were skipped in determining which unpaired scores were too close to each other. Thus, a higher score is indicative of greater CSRFAB expression for the genotype. Figure 1 shows CSRFAB and the scoring scale.

Data analysis

Growth model analysis. Growth models were estimated using a multilevel, mixed model framework described by Payne (2009) in GenStat 18th Edition. Data was re-arranged to have all the four-time point observations in a single variate, with accompanying factors for location, season, harvest time, genotype and replication. All factors were duplicated for each of the harvest times, and a factor, harvest time, was set up to record the number of the stacked columns corresponding to each row of the new sheet. Variates were calculated to hold the harvest time and the square of harvest time using "calculate menu" in Genstat spread menu. Each of the 130 genotypes was maximally compared (4160 times) with the other genotypes in a model with two replications, four harvest times, two seasons and two locations.

To better understand the details in the storage root development patterns across the four harvest times; we included linear and quadratic variates in the model to detect trends, followed by HT as a factor variate to detect lack of fit. We analyzed piecewise, storage root growth patterns in different phases of the trial and selected individuals to represent different growth pattern characteristics. Means were plotted to visualize the growth patterns using Genstat 18th edition

Table 3. Description of study sites used for screening sweetpotato genotypes for continuous storage root formation and bulking in Uganda.

Location	Elevation	Temperature	Rainfall	Soil			
	(masl)	(°C)	(mm)	pH	OM	K	P
					(%)	Cmol/kg	Cmol/kg
NaCRRI (2016B)	1150	24–30	1400–1600	4.8	3.8	0.11	Trace
NaSARRI (2016B)	1140	25–32	1100–1300	4.9	3.7	0.19	Trace
NaCRRI (2017A)	1150	22–29	1550	5.2	3.4	0.76	1.66
NaSARRI (2017A)	1140	23–31	1150–1350	4.9	3.6	0.56	0.92

Note. NaCRRI: National Crops Resources Research Institute; 2016B: 2016 second season; NaSARRI: National Semi-Arid Resources Research Institute; 2017A: 2017 first season; masl: meters above sea level; °C: degrees celcius; mm: millimeters; OM: organic matter; K: potassium; P: phosphorus

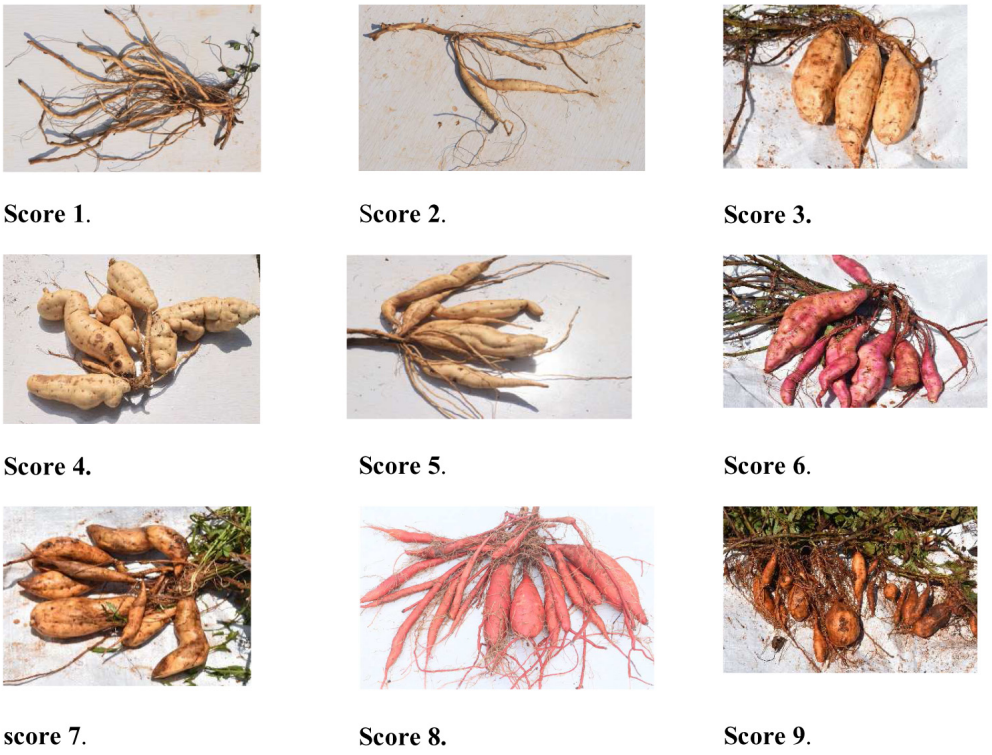

Figure 1. A 1 to 9 scoring scale for continuous storage root formation and bulking in which score: 1 = no visual detectable storage root initiation (SRI) and no visually detectable bulking; 2 = Storage root formation and bulking detectable; 3 = no visually SRI and has unclear levels of bulking; 4 = distinct SRI and 2 clear levels of bulking; 5 = distinct SRI and 3 clear levels of bulking; 6 = distinct SRI and 4 clear levels of bulking; 7 = distinct SRI and 5 clear levels of bulking; 8 = distinct SRI and 6 clear levels of bulking; and 9 = distinct SRI and 7 clear levels of bulking.

Restricted maximum likelihood (REML) variance components analysis of the phenotypic data was performed using the following general linear mixed model;

$$Y_{ijklcqm}=\mu+S_i+L_j+SL_{ij}+SLR_{ijk}+H_l^1+H_q^2+H_c^3+SH_{il}+LH_{jl}+SLH_{il}+E_m+EH_{lm}^1+EH_{qm}^2+EH_{cm}^3+SE_{im}+LE_{jm}+SLE_{ijm}+\epsilon_{iml}+LEH_{jml}+SLEH_{ijml}+\varepsilon_{ijklcqm}$$

Where

Y_{ijklm} is the observed overtime response of genotypes across location and season.

μ, is the overall mean, S_i is the effect of the ith season, L_j is the effect of the jth location, SLR_{ijk} is the effect of the interaction between the ith season in the jth location and the kth replication, HT_l^1 is the effect of linear term l in polynomial model, HT_q^2 is the effect of the quadratic term q in polynomial model, HT_c^3 is the random effect of the cubic term in the polynomial model, SH_{il} is the interaction between season and harvest time, LH_{il} is the random effect of interaction between jth location and h^{th} harvest time, SLH_{iil} is the effect of the interaction between the ith season and the jth location at the mth harvest time, E_m is the effect of the m^{th} genotype, EH_{lm}^1 *is the* effect of interaction between mth genotype and lth linear term, EH_{qm}^2 is the effect of the interaction between ith genotype and qth quadratic term in the polynomial model, EH_{cm}^3 is the effect of interaction between ith genotype and cth cubic term in the polynomial model, SE_{im} is the effect of interaction between season and genotype, LE_{jm} is the effect of interaction between location and genotype, SLE_{ijm} is the random effect of the interaction between season, location and genotype. ϵSEH_{iml}, is the effect of the interaction between season, harvest time and genotypes, LEH_{jml} is the random effect of the interaction between location, harvest time and harvest time, $SLEH_{ijml}$ is the interaction season, location and harvest time, $\varepsilon_{ijklcqm}$ is the error associated with all factors involved in the polynomial model.

We recalculated the F-test denominator for genotypes tested in different locations and seasons (Bararyenya *et al.*, 2018b). This was relevant to factors other than genotypes that were tested across two environmental factors that should be considered random. The choice of the F-test denominator was guided by whether a particular variance component had an estimated value greater than 0. This could be seen in the relative sizes of the mean squares of error and the three environmental interactions with genotypes. If all three GxE interaction variance components (GxLxS, GxL, GxS) were positive (greater than 0), then Satterthwaite's formula was appropriate for determining the appropriate MS to use as the T-test denominator for genotypes.

Satterthwaite's formula for the "composite" F-test denominator for genotypes is as shown:

$$Den\ MS = MS(GL) + MS(GS) + MS(GSL)$$

$$Den\,df = \frac{[MS(GL) + MS(GS) + MS(GSL)]^2}{\frac{MS(GL)^2}{df(GL)} + \frac{MS(GS)^2}{df(GS)} + \frac{MS(GSL)^2}{df(GSL)}}$$

Satterthwaite-type approximation of mean squares (MS) and degrees of freedom (df).

Where MS = mean square, G = genotype, S = season, L = location, df = degree of freedom, Den df = denominator degrees of freedom.

In calculating the F-test, there is no problem using the fractional effective Den df obtained by the formula above (Satterthwaite, 1946; Snedecor & Cochran, 1967). The "Fdist" and "Finv" functions in Excel handle fractional df without a problem.

Results and discussion

Growth pattern analysis and phenotypic variability across selected CSRFAB sweetpotato traits.

We used a linear mixed model to decompose phenotypic variance (P) into different components: genetic (G) and environmental (E) sources, and their interaction effects (GxE). For most of the traits, their three-way interactions were significant which means in reality that at least one of the 2-way interactions changes across the third factor. Thus, the interaction between season, location and replication (SLR) was highly significant across all the parameters. This is because the replication differences were large in some environments as previously observed by Tumwegamire *et al.* (2016). The variability in replication for an experiment involving clonal crops can easily occur. The main effects for season and location were not significant, as were their interactions. The interaction between season, location and harvest time (SLH) was highly significant (P<0.001) for all the parameters in this study, resulting in non-significance of SL, SH and LH interactions. This implies that harvest time effect differs depending on the level of the location and season on storage root yield (SRY), CSRFAB, storage root diameter (SRD), storage root length (SRL), CRW, CRN, HI and SEN (Table 4). These results require further investigation to identify the level of influence (Table 4). The average effect of linear, quadratic and cubic predictors was not significant due to the large mean square of LH. For all the traits in this study, the interaction between season, location and genotype (SLE) was highly significant (P<0.001). This indicates that there was wide variability of genotype across locations and seasons and this wide variability can be used for sweetpotato yield improvement in a specific location. However, there is a need to study the stability across locations and seasons for easy selection of the CSRFAB trait.

