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Heterosis and combining ability for storage root, flesh color, virus disease resistance and vine weight in Sweet potato [*Ipomoea batatas* (L.) Lam.]

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This study was done to determine the mid-parent heterosis, the general (GCA) and specific (SCA) combining abilities of storage root yield, sweet potato virus resistance (SPVD), flesh color and vine weight of candidate sweet potato clones. Sixteen selected genotypes from two gene pools were crossed in an 8B×8A cross having 64 families. Trials were conducted with 1,896 offsprings and 16 parents during two seasons at the National Crops Resources Research Institute in Uganda (NaCRRI) using a Westcott design (only checks were replicated). Significant differences in performance were noted among families for all traits in both seasons ($P \leq 0.001$). Magabali×NK259L and Resisto×Naspot 7 were the best crosses for improving total storage root while Naspot 5×Naspot 7 stood out as the best cross for flesh color. The ratio of general combining ability to specific combining ability (GCA/SCA) for storage root, flesh color and SPVD ranged from 0.55 to 0.79, implying that additive gene effects were more important than non-additive gene effects for these traits. For vine weight, non-additive gene effects tended to be predominant. A susceptible parent Magabali and a moderately susceptible parent Naspot 1 had the most resistant progenies. This suggests that SPVD resistant alleles could be homozygous recessive, which may be confirmed in further studies. Correlation studies between traits were almost all significant except for flesh color and storage root yield. There was a positive and significant correlation ($P \leq 0.001$) between flesh color and SPVD resistance, with orange roots being the most resistant to SPVD. This important finding can help breeders to come up with orange-fleshed sweet potatoes that are highly resistant to virus diseases.

Key words: Sweet potato combining ability, heterosis, genetic effect, storage root, sweet potato virus resistance (SVDP), flesh color, vine weight.

INTRODUCTION

Undernourishment and severe food insecurity continue to be major concerns in most parts of the world especially in Africa. New statistics indicate a rise in world hunger in recent years after a prolonged decline. An estimated 821 million people, approximately one out of every nine people in the world are undernourished. Therefore, considerable efforts need to be done to achieve the objective of a world without hunger (WFP, 2018). In order to meet that goal, crops that can be resilient under a wide range of environmental conditions need to be promoted worldwide. In that regard, root and tuber crops can play a significant role as solutions. Among tuber and root crops, sweet potato [*Ipomoea batatas* (L.) Lam] plays an important role in human and animal nutrition and is known to have the potential to be resilient to climate change thanks to its plasticity to adapt to different environments and agro-systems, its productivity and short growth cycle (Glato et al., 2017).

Sweet potato is grown for food and nutritional security with the white- and cream-fleshed storage roots usually consumed as raw, boiled or fried as calorie sources, while the orange-fleshed sweet potato (OFSP) having sufficient beta-carotene levels to alleviate vitamin A deficiency (Gurmu et al., 2014). Additionally, sweet potato leaves are used as vegetable and aboveground biomass is widely used as animal feed (David et al., 2018). Bearing in mind the importance of this crop, efficient sweet potato breeding programs are vital to increase food security and improve health worldwide (in sub-Sahara Africa specifically). Two keystones of any breeding program being the characterization of the crossing parents and evaluation of their performances, bringing about two concepts core to any crop improvement program: combining ability and heterosis. The former is defined as a cultivar’s ability to transmit desirable genes or characters to their progenies in a very efficient way (Fasahat et al., 2016). Combining ability analysis helps breeders in identifying the potential parents and also informs on the genetic action governing the expression of a given trait (Rukundo et al., 2017). When crossing a genotype to several others we can calculate its mean performance in all crosses: this is referred to as the general combining ability (GCA) (Fasahat et al., 2016). GCA is directly related to the breeding value of a parent and is associated with additive genetic effects, while specific combining ability (SCA) is the relative performance of a cross and is mostly associated with non-additive gene actions, such as dominance, over dominance, epistasis (Rukundo et al., 2017). Therefore, both GCA and SCA effects are important in a breeding program (Rukundo et al., 2017).

On the other hand, heterosis, also referred to as hybrid vigor, is of sound interest to breeding programs especially for cross-pollinated crops like sweet potato (Singh, 2015). It is defined as the superiority of F1 hybrids over both parents in terms of yield or some other characters (Chaurasia, 2012). The exploitation of heterosis in crop plants is considered to be one of the milestones in modern agriculture and is of huge economic importance (Hochholdinger and Baldauf, 2018). The utilization of heterosis has become a major practice for increasing productivity of plants, which has contributed to the great increase of agricultural products worldwide in the last several decades. However, studies on yield components, qualitative traits and heterosis in sweet potato are limited and very few as compared to other crops like corn and potato. Several hypotheses have been proposed to explain heterosis such as: masking of deleterious mutations by heterozygosity; overdominance of additive loci between genotypes; protein metabolism, dosage-sensitive genes; and possible epigenetic effects (McKeown et al., 2013). In other major crops such as maize (Matin et al., 2017) and cotton (Khokhar et al., 2013), combining ability and heterosis have been heavily studied. Genetic studies in sweet potato are limited due to several barriers, namely: it is self and cross-incompatibility, high level of polyploidy and limited flowering ability and seed setting (Mwanga et al., 2017). Keeping in view the economic importance of yield contributing traits (storage root weight, vine weight) in sweet potato and also the importance of flesh color as well as resistance to SPVD, the objectives of the present study were: (1) to evaluate the general combining ability effects (GCA) of parents, (2) to estimate the specific combining ability (SCA) effects of different cross combinations with regard to the aforementioned traits, (3) to calculate the extent of the mid-parent heterosis for all progenies, and (4) to infer the correlations between the measured traits.