This can be explained by the large population effect combined with sample size. The main effect for genotype was highly significant for all the parameters except SRY providing evidence for presence of genetic variability for CSRFAB trait improvement. While the main effects for L and S were not significant, their interactions (SE and LE) with genotype showed strong effects on all parameters except SRY. SE and LE interactions with a linear predictor was significant across all the parameters except SRY and SEN, so any variation in genotype across location and season is linearly explained. In other words, the performance of genotype increases linearly with time. However, the interaction between entry (genotype) and quadratic predictor as well as cubic predictor was not significant, indicating that with 1 df, HC cannot differentiate cubic effects from higher-order effects. This implies that the overall genotype performance increases overtime in any of the parameters in this study is linearly explained. The two-way interaction with genotype (SE and LE) was significant for CSRFAB, SRNO, SRD, CRW, CRN, and SEN. For SE and LE, the F-values are not large, but with many degrees of freedom, they are significant. None of the time predictors alone was significant except for the CRW, however, the overtime means show a pattern that is stationary from 90 DAP to 120 DAP, followed by a slight overall increase from 120 DAP to 150 DAP. The late phase on average decreased. In summary, one can identify three growth patterns, including an early increasing linear growth, a stationary growth and a late increase then decrease growth pattern. The observation of derived overall means (Table 5) from linear and quadratic models suggests the existence of determinate and extended growth maturity stages among genotypes. High variation (P<0.001) of storage root formation and bulking was observed using the 1 to 9 scoring scale for CSRFAB. This suggests that the scale can be used to differentiate and evaluate the CSRFAB trait among sweetpotato genotypes.

Variance component analysis and heritability estimates of selected sweetpotato growth traits

Variance component analysis and heritability estimates of selected sweetpotato growth traits in a nonlinear model structure. The genotypic variance among the nine traits associated with CSRFAB varied from 0.9 (CRW) to 7.7 (SRNO). Genotypic variance was high for SRNO (7.7), CRN (5.0) and CRW (5.0) (Table 5). The overall contribution of the GxE variance was always high compared to the genetic variance alone. The error variance was also high compared to other variance components. This can be partly explained by the population size, the genotypic variability within the population and the sample size. The phenotypic variance was high for VY (449.8), SRL (378.5) and SRY (84.6) and varied from 2.4 (CSRFAB) to 449.8 (VY). The residual variance was extremely high for VY (412.5) and SRL (339.6). These two particular traits are influenced by continuous growth. While some genotypes continue to increase biomass weight, others die by senescence, likewise for vine length. The error and the GxE variances for CSRFAB are not big compared to its genetic variance. This implies that the scale used to measure the trait is precise and the trait is not influenced much by the environment. The overall broad sense heritability for each trait was not high. This can also be explained by the population size, the variability within the genotypes used and the overall sample size. However, heritability was relatively high for SRNO (67.2%) and CSRFAB (50.5%). The low residual variance and high heritability observed for CSRFAB imply that the CSRFAB trait in this study was not greatly influenced by environment and the scale used to measure the trait is precise.

Table 4. Mean squares and F-test of significance for continuous storage root formation and bulking (CSRFAB), storage root yield (SRY) (tons/ha), storage root number (SRNO), vine yield (VY) (tons/ha), storage root diameter (SRD) (mm), storage root length (SRL) (mm), commercial root number (CRN) and weight (CRW), harvest index (HI) and senescence (SEN) of 130 sweetpotato genotypes from Uganda.

SOV	d.f.	CSRFAB	SRY	SRNO	VY	SRD	SRL	CRW	CRN	HI	SEN
S	1	1223.56^{ns}	2263.89^{ns}	15284.37^{ns}	73832.70^{ns}	2821.05^{ns}	89273.20^{ns}	125.34^{ns}	4381.50^{ns}	383.10^{ns}	21.90^{ns}
L	1	243.40^{ns}	415.52^{ns}	1609.44^{ns}	77317.50^{ns}	1246.97^{ns}	16297.00^{ns}	42.99^{ns}	0.024^{ns}	22744.50^{ns}	7.57^{ns}
SL	1	0.037^{ns}	906.99^{ns}	249.05^{ns}	28398.30*	4147.13^{ns}	9217.60^{ns}	92.14*	281.46^{ns}	1855.40^{ns}	9.24^{ns}
SLR	4	13.14***	595.92***	147.08***	3278.10***	1021.48***	4815.60***	7.57***	42.20***	1235.5***	1.65***
HLin	1	134.56^{ns}	5039.56^{ns}	661.59^{ns}	3801.60^{ns}	276.73^{ns}	2692.20^{ns}	176.72*	107.95^{ns}	22840.60^{ns}	0.01^{ns}
HQ	1	0.037^{ns}	310.48^{ns}	43.89^{ns}	1670.50^{ns}	52.76^{ns}	34.80^{ns}	14.44^{ns}	45.44^{ns}	60.00^{ns}	6.35^{ns}
HC	1	33.212^{ns}	270.43^{ns}	35.27^{ns}	204.70^{ns}	0.22^{ns}	1170.50^{ns}	7.39^{ns}	4.39^{ns}	4655.80^{ns}	8.29^{ns}
SH	3	21.58^{ns}	172.93^{ns}	203.05^{ns}	13015.70^{ns}	100.56^{ns}	1998.90^{ns}	13.28^{ns}	11.99^{ns}	5152.80^{ns}	6.14^{ns}
LH	3	61.12^{ns}	1113.99^{ns}	1062.79^{ns}	1937.90^{ns}	4904.45^{ns}	34388.40^{ns}	3.83^{ns}	847.82^{ns}	7276.10^{ns}	3.55^{ns}
SLH	3	27.55***	242.29**	561.79***	1626.00**	728.56***	6705.80***	17.01***	134.57***	111.8***	2.90***
E	129	12.26***	262.85^{ns}	246.97***	1370.60*	503.38***	3801.90***	4.23***	103.32***	2569.60***	2.13***
HLinE	129	2.73***	71.90^{ns}	39.94***	613.30***	96.35*	522.20**	1.24*	19.72***	269.70^{ns}	1.13^{ns}
HQ.E	129	0.99^{ns}	38.08^{ns}	11.87^{ns}	215.40^{ns}	39.75^{ns}	141.40^{ns}	0.81^{ns}	7.32^{ns}	154.80^{ns}	0.46^{ns}
HC.E	129	1.40^{ns}	46.53^{ns}	17.32^{ns}	329.70^{ns}	38.37^{ns}	192.40^{ns}	0.69^{ns}	7.78^{ns}	183.10^{ns}	0.41^{ns}
SE	129	4.98***	175.22^{ns}	78.07***	1089.30^{ns}	194.50**	1451.00*	1.94**	36.73**	1115.90***	1.35*
L.E	128	4.02*	177.72^{ns}	81.34***	988.80^{ns}	189.38**	1263.80^{ns}	1.95**	33.26*	1009.30***	0.97***
SLE	126	2.90***	119.02^{ns}	45.69***	995.00***	112.38***	1029.10***	1.25***	24.18***	807.70***	0.89***
SHE	385	1.24^{ns}	50.31*	15.50^{ns}	399.80^{ns}	54.21^{ns}	289.10^{ns}	0.74^{ns}	7.79^{ns}	202.40^{ns}	0.77***
LHE	377	1.19^{ns}	57.48*	17.24^{ns}	367.00^{ns}	72.13^{ns}	364.60*	0.93^{ns}	8.67^{ns}	254.50***	0.50^{ns}
SLHE	331	1.44^{ns}	52.67^{ns}	19.74*	363.80^{ns}	59.75^{ns}	295.50^{ns}	0.82***	7.84^{ns}	177.40^{ns}	0.31^{ns}
Residual	1983	1.36	51.05	16.32	412.50	52.54	339.60	0.45	7.35	193.4^{ns}	0.46

Note: SOV = source of variation; df: degrees of freedom; CSRFAB = continuous storage root formation and bulking (scored on a scale of 1 to 9, where 1 = no storage initiation and no bulking, and 9 = high storage root initiation & bulking); SRY = storage root yield; SRNO = storage root number per plant; VY = vine yield; SRD = storage root diameter; SRL = storage root length; CRW = commercial storage root weight; CRN = commercial storage root number; HI = harvest index; SEN: senescence (scored on a scale of 1 to 9, where 1 = no senescence, 9 = severe senescence, and death/drying); S = Season; L = location; H = harvest time; E = genotype; HLin: Harvest time linear; HQ = harvest time squared; HC = harvest time cubic (ie. lack-of-fit); SL = season by location interaction; SLR = season by location by replication interaction; SH = season by harvest time interaction; LH = location by harvest time interaction; SLH = season by location by harvest time interaction; SE = season by genotype interaction; L.E = location by genotype interaction; SLE = season by location by genotype interaction; SHE = season by harvest time by genotype interaction; LHE = location by harvest time by genotype interaction; SLHE = season by location by harvest time by genotype; * = significant at 0.05; ** = significant at 0.01; *** = significant at 0.001; ^{ns}= non-significant.

Genetic effects on yield of CSRFAB genotypes in sweetpotato

We performed a harvest basis analysis and calculated the corresponding heritability for each trait to study the dynamics of breeding values across harvest times. We focused on the traits that can affect the final yield and we compared the dynamic genetic variances and heritability of traits. Thus, the genotypic variances among seven main traits associated with CSRFAB varied from 0 to 72.46 (Table 6). Genotypic variance was high for HI at 120 DAP (72.46) and VY at 180 DAP (59.91) (Table 6). Zero variance was recorded for VY (120 DAP), HI (150 DAP), SEN (180 DAP) and weevils (180 DAP). The zero (or negative) variance components could be due to an artifact of the optimization algorithm that includes a non-negative constraint; a negative variance component could also represent competition effects between adjacent plots in the same block in the field. These results imply that there is no significant change in VY, HI, SEN and weevil damage within the population for the respective growth periods. Heritability is the proportion of variance in a phenotypic trait that is accounted for by genetic variance. Therefore, these results affected the value of heritability in the respective traits at the same harvest periods (varied from 0 to 67%). The 0% heritability implies that the effect of the traits is moving to fixation, that is, its frequency in the population is close to 100%. If we score the effect of the allele (s) regulating the trait having no heritability in the population, the result would mean in genetic terms, that the allele frequency in the population is 100%, therefore the genetic variance at the loci of these genes is zero, so any variance in the corresponding phenotypic traits cannot be attributed to the non-existent genetic variance. These results

need further investigation especially in the case of weevil resistance mechanisms as no significant increase in weevil infestation was observed in late harvest (Bararyenya *et al.*, 2018b). The rate in storage root bulking resulting in the available high green biomass may compete with weevil infestation. Broad sense heritability was relatively high for CSFRAB (50.5%) compared to other yield component traits indicating a better yield prediction using the scale.

We found temporal dynamics of genotypic influence on overall trait development (Table 6). In the early growth phase, genotypic variance was mostly low. As plants grew, genotypic factors became in general more important. The increasing genetic effect was observed up to about 120 DAP and decreased thereafter. After 120 DAP, the genetic effect became relatively less important. This can be partly explained by the drought stress which became more important 4 months after planting (MAP). Although less obvious, the opposite pattern was seen in the growth recovery phase (after 5 MAP), likely due to growth resumption resulting in the decline in overall phenotypic differences between CSRFAB and DCSRFAB plants. The investigated highly correlated traits with CSRFAB showed dynamic changes in heritability during the entire plant growth stage (Table 6). SRNO and CSRFAB showed similar patterns of heritability over time. We found that heritability of SRNO and CSRFAB increased in early growth stages and then decreased during drought stress, usually occurring between two consecutive rainy seasons and then increased thereafter during the growth recovery period occurring with the onset of the rainy season. These results are supported by Tuberosa (2012); quantitative traits reflecting the performance of crops under drought conditions tend to have low to modest heritability (Table 6).

Table 5. Variance components, within and across environment heritability estimation for nine characters associated with continuous storage root formation and bulking in sweetpotato.

Trait	σ^2_R	σ^2_{SLG}	σ^2_{LG}	σ^2_{SG}	σ^2_G	*H1*	*H2*	H(%)
CSRFAB	1.4	0.2	0.1	0.1	0.2	68.2	53.7	50.5
SRY	51.1	8.8	3.8	3.7	0.9	77.2	30.9	11.1
SRNO	16.3	3.9	2.4	2.2	7.7	74.9	53.2	67.2
VY	412.5	8.8	3.8	3.7	4.7	68.2	24.9	19.9
SRD	52.5	9.2	4	3.8	4.9	67.2	63.1	38.3
SRL	339.6	9.2	4	3.8	4.9	73.5	60.8	22.5
CRW	0.4	9.4	4.1	3.9	5	69.9	69.4	44
CRN	7.4	9.4	4.1	3.9	5	73.1	56.8	43.2
SEN	0.5	9	3.9	3.7	4.8	46.7	58.0	44

Note. H: broad sense heritability across location and season; H1: within environment broad sense heritability across 2 seasons for NaCRRI; H2: within environment broad sense heritability across 2 seasons for NaSARRI; σ^2_R: residual variance; σ^2_G: genotypic variance; σ^2p: phenotypic variance; σ^2_{SLG}: variance due to season by location by genotype interaction; σ^2_{LG}: variance due to location by genotype interaction; σ^2_{SG}: variance due to season by genotype interaction; σ^2_{GxE}: genetic by environmental variance; SRNO: storage root number per plant; SRY: storage root yield; VY: vine yield; SRDIA: storage root diameter; SRLG: storage root length; CRW: commercial root weight: CRN: commercial root number; VW; vine weight; CSRFAB: continuous storage root formation and bulking; SEN: senescence

Identification of storage formation and bulking growth patterns and their characterization

We have proposed in this study a method that can be used to estimate changes (Figure 2 to Figure 5) in the CSRFAB trait and therefore estimate the potential maximum yield of a sweetpotato genotype. We characterized in this study growth patterns associated with CSRFAB in sweetpotato and compared the accuracy of CSRFAB scores and the classic method used to measure growth change overtime (compared yield change overtime). The scoring method developed in this study accurately measured changes in the CSRFAB trait. This is supported by its low residual variance (1.4) compared to SRN (16.3) and SRY (51.1) (Table 4) and its high broad sense heritability of 50.5% compared with heritability of SRN (67.2%) and yield (11.1%) (Table 5). The within environment heritability, H1 and H2, are high for all traits compared to across environment heritability, indicating the consistency of the measurement of the variable. The high GxE variance components indicate actual differences in

Table 6. Estimates of genotypic (σ^2g) variance and broad sense heritability (H) within harvest time across environments for seven traits associated with continuous storage root formation and bulking.

	Genetic variance (σ^2g)					Broad sense heritability H (%)				
Trait	90DAP	120DAP	150DAP	180DAP	Comb.	90DAP	120DAP	150DAP	180DAP	Comb.
SRNO	3.29	10.08	6.46	8.06	8.84	47	67	62	58	70
SRY	2.84	2.32	4.04	0.81	2.43	26	20	23	4	24
VY	14.53	0.00	4.57	59.91	26.50	19	00	6	35	46
HI	29.80	72.46	0.00	36.25	75.26	43	61	0	29	61
SEN	0.01	0.02	0.07	0.00	0.07	12	19	22	0	56
WEEVIL	0.02	0.00	0.24	0.00	0.08	31	0	13	0	45
CSRFAB	0.23	0.51	0.10	0.43	0.45	35	62	49	55	69

Note. σ^2**g**: Genetic variance; DAP: days after planting; Comb.: combined estimate; SRNO: storage root number; SRY: storage root yield; VY: vine yield; HI: harvest index; CSRFAB: continuous storage root formation and bulking; SEN: senescence.

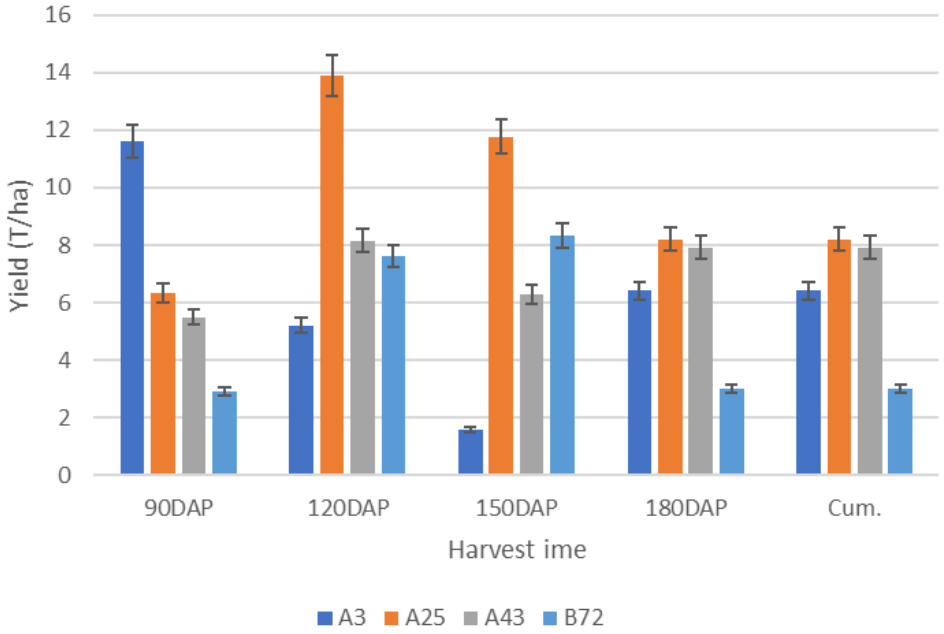

Figure 2. Growth pattern for discontinuous storage root formation and bulking (DCSRFAB) of four sweetpotato genotypes representing different growth patterns over four harvest times (averaged across four environments). Growth trend for genotypes A3, A25, A43 and B72 showing a fully DCSRFAB trait which generally increases the yield up to 120 days after planting (DAP) and then decreases overtime. The cumulative yield is generally lower than the maximum yield due to the yield decreasing in late stages. Note: DAP = days after planting, Cum. = cumulative yield.

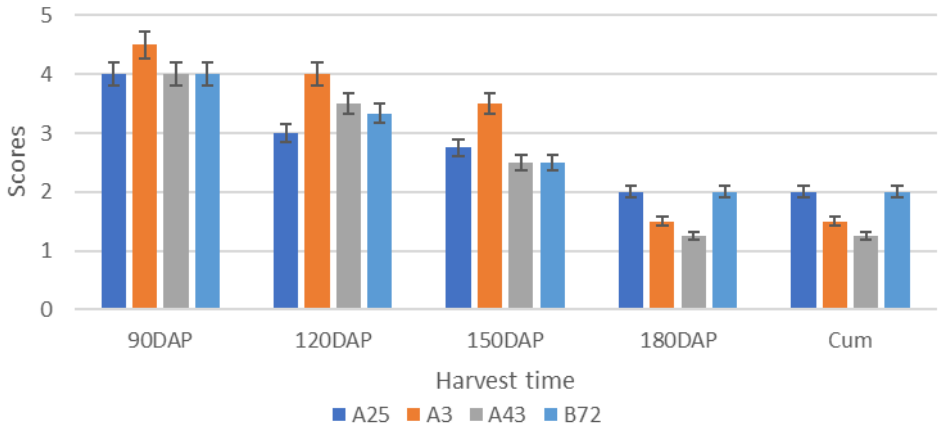

Figure 3. Growth trend of scores over four harvest times for discontinuous storage root formation and bulking genotypes A3, A25, A43 and B72 decreases due to progressive reduction of newly formed storage roots and similar bulking across all storage roots of the same genotype. Note: DAP = days after planting; CSRFAB = Continuous storage root formation and bulking; Cum. = Cumulative scores. DCSRFAB = discontinuous storage root formation and harvesting. Trend of scores over four harvest times for DCSRFAB genotypes A3, A25, A43 and B72 decreases due to progressive reduction of newly formed storage roots and similar bulking across all storage roots of the same genotype. The cumulative scores are generally lower than the respective maximum scores due to to the rate of CSRFAB decreasing in late stages.

the growth pattern responses of the genotypes across environments. The within environment effects reduce environmental variation to near zero implying that nearly all phenotypes, variation associated with environmental effect will be eliminated, and the only variation left will be mostly associated with genetic differences. Two types of growth patterns were identified according to the lifetime of sweetpotato genotypes. The first type which has determinate storage root formation and bulking is characterized by a rapid and short vegetative growth period followed by a senescence period until the leaves die off. This period is also characterized by a quick maximum yield obtained about 90 to 120 DAP (Figure 2) for most DCSRFAB genotypes. Respective CSRFAB

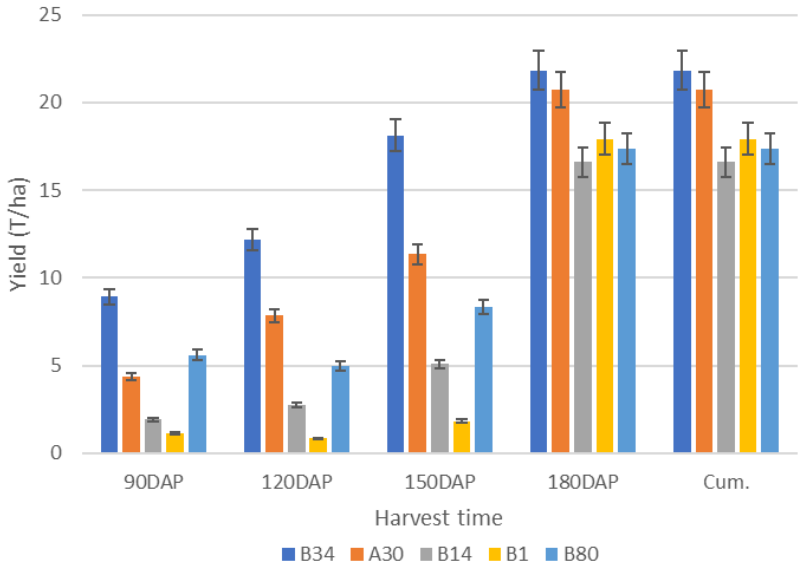

Figure 4. Growth pattern of continuous storage root formation and bulking of four sweetpotato genotypes representing different growth patterns over four harvest times (averaged across four environments). Note: DAP = days after planting; Cum. = Cumulative yield. Growth trend for genotypes A30, A14, B1 and B80 shows CSRFAB with increased yield overtime. The yield increase starts slowly and drastically increases at a late stage (150 DAP). The cumulative yield is the same with the last harvest (180 DAP).

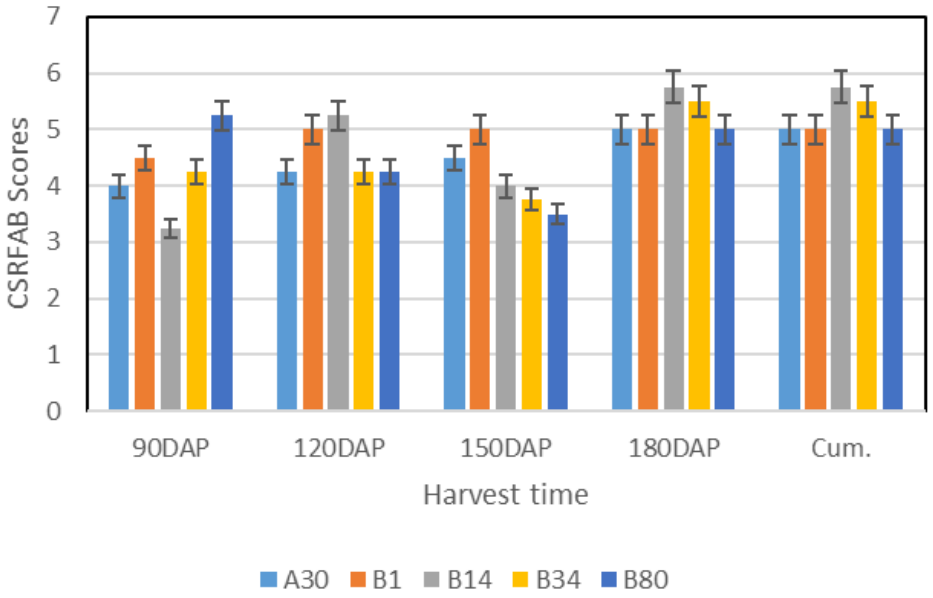

Figure 5. Growth pattern for continuous storage root formation and bulking (CSRFAB) of four sweetpotato genotypes representing different growth patterns over four harvest times (averaged across four environments). Note: DAP = days after planting; CSRFAB = Continuous storage root formation and bulking; Cum. = Cumulative scores. Scores show a trend which is similar across the four harvest times suggesting a possibility of predicting CSRFAB genotypes from early stages upwards. Genotypes A30, B1, B14 and B80 exhibit continuous bulking over the four harvest times. Cumulative scores were the same with 180DAP confirming the precision of the scale.

scores for the same genotypes declined overtime due to lack of new root formation and similar level of bulking for mature storage roots (Figure 3). Changes between successive harvest times were generally negative for DSRFAB genotypes. The cumulative yield changes, as were the cumulative score changes of DCSRFAB genotypes were therefore lower than the respective maximum single harvest yields and the rate of CSRFAB decreases in late stages. The second type of growth is characterized by a prolonged vegetative growth and a late switch-over time to reproductive phase (Figure 3 and Figure 5). The cumulative yield

changes over time, as were as the cumulative score changes, of CSRFAB genotypes displayed similar results with the last harvest (180 DAP) confirming the accuracy of the scale to predict yield changes over time. The change responses were positive for CSRFAB genotypes and the cumulative responses increased overtime (Figure 4) for yield and the increase was not significant (Figure 5) for the CSRFAB scores suggesting a possibility of predicting CSRFAB genotypes responses from early growth stages. During this period the yield increase starts later and increases drastically after 150 DAP (Figure 4) for most CSRFAB genotypes. Respective CSRFAB scores of the same genotypes did not change overtime due to continuous root formation and bulking (Figure 5) suggesting the ability of the scoring scale to predict CSRFAB genotypes at early growth stages. This period increased drastically yields of CSRFAB genotypes, however, the maximum yields were not observed in this trial due to persistent vegetative growth. According to Paltridge & Denholm (1974) the variation in yield observed may be due to the variation in their actual rates of dry matter production and the individual switchover time of the genotype to raise its maximum yield, referred to as the optimum growth pattern. The optimum growth pattern for determinate sweetpotato genotypes is of a two-phase plant growth, with the switchover occurring at the instant the plant becomes limited by restriction of its access to light (senescence). Subsequent values of the growing cycle which give maximum yield per unit time of harvest occur after these periods for indeterminate growth which are functions of above ground vegetative (leaves) lifetime. Each successive maximum is larger than the last, so one might expect the plants to evolve longer lifetimes and correspondingly longer periods of indeterminate (CSRFAB) growth. The intensity of senescence strongly varied ($P<0.001$) among genotypes and was negatively correlated with CSRFAB (Table 7). The yield rate of change between the 120 DAP and the 150 DAP was always negative. For the CSRFAB (Figure 3 & Figure 5), all the mean predictions and changes were positive. Yield increased up to more than 20-fold and the increase was genotype dependent.

These results are in agreement with the basic growth curves in many crop plants (Schurr *et al*., 2006; Yanfu *et al*., 1989). The rapid growth in the first stage for determinate or DSRFAB genotypes could be attributed to early maturing genotype properties in which there is more energy invested in biomass production for early remobilization for storage root bulking and this plant growth expression is also reported in other annual crops (Wenk & Falster, 2015). However, the maximum yield in this period was low and was limited by the available amount of green biomass which affected the bulking rate. Paltridge *et al*. (1984) reported similar common characteristics in which many plants have a rather sharp transition between the vegetative and the reproductive stages of growth. If the time of switch over is small, the amount of green leaf would be small and the subsequent rate of

Table 7. Overall growth mean trend over four harvest times across locations and seasons.

Location	Season	Traits	90DAP	120DAP	150DAP	180DAP	% change	a	b1	b2	R^2 (L)	R^2(L+Q)
NaCRRI	2016B	SRNO	1.19	1.82	1.7	2.11	16	0.77	0.54	-0.05	0.81	0.81
NaCRRI	2017A	SRNO	2	2.09	2.51	1.67	-20	1.05	1.1	-0.23	0.04	0.65
NaSARRI	2016B	SRNO	0.46	0.64	0.42	1.02	59	0.79	-0.37	0.1	0.47	0.68
NaSARRI	2017A	SRNO	0.99	1.6	2.03	2.33	46	0.23	0.83	-0.07	0.97	0.99
NaCRRI	2016B	SRY	1.35	4.53	6.75	12.75	181	0.76	0.12	0.7	0.95	0.98
NaCRRI	2017A	SRY	4.12	4.42	7.74	6.92	57	1.4	2.6	-0.28	0.7	0.74
NaSARRI	2016B	SRY	0.45	0.51	0.36	5.1	900	4	-4.5	1.17	0.58	0.92
NaSARRI	2017A	SRY	1.35	6.29	17.63	27.57	338	-3.04	2.75	1.25	0.97	0.99
NaCRRI	2016B	VY	26.54	22.56	24.58	24.58	9	30.5	-5.36	0.99	0.09	0.54
NaCRRI	2017A	VY	25.51	27.41	30.61	26.44	-4	18.4	8.18	-1.5	0.12	0.74
NaSARRI	2016B	VY	16.98	10.91	10.46	0.32	-97	17.18	0.04	-1.01	0.54	0.91
NaSARRI	2017A	VY	57.95	48.6	62.76	72.67	50	69.9	-18.24	4.81	0.34	0.87
NaCRRI	2016B	HI	4.41	19.04	20.37	31.53	66	-6.17	12.6	-0.87	0.93	0.92
NaCRRI	2017A	HI	13.51	13.36	19.48	19.78	48	10.86	1.93	0.12	0.8	0.8
NaSARRI	2016B	HI	2.35	4.17	2.91	99.31	2282	73	-89.26	23.64	0.6	0.92
NaSARRI	2017A	HI	2.1	12.24	18.34	21.39	75	11.33	15.25	-1.77	0.94	0.99

Note. DAP: Days after planting; a: intercept of the growth curve; b1: linear slope of the growth curve; b2: quadratic slope of the polynomial growth; R^2: coefficient of determination; % change: rate of change between the normal harvest time (120 DAP) and the extended harvesting time (180 DAP); L: Linear; Q: Quadratic. NaCRRI: National Crop Resources Research Institute; NaSARRI: National Semi-arid Resources research Institute.

production and final yield would be also low. In this phase, the time of switchover was before 90 DAP. Sweetpotato continues to grow and branch if environmental conditions are favorable, due to its perennial habit, but the leaves formed earlier in the growing season start to fall and the total number of leaves and leaf area decrease toward the end of the growing season (Somda & Kays, 1990). Determinate or DSRFAB genotypes lost their ability to initiate new shoots at around 120 DAP and the VW decreased drastically. These results agree with findings of Paltridge & Denholm (1974) and Bhagsari (1990) in which most annuals exhibit a single reproductive phase, often with a sudden onset.

The senescence phenotype was less observed in indeterminate types, although greenness intensity was reduced at 120 DAP which resumed and drastically increased (high positive quadratic slope) from 150 DAP when rains came back. Bhagsari (1990) reported similar results that sweetpotato cultivars maintained leaf area index to intercept a major portion of sunlight until harvest, and leaf area growth significantly differed depending on cultivar.

The slow increase in most of the yield component parameters in CSRFAB genotypes resulted in low storage root yield in the first growth phases (Figure 3 & Figure 5). This can be explained by the fact that indeterminate genotypes invest resources for maintenance at earlier stages including root elongation for nutrition purposes and biomass production to maintain vegetative growth. This resulted in strong vegetative quadratic biomass increase (Table 7) for CSRFAB genotypes. For these genotypes the time of switchover to reproduction was very late (around 150 DAP). This was the last growth phase where yield increased drastically in CSRFAB corresponding to the switch to reproduction (onset of flower and seed) and storage root remobilization in sweetpotato in which the plant invests its vegetative resources in increasing the sink capacity. Because of high availability of resource/energy in upper biomass, sink strength is increased leading to increased productivity.

For sweetpotato breeders and practitioners, harvest index (HI) is difficult to estimate due to the problem of measuring its components. For instance, the time of harvest influences greatly the value of HI because storage root bulking is likely to vary progressively from the onset of the storage roots and increases with the biomass translocation into storage roots. However, the senescence reduces the above-ground biomass progressively leading to high and unrealistic values (e.g. HI of 99.31%) (Table 7). Therefore, HI of sweetpotato varies greatly with the time of harvest. This variation is also influenced by other environmental factors including wet or dry conditions during harvest which increase or decrease weight due high or less moisture. Similar results in other roots and tubers are reviewed by Hay (1995).

Overall, the yield started low, at 90 DAP (overall mean) and increased progressively as growth time increased (Table 7 and Table 8). This relationship is well explained by the variation in the data (R^2 varied from 38% to 65%). High yielding genotypes showed consistently maximum yields in the population (R^2>0.99) while low yielding genotypes showed inconsistent relationship (low R^2). The maximum yield recorded across locations and seasons was 16.7 t/ha and 28.6 t/ha at the first harvest

Table 8. Yield means of 10 most distinct discontinuous (DSRFAB) and continuous (CSRFAB) genotypes at different harvest times showing overall best yielding genotypes in combined environments.

DSRFAB genotypes					CSRFAB genotypes				
Genotype	**90DAP**	**120DAP**	**150DAP**	**180DAP**	**Genotype**	**90DAP**	**120DAP**	**150DAP**	**180DAP**
MPG1146	8.23	10.49	17.46	13.17	SPK004	6.47	4.43	10.34	28.64
Ndimbuka	7.18	3.47	6.29	5.83	Kala	4.18	6.72	7.41	24.26
NASPOT 1	6.56	3.19	7.63	3.99	BSH740	5.31	5.67	8.15	18.62
Otada	6.49	3.56	9.03	4.08	KML872	4.31	6.59	12.16	21.44
MPG1128	6.11	6.41	17.33	5.29	NASPOT 9 O	3.52	8.83	4.17	10.37
MSK1040	5.97	9.12	11.97	11.83	Mayai	9.69	11.6	3.63	9.72
RAK786	5.13	2.8	6.36	2.96	Ukerewe	5.47	5.1	5.5	11.59
KMI88	5.03	6.4	7.91	8.52	NASPOT 7	2.68	6.98	7.89	13.88
KBL648	4.6	9.54	8.95	9.33	APA352	1.12	2.95	2.95	8.87
Jonathan	4.6	7.62	17.36	9.54	RAK819	2.92	8.3	5.19	11
Mean	6.29	4.48	7.35	4.87	**Mean**	3.54	5.95	7.09	9.83
Max	16.71	12.98	17.6	13.17	**Max**	9.82	15.45	19.57	28.64
Min	1.24	0.1	0.97	0.3	**Min**	0.21	0.65	0.22	2.41
SED	7.67	6.4	7.43	8.55	**SED**	7.67	6.4	7.43	8.55

DAP: Days after planting; DSRFAB: discontinuous storage root formation and bulking; CSRFAB: continuous storage formation and bulking; Comb.: combined; Max: maximum; Min: minimum; SED: standard error difference.

and the last harvest, respectively. This implies that the frequency of genotypes that increase yield overtime is high. In this trial, some genotypes reached maximum growth earlier, others late, leading to high variability in growth related parameters.

On average, there was a two-fold increase in yield from the 90 DAP to 180 DAP. The 10 most distinct DSRFAB genotypes were MPG1146 (A26), Dimbuka-Bukulula (A34), NASPOT 1 (A24), Otada (A40), MPG1128 (A11), MSK1040 (A33), RAK786 (A10), KMI88 (A42), KBL648 (A14) and the 10 most distinct CSRFAB were SPK004 (A19), Kala (A13), BSH740 (A16), KML872(A32), NASPOT 10 O (A22), Mayai (A3), Ukerewe (A41), NASPOT 7 (A30), APA352 (A27) and RAK819 (A18). These contrasting genotypes for CSRFAB can be used in breeding programs to study and improve sweetpotato yield in CSRFAB genotypes. The average yield at two locations in two seasons shows that you can more than double sweetpotato production by choosing high yielding genotypes (Table 7 with maximum yield of 13.17 t/ha for DSRFAB versus maximum of 28.64 t/ha for CSRFAB). Similar results have been reported (Çalişkan *et al.*, 2007) in which there were significant differences among the locations, 60 to 70 t/ha of storage root yield being obtained by choosing high-yielding varieties.

Variability and distribution of 130 genotypes over 4 harvest times

For SRY and VY the first two box plots are comparatively equally shorter than the third and fourth box plots (Figure 6). This suggests that, overall, genotypes have little variation over the first two harvest times. It also suggests low variation between time of harvest during this phase. The third and fourth box plots are higher than the first two box plots for SRY and VY. This suggests that genotypes have quite different growth patterns from the two first harvest times and the two last ones. It also suggests high variation among the genotypes. The last two box plots in each sub-figure show obvious differences within each box plot and the two first box plots. This suggests an area of difference that could be explored further. The four sections of the box plots are uneven in size. This shows that many genotypes have a similar growth pattern during the early growth phase, but in a later phase genotypes are more variable in their growth pattern. The long upper whisker shows that genotype growth varied amongst the most positive quartile group, and very similar for the least positive quartile group. This suggests a need for further exploration. The medians of the two first harvest time plots (which generally will be close to the average) are at the same level. However, the box plot of the last two harvest times shows very different distribution means.

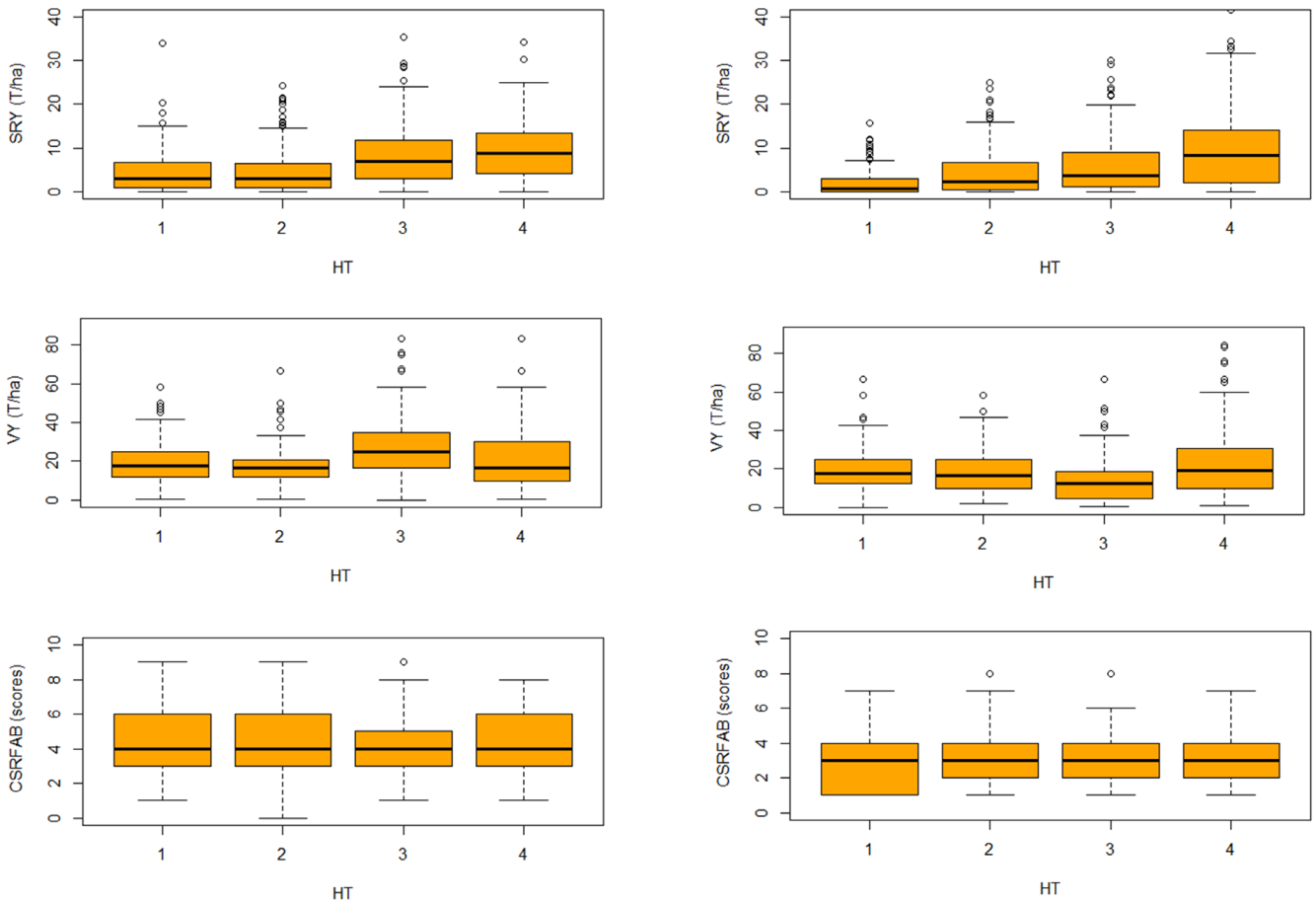

Figure 6. Two seasons (2016B & 2017A) boxplot comparison showing overall variability and dispersion of storage root yield (SRY), vine yield (VY) and continuous storage root formation and bulking (CSRFAB) over 4 harvesting times (HT) among 130 sweetpotato genotype at the National Crops Resources Research Institute (NaCRRI), Namulonge.

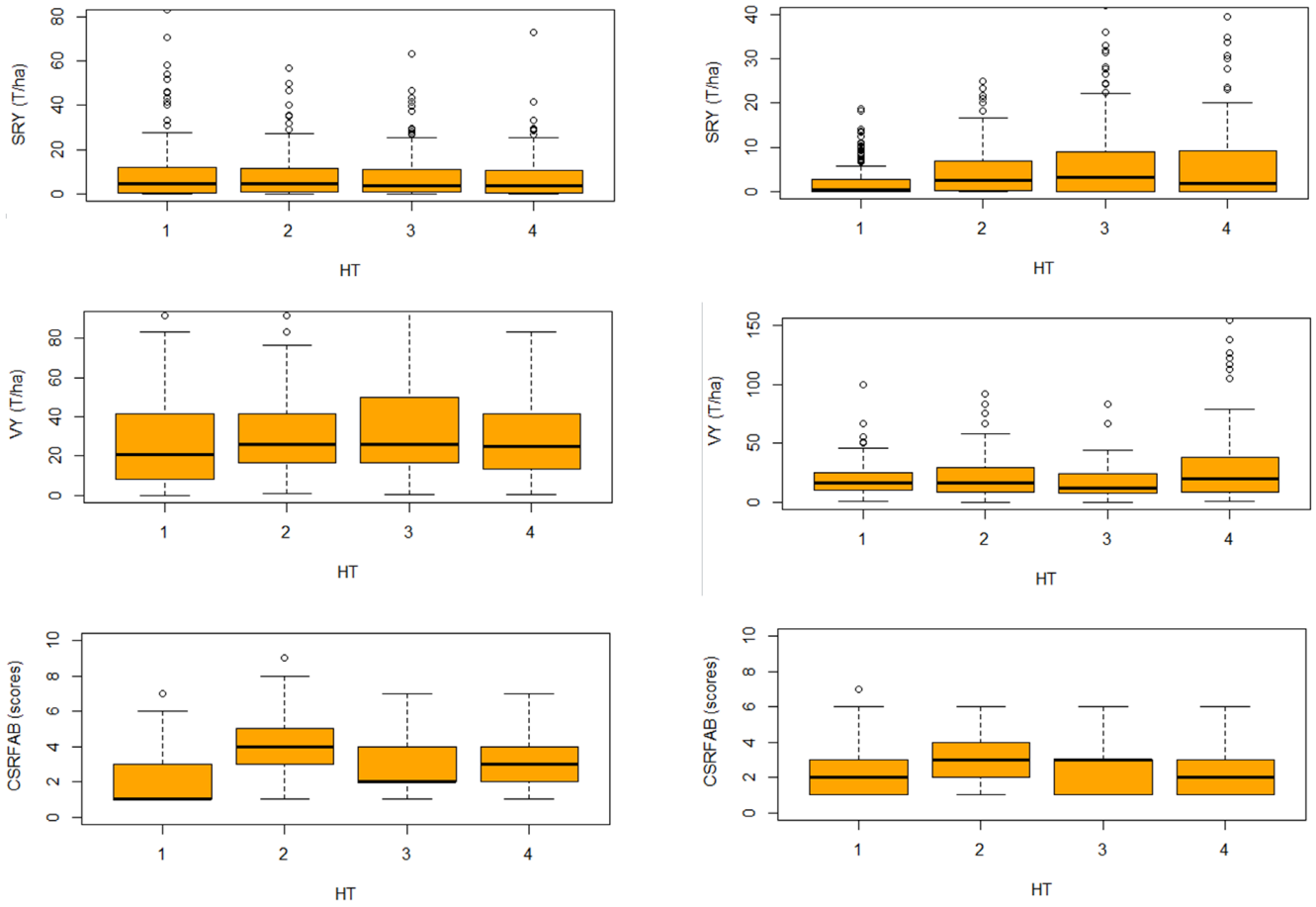

Figure 7. Two seasons (2016B&2017A) boxplot comparison showing overall variability and dispersion of storage root yield (SRY), vine yield (VY) and continuous storage root formation and bulking (CSRFAB) over 4 harvest times (HT) among 130 sweetpotato genotypes at National Crop Resources Research Institute (NaCRRI) Serere. Note: SRY=storage root yield; VY=vine yield; HT=harvesting time; 1=90DAP; 2=120 DAP; 3=150 DAP; 4=180 DAP.

Variation and distribution of CSRFAB scores across location and seasons consistently remained almost the same, suggesting an accurate response prediction of the scores from the beginning.

Relationship between associated growth traits and CSRFAB in sweetpotato

CSRFAB scores were highly and positively correlated with most of the yield component traits (Table 9). This implies that CSRFAB is also a component of yield. In other words, the higher the CSRFAB scores of a sweetpotato genotype, the higher the yield of the genotype. CSRFAB scores were negatively correlated with SEN which confirms our hypothesis in which a CSRFAB genotype should maintain vegetative growth to continuously provide source/inputs for sink storage roots. The negative correlation with VW needs further investigation, however, we believe the competition of source and sink activities in the plant, effects of pests and diseases such as nematodes and Alternaria stem blight (*Alternaria bataticola*) and SPVD could be among the factors. It is possible to cease vegetative growth and continue survival for an extended period, but most varieties reduce their vegetative weight following the storage root bulking peak (Venus & Causton, 1979). The comparison of a classic method of evaluating growth change (analyzing yield mean change between two consecutive harvests) and the developed scale for measuring CSRFAB traits produced similar results, however, CSRFAB was more accurate. This is supported by high heritability and low residual variance observed for CSRFAB versus yield and other component parameters. Using the developed scale, 48 genotypes were clustered among CSRFAB genotypes, whereas 62 genotypes clustered among DSRFAB (Figure 5). These results were reproduced in the following season, and 41% were common to the two methods in 2017A versus 46% in 2017B (Figure 8).

Accuracy of CSRFAB scoring method

It was hypothesized that CSRFAB genotypes potentially increase yield over time, therefore, the trait can be screened for by measuring yield change overtime. This method, holding other factors constant, shall produce the same results of scoring for the trait using the developed 1 to 9 scale. We investigated this

Table 9. Pearson's correlation coefficients of CRN, CRW, CSRFAB, HI, SEN, SRD, SRL, SRY, VW and VY for 130 sweetpotato genotypes across two locations (Namulonge and Serere) and two seasons (2016B and 2017A) (N = 4160).

	CRN	CRW	CSRFAB	SEN	SRD	SRL	SRNO	SRY	VY
CRN	-								
CRW	0.84***	-							
CSRFAB	0.67***	0.46***	-						
SEN	0.08	-0.05	0.01	-					
SRD	0.74***	0.70***	0.63***	-0.12	-				
SRL	0.75***	0.68***	0.71***	-0.12	0.86***	-			
SRNO	0.90***	0.65***	0.82***	0.09	0.68***	0.72***	-		
SRY	0.74***	0.74***	0.53***	-0.08	0.80***	0.72***	0.70***	-	
VY	-0.29***	-0.25***	-0.16*	-0.21*	-0.17*	-0.18**	-0.25**	-0.14	-

Note. CRN: commercial storage root number; CRW = commercial storage root weight; CSRFAB = continuous storage root formation and bulking (scored 1–9); HI = harvesting index; SEN = senescence (scored 1 to 9); SRD: storage root diameter; SRL: storage root length; SRN storage root number; SRY = storage root yield; VW = vine weight; VY = vine yield.

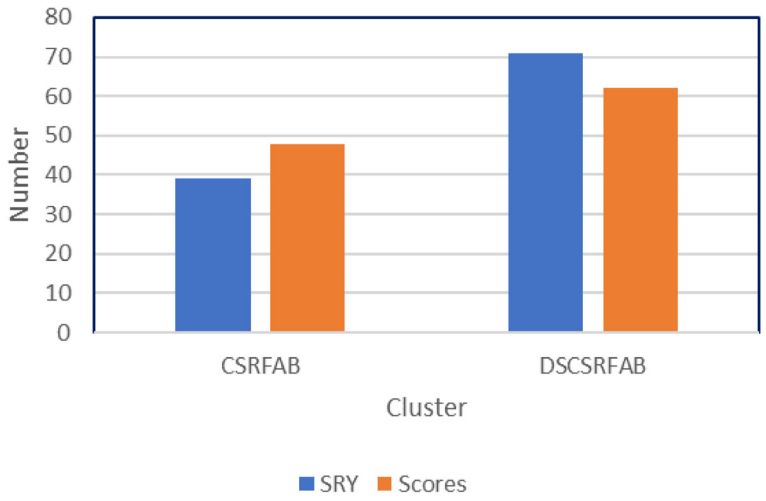

Figure 8. Comparative accuracy of screening continuous growth using yield increase overtime evaluation and using a 1 to 9 scale (discontinuous storage root formation and bulking (DSRFAB) and continuous storage root formation and bulking (CSRFAB). Note. SRY: storage root yield.

relationship in our data. Overall, the yield change analysis over four harvest times grouped the 110 genotypes (without missing data) into 39 CSRFAB and 71 DSRFAB genotypes. Using the developed scale, 48 genotypes clustered among the CSRFAB genotypes, whereas 62 genotypes clustered together as DSRFAB (Figure 8).

CSRFAB scores represent a measure of changes in CSRFAB on a scale of 1 to 9. Figure 9 shows the total number of clones that exhibited CSRFAB and DSRFAB in 2017A, the respective proportion of each category in the total population, the respective total number of clones that are common to a different method of screening and their respective proportions under each method of screening. The overall picture shows similarities, although the accuracy differs between methods. Comparing the score results of 2017A and 2017B, there is high reproducibility of the results. This implies that the CSRFAB scale of 1 to 9 can be used accurately to estimate changes in CSRFAB genotypes and yield progress in sweetpotato crops overtime.

HI captures the allocation of biological yield into above-ground biomass and root biomass (with commercial and non-commercial storage and non-storage roots). Estimating the amount of non-storage and non-commercial roots is extremely difficult (Grüneberg *et al.*, 2015) because of newly initiated and immature storage roots that will affect the final yield of indeterminate genotypes.

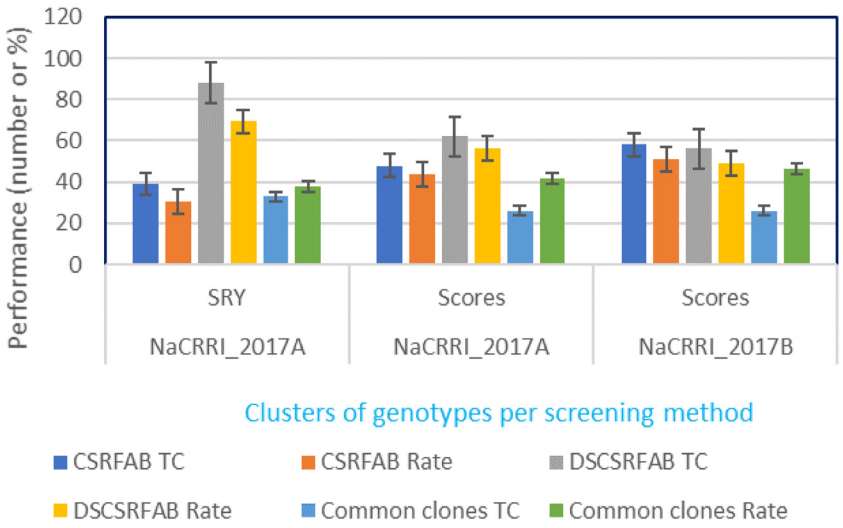

Figure 9. Number of genotypes clustered into discontinuous storage root formation and bulking (DSRFAB) and continuous storage root formation and bulking (CSRFAB) using yield mean change over time and scores at NaCRRI in 2017A. The number of genotypes clustered in the same category under both screening methods. Note. SRY: storage root yield; NaCRRI: National Crops Resources Research Institute; 2017A and 2017B: first and second rainy seasons of 2017; CSRFAB rate: the fraction of number of CSRFAB genotypes over the total genotype number assessed; DSRFAB rate: the fraction of number of DCSRFAB out of the total number of genotypes assessed; TC: total number of genotypes; Common clones TC: the total number of same genotypes clustered among CSRFAB using the two screening methods; Common clone rate: the percentage of same genotypes under each method out of the total common genotypes.

Usually, HI is calculated by storage root yield divided by above-ground biomass and storage root production which over-estimates HI values. HI values are likely to increase with time of harvest for CSRFAB genotypes because the number and weight of storage roots increase overtime. CSRFAB, newly investigated in this research, highlights the need to integrate these complex yield components by estimating their effects leading to the final maximum yield, and introgressing genes controlling the trait into genotypes with other major desirable traits such as SPVD resistance, weevil resistance and drought tolerance to unleash the potential of sweetpotato.

Conclusion

This study highlights three important results: 1) the CSRFAB trait can be exploited to provide additional yield in sweetpotato 2) the 1 to 9 scale developed provided consistent scores across replications, and reflected well the growth patterns observable phenotypically, 3) the method of analyzing growth variables over harvest times revealed distinct growth patterns among genotypes. These patterns identify which sweetpotato genotypes are likely to be suited to piecemeal harvesting. The methodolgy introduced here is expected to be useful in other root crops as well.

This study showed that CSRFAB genotypes differentially increased yields up to 779% and discontinuous genotypes reduced yield after crop maturity up to 85% for determinate genotypes. Five months after planting (150 DAP) is proposed as the ideal scoring time for this scale, however, there is need for further work in different agroecologies to validate the reliability of the results. The sweetpotato genotypes used in this study are highly variable for CSRFAB and breeding to improve the trait should be feasible due to its high heritability. Genotypes most distinct for CSRFAB were, SPK004, Kala, BSH740, KML872, NASPOT 9 O, Mayai, Ukerewe, NASPOT 7, APA352 and RAK819, and those distinct for DCSRFAB were, MPG1146, Dimbuka-Bukulula, NASPOT 1, Otada, MPG1128, MSK1040, RAK786, KMI88, and KBL648. The highest CSRFAB yielder, SPK004 (28.6 t/ha) outperformed by 15.4 t/ha (117%) the highest DCSRFAB yielder, MPG1146 (13.2 t/ha) across locations and seasons. Delaying in harvest leads to final yield losses for DCSRFAB while it enhances final yield of CSRFAB genotypes. These genotypes can be used in conventional sweetpotato breeding for yield improvement. For sweetpotato breeding, the CSRFAB genotypes are recommended for the improvement of sweetpotato varieties suitable for piecemeal harvesting in small scale farming systems, while the discontinuous genotypes are recommended for the development of early maturing sweetpotato varieties. However, the trait needs much more understanding of the physiology of sweetpotato. Therefore, linking these phenotypic patterns with causal genomic variations can provide a clear understanding of selection scenarios and speed up the breeding for this important trait in sweetpotato.

Data availability

The data underlying this study is available from International Potato Center (CIP) Dataverse.

CIP Dataverse: Dataset 1. Dataset for: Continuous Storage Root Formation and Bulking in Sweetpotato http://dx.doi.org/10.21223/P3/IC6ZEY (Bararyenya *et al*., 2018b)

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Acknowledgements

The authors thank the National Agricultural Research Organization of Uganda for providing sites for the trials, and CIP and NARO for kindly providingtechnical support and the sweetpotato genotypes.

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Version 2

Reviewer Report 20 January 2020

https://doi.org/10.21956/gatesopenres.14205.r28324

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This study was aimed to determine how continuous storage root formation and bulking vary over diverse genotypes of sweet potatoes from Uganda. This remarks that some genotypes with good CSRFAB can be identified and have the potential to be used to enhance sweet potato productivity.

It is evident that identifying sources of good traits is significant to promote advances in breeding and agriculture. From that standpoint this study has merit. However, the reviewer finds this manuscript doesn't have good flow and it is difficult to follow.

One criticism is that the authors build the discussion including excessive statistics and excessive technical details of the statistical analysis. In many cases it was not clear what the findings were as information and concepts become unclear. I would advise the authors to make it simpler, you have to take into consideration that this paper will reach a broad audience with different backgrounds. This study has practical implications, giving a clear view of the results, discussions and analyses could enhance its outreach and practical application from breeding groups in the region.

In summary, this manuscript needs major revision. It needs to simplify the statistical analysis to a point of showing what is truly relevant with respect to the variation in traits assessed to explain CSRFAB and the variation among genotypes. This manuscript is too long.

Some additional comments:

- In Introduction: The second paragraph, it seems to me that the authors should clarify better if yield increase was because of the effect of breeding or just an increase of planting areas. If the latter this doesn't help much justifying the addition of new breeding forms.

- In Methods: What is a mega-environment for selection? I assume it was as reference to environmental diversity but the term *mega-environment* is a bit misleading in my view.

- Results: It is not new to report that clonal forms can respond differently in different environments. Variation levels across multiple environments is often high in field experiments in any crop. How is this result original? Then, you indicate that there is high variability among genotypes across locations + seasons. Wasn't this expected from a variable set of genotypes?

- When the authors indicate that "*this can be explained by the large population effect combined with sample size",* I would suggest clarification in that sentence since I understand the same number of plants and populations were used in the experiments. How were the effects compared on that basis?

- The parameters that the authors have used are related to storage root development, it seems that indicating that genotype performance increases overtime and is linearly explained is a logical outcome and fully expected. Storage root formation is related to maturity and developmental stages (=time). Maybe you need to clarify that result and explain better.

Is the work clearly and accurately presented and does it cite the current literature?
Yes

Is the study design appropriate and is the work technically sound?
Partly

Are sufficient details of methods and analysis provided to allow replication by others?
No

If applicable, is the statistical analysis and its interpretation appropriate?
No

Are all the source data underlying the results available to ensure full reproducibility?
No source data required

Are the conclusions drawn adequately supported by the results?
Partly

Competing Interests: No competing interests were disclosed.

Reviewer Expertise: Plant breeding and Genetics and, Conservation Genetics.

I confirm that I have read this submission and believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard, however I have significant reservations, as outlined above.

Version 1

Reviewer Report 20 February 2019

https://doi.org/10.21956/gatesopenres.13991.r26950

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Hussein Shimelis
African Centre for Crop Improvement, School of Agricultural, Earth and Environmental Sciences , College of Agriculture, Engineering and Science, University of KwaZulu-Natal (UKZN), Pietermaritzburg, South Africa

I suggest the following points for possible consideration:

Title:

- It can be adjusted to read: “Variation for Continuous Storage Root Formation and Bulking in Sweetpotato”.

Abstract:

- Some of the acronyms must be written in full during the first mention e.g. CSRFAB, NaCRRI etc.
- The conclusion is not clear, e.g., which genotypes were selected and recommended for continuous storage root formation and bulking and what yield advantage?

Introduction:

- The authors have provided long and detailed information on the overall productivity issues of sweetpotato. Instead, the authors should refocus on the challenges and opportunities of piecemeal harvesting under field conditions, and data and literature on continuous storage root formation and bulking. Problems such as termites, terminal drought stress, multiple and intercropping systems, and limited agricultural lands etc. can be pressing issues for piecemeal harvesting.

Materials and methods:

- Provide information on the maturity period (in months) of the test genotypes in Table 2. This will influence genotype comparison and recommendation for piecemeal harvesting.
- The 1 to 9 senescence scale should be described in detail, e.g. what is 1, 2, 3, 4, 6, 6, 7, 8 and 9.

Results:

- In all the Figures it will be interesting if the final yield/score (cumulative yield) of test genotypes are included, not only at 90, 120, 150 and 180 DAP.
- Is there a control harvest (e.g. normal harvest/once off harvest of a given genotype) to compare with cumulative yields over 90, 120, 150 and 180 DAP?

Is the work clearly and accurately presented and does it cite the current literature?
Partly

Is the study design appropriate and is the work technically sound?
Yes

Are sufficient details of methods and analysis provided to allow replication by others?

Partly

If applicable, is the statistical analysis and its interpretation appropriate?
Yes

Are all the source data underlying the results available to ensure full reproducibility?
Yes

Are the conclusions drawn adequately supported by the results?
Partly

Competing Interests: No competing interests were disclosed.

Reviewer Expertise: Plant Breeding, Plant Genetics, Crop Improvement, Quantitative Genetics

I confirm that I have read this submission and believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard.

Reviewer Report 15 February 2019

https://doi.org/10.21956/gatesopenres.13991.r26921

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Arthur Villordon
LSU Agcenter Sweet Potato Research Station, Chase, LA, USA

Introduction:

This work addresses the subject of what the authors have termed “continuous storage root formation and bulking” in sweetpotato. The stated objective of this study was to investigate the genetic variability of “continuous storage root formation and bulking” and characterize growth patterns at different development stages to identify possible “continuous storage root formation and bulking” sweetpotato genotypes in a Ugandan germplasm collection for possible use as parents in trait improvement.

Merits:

The work addresses an important issue of relatively low sweetpotato storage root yields in Sub Saharan Africa where the crop is considered an important component of food security. Therefore, any work that seeks to understand the biological and environmental constraints of storage root yield has merit for advancing the fundamental understanding of the problem and development of solutions to improve productivity.

Critique:

Although the premise of the study was reasonable, the manuscript has a number of general and specific

concerns, chief among this is the apparent oversight of previous work on the subject of storage root formation. There is general scientific consensus of the definition of “storage root formation” within the context of storage root developmental stages. It is unfortunate that the manuscript failed to acknowledge this scientific consensus and how it could have informed the current work and led to the advancement of the understanding of storage root formation in general, and within the context of the study location in particular. A short list of such work is provided in the references section below. I do encourage the authors to review some or all of the listed references, particularly the work of Lowe and Wilson (1974[1]). There are many similarities and parallels between the current work and Lowe and Wilson’s methodology and approach. I do believe there is valuable data to be published from this research, but as it stands, I am recommending revision for the manuscript, as I believe that conceptual and structural changes need to be made on the manuscript. I hope that the following critiques will aid the authors in the refining of this manuscript to allow for revision in the future.

There has been prior work looking at abiotic and biotic constraints on early storage root development (between 30 and 50 days) wherein storage roots were anatomically examined to confirm storage root formation and then storage root number was used to measure the response (please see Solis *et al.* (2014[2]) and Gajanayake *et al.* (2014[3]) below). A common thread in these prior reports is the confirmation of the anatomical markers of storage root formation or lignification (generally lignified adventitious roots typically do not undergo storage root formation). These anatomical observations are relatively quick and require very basic tools and equipment. In contrast, the present work used visual assessments to indicate “storage root formation” or lignification (third paragraph and figure on page 6). For example, a score of 1 is based on visual observations of “no storage root initiation and no bulking.” Unfortunately, as prior work will show, non-swollen or non-thickened adventitious roots cannot be visually classified as undergoing storage root formation or lignification without anatomical confirmation. As it stands, any analyses or models based on this scale is based on the assumption that a score of 1 or 2=”no storage root initiation”, which may not be accurate. Lowe and Wilson (1974[1]) used the same approach as the current work and used an index to quantify thickened storage roots. They made very clear assumptions about their rating scale, in part as a result of their detailed anatomical work on storage root formation, as detailed in another study by Wilson and Lowe (1973[4]). The authors are encouraged to review Wilson and Lowe (1974[1]) and consider revising along these lines. I encourage the authors to reconsider using the “CSRFAB index” and instead use the quantitative measurements that they are already collected to describe the variation in storage root development and yield among the genotypes.

If there is one single problem that stands out, one that I find very unfortunate, is this statement found on the 2nd paragraph on page 4: “no study attempted to understand the storage root formation and bulking patterns overtime under field conditions.” Lowe and Wilson (1974[1]), referenced above and listed below, conducted such a study, not very different in its conceptual approach from the current work. Lowe and Wilson grew six sweetpotato cultivars in field plots, and subsequently sampled and assessed storage formation and storage root development at weekly intervals during the first 8 weeks of growth, and then at monthly intervals after 8 weeks, for up to 24 weeks. Lowe and Wilson were very keen to recognize that storage root formation can only be determined anatomically, so they developed an index to quantify storage root development based on thickness of roots.

Finally, I looked up Yanfu *et al.* (1989) and was unable to find the data about storage root initiation occurring as early as 7 days. At this stage, adventitious roots are typically still undergoing primary growth, even in high yielding cultivars. Please cite cultivar or genotype or primary source, if available. In addition, I am unable to locate the data on storage root number ranging from 30 to 112 depending on genotype. Please verify this citation. Perhaps this refers to 30 to 112 g/plant (average root yield)?

Discussion:

The research on which this manuscript is based has generated valuable data on the variability of storage root yields of the sweepotato genotypes in the collection and once the recommended structural and conceptual changes are made, the authors are encouraged to revise. Lowe and Wilson's (1974[1]) work was titled "Comparative Analysis of Tuber Development in Six Sweet Potato (Ipomoea batatas [L.] Lam) Cultivars." Other than the unfortunate use of "tuber" in this case, perhaps the authors will take a cue from this very relevant prior work. Given that the subject of phenotypic variability of storage root development is under-researched in this geographic area, these findings will have undoubtedly have fundamental and applied merit.

However, if the authors insist on applying the term "storage root formation" in the context of their work, then they must implicitly define the contextual usage and exceptions relative to what the scientific community has adopted as the generally accepted conceptual and functional definition (please see a sampling of references below). In particular, they need to make the needed assumption that all non-swollen adventitious roots (Score 1) and not all slightly swelling adventitious roots (Score 2) are not undergoing storage root initiation and that anatomical examinations were not conducted. However, I strongly urge the authors to avoid this route as it does not advance our understanding of sweetpotato storage root formation and unnecessarily deviates from the scientific consensus.

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Is the work clearly and accurately presented and does it cite the current literature?
Partly

Is the study design appropriate and is the work technically sound?
Partly

Are sufficient details of methods and analysis provided to allow replication by others?
No

If applicable, is the statistical analysis and its interpretation appropriate?
Partly

Are all the source data underlying the results available to ensure full reproducibility?
Partly

Are the conclusions drawn adequately supported by the results?
Partly

Competing Interests: No competing interests were disclosed.

Reviewer Expertise: Relationship between sweetpotato root architecture and storage root development.

I confirm that I have read this submission and believe that I have an appropriate level of expertise to state that I do not consider it to be of an acceptable scientific standard, for reasons outlined above.

Comments on this article

Version 2

Author Response 25 Mar 2020

Robert Mwanga, International Potato Center (CIP), Kampala, Uganda

Response to Reviewer's (Dr. Alfonso del Rio) Report (responses are in italics).
In general, and in specific instances the reviewer's comments were very helpful and have been responded to in order to help readers to follow the work as suggested by the reviewer.

This study was aimed to determine how continuous storage root formation and bulking vary over diverse genotypes of sweet potatoes from Uganda. This remarks that some genotypes with good CSRFAB can be identified and have the potential to be used to enhance sweet potato productivity.
It is evident that identifying sources of good traits is significant to promote advances in breeding and agriculture. From that standpoint this study has merit. However, the reviewer finds this manuscript doesn't have good flow and it is difficult to follow.

Significant revisions have been made to improve on the flow; all changes have been highlighted.

One criticism is that the authors build the discussion including excessive statistics and excessive technical details of the statistical analysis. In many cases it was not clear what the findings were as information and concepts become unclear. I would advise the authors to make it simpler, you have to take into consideration that this paper will reach a broad audience with different backgrounds. This study has practical implications, giving a clear view of the results, discussions and analyses could enhance its outreach and practical application from breeding groups in the region.

Details on statistics and technical details have been drastically reduced while maintaining content wherever it makes the flow and the text easier to understand.

In summary, this manuscript needs major revision. It needs to simplify the statistical analysis to a point of showing what is truly relevant with respect to the variation in traits assessed to explain CSRFAB and the variation among genotypes. This manuscript is too long.

Major revisions have been made on the manuscript; methods section and experimental details have been modified and statistical analysis details reduced drastically.

Some additional comments:
•In Introduction: The second paragraph, it seems to me that the authors should clarify better if yield increase was because of the effect of breeding or just an increase of planting areas. If the latter this doesn't help much justifying the addition of new breeding forms.

A modification has been made to the text: "The increase in production was due to a combination of factors varying in different countries but mainly due to increase in area and breeding efforts."

•In Methods: What is a mega-environment for selection? I assume it was as reference to environmental diversity but the term mega-environment is a bit misleading in my view.

A modification has been made to the text to reflect environmental diversity; "mega-environment" has been dropped.

•Results:
It is not new to report that clonal forms can respond differently in different environments. Variation levels across multiple environments is often high in field experiments in any crop. How is this result original? Then, you indicate that there is high variability among genotypes across locations + seasons. Wasn't this expected from a variable set of genotypes?

The confusing, rather long text has been deleted and the remaining text modified to refer to the CSRFAB trait.

•When the authors indicate that "this can be explained by the large population effect combined with sample size", I would suggest clarification in that sentence since I understand the same number of plants and populations were used in the experiments. How were the effects compared on that basis?

The details have been deleted and the remaining text modified for clarity.

•The parameters that the authors have used are related to storage root development, it seems that indicating that genotype performance increases overtime and is linearly explained is a logical outcome and fully expected. Storage root formation is related to maturity and developmental stages (=time). Maybe you need to clarify that result and explain better.

The terms used in the manuscript are "storage root formation" or "storage root initiation" and "bulking". Bulking is related to development and maturity. However, storage root formation or initiation, when continuous in the life of the genotype is a different component which has been identified in some

genotypes in this study and can be exploited to benefit farming systems where there is piecemeal harvesting. A small modification has been made in the text by using both storage root formation and storage root initiation.

Is the work clearly and accurately presented and does it cite the current literature?
Yes
Is the study design appropriate and is the work technically sound?
Partly

Modifications have been made under the Methods section for the reader to follow the design.

Are sufficient details of methods and analysis provided to allow replication by others?
No

The Methods and Analysis sections have been modified while avoiding expanding technical details.

If applicable, is the statistical analysis and its interpretation appropriate?
No

Details of the statistical analysis and technical details have been reduced for clarity.

Are all the source data underlying the results available to ensure full reproducibility?
No source data required
Are the conclusions drawn adequately supported by the results? Partly

The text in the Methods and analysis and results have been modified for smooth flow and clarity.

Competing Interests

No competing interests were disclosed.

A statement on competing interests has been added to the text.

Reviewer Expertise
Plant breeding and Genetics and, Conservation Genetics.
I confirm that I have read this submission and believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard, however I have significant reservations, as outlined above.

Competing Interests: The authors declare that they have no competing interests.