MATERIALS AND METHODS

Origins of parental lines

The parental lines originated from different countries in Africa, United States of America and Peru as shown in the Table 1. They are part of the parental materials of the International Potato Center’s East and Central Africa sweet potato breeding support platform based in Uganda. The list of the parents is shown in Table 1.

Plant materials and crosses

The population used in this study (Mwanga Diversity Panel) is an 8B×8A cross comprising 16 parents without reciprocals and 1,896 progenies. The 16 parental accessions were chosen from a pool of other 80 and 50 sweet potato accessions based on two heterotic

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Table 1. Background information of the parents crossed in this study.

Parent code	Name of cultivar	SPVD status	Country of origin
A1	Ejumula	S	Uganda
A2	NASPOT 1	MR	Uganda
A3	Dimbuka-Bukulula	S	Uganda
A4	NASPOT 5/58	S?	Uganda
A5	NASPOT 7	MR	Uganda
A6	SPK004	MR	Kenya
A7	NASPOT 10 O	MR	Uganda
A8	NK259L	MR	Uganda
B1	Resisto	S	USA
B2	Magabali	S	Uganda
B3	NASPOT 5	MR	Uganda
B4	Wagabolige	MR	Uganda
B5	Mugande	MR?	Uganda
B6	NASPOT 11	MR	Uganda
B7	New Kawogo	MR	Uganda
B8	Huarmeyano	S?	CIP/Peru

SPVD: Sweet potato virus disease, S: sensitive, MR: Moderately resistant, S? and MR? status not yet established but close to be sensitive or moderately resistant, respectively.

groups separated by 18 SSR markers (David et al., 2018). 64 crosses (B×A: B being the female parent and A being the male parent) were done to generate seeds that were established *in vitro* (at BecA) and later transferred to Uganda for phenotypic evaluation. Crosses and field trials were conducted at the National Crops Resources Research Institute (00°31′30″N, 32°36′54″E), Namulonge, Uganda. Experiments were conducted for two seasons in 2018 (season A running from March to July and season B running from August to December). 10 plants were established for each progeny at the beginning of the trials. Among the traits that were looked at are sweet potato virus disease (SPVD), flesh color, vine weight and total storage root.

Traits measurements

Two quantitative traits and two qualitative traits were measured in this study. Data were recorded for storage root and vine weights (in kg per plot and each plot was 3 m^2), for flesh color (ranked from 1 to 9 where 1 represents a white flesh and 9 deep orange-fleshed root) and for SPVD status (also ranked from 1 to 9 where 1 represents minimum signs of infection and 9 very high level of infection).

Phenotypic data analysis

Data were obtained from a population of 1896 progenies and 16 parents (including 2 checks: Naspot 11 and Ejumula). BLUPs (Best Linear Unbiased Prediction) were generated for each residual across all traits for the two seasons (separately) with the following model using ASREML software implemented in R (Version. 3. 6):

$$Y_{ijk} = \mu + g_i + r_j + c_k + e_{ijk}$$

where Y_{ijk} is the phenotypic performance of the ith genotype in the jth row and kth column, μ is the oval mean, g_i is the effect of the genotype, r_i, is the effect of the ith row, c_k is the effect of the kth column, and e_{ijk} is the experimental error. It was assumed that row and column effects were random. Co-analysis of the two seasons together did not allow the combined mixed model to converge.

Descriptive statistical analyses were then done on BLUPs of checks, parents, all progenies and 10% of the best performing progenies for every trait in each season. Mid-parent heterosis was calculated for the overall population and per family using the following formula:

$$\text{Mid-parent Heterosis (\%)} = [(\text{F1} - \text{MP})/\text{MP}] \times 100$$

where F1 and MP represent the mean performance of the progenies and the two parents, respectively. Correlation of BLUPs was evaluated between seasons and between pairs of traits. All analyses were conducted using R software (Version 3.6.1). The combining ability of parental lines was calculated as the deviation of the mean performance of the line in all its crosses from the mean of all crosses, while the specific combining abilities of crosses were computed as the deviation of the mean for each cross from the sum of general combining abilities of its two parental lines as defined in Griffin's method (Olfati et al., 2012a). The relative importance of GCA and SCA was estimated using the general predicted ratio (GPR) for the traits observed as follows (Baker, 1978):

$$\text{GCA/SCA} = (2\text{MSGCA}) / (2\text{MSGCA} + \text{MSSCA})$$

RESULTS AND DISCUSSION

Descriptive statistics on the overall population

Total storage root weight was better for the season A

Table 1. Descriptive statistics for BLUPs of the full population, checks and the best 10% clones for every trait in each season.

Statistics	TSRW (Kg/plot)		Flesh color (1-9)		SPVDR (1-9)		Vine weight (kg/plot)	
	SA	SB	SA	SB	SA	SB	SA	SB
Overall mean	2.39	0.83	2.15	4.18	2.79	2.84	3.99	3.23
Overall Min	1.68	0.69	0.7	1.2	2.42	1.83	1.83	1.84
Overall Max	6.87	2.26	7.76	8.51	3.88	4.57	10.67	8.82
Mean Checks	3.92	1.16	3.17	3.84	3.21	3.30	4.72	4.18
Mean best 10%	2.95	0.92	6.55	6.85	2.57	2.04	6.06	5.10

TSRW: Total storage root weight, SPVDR: sweet potato virus disease resistance, SA: season A, SB: season B.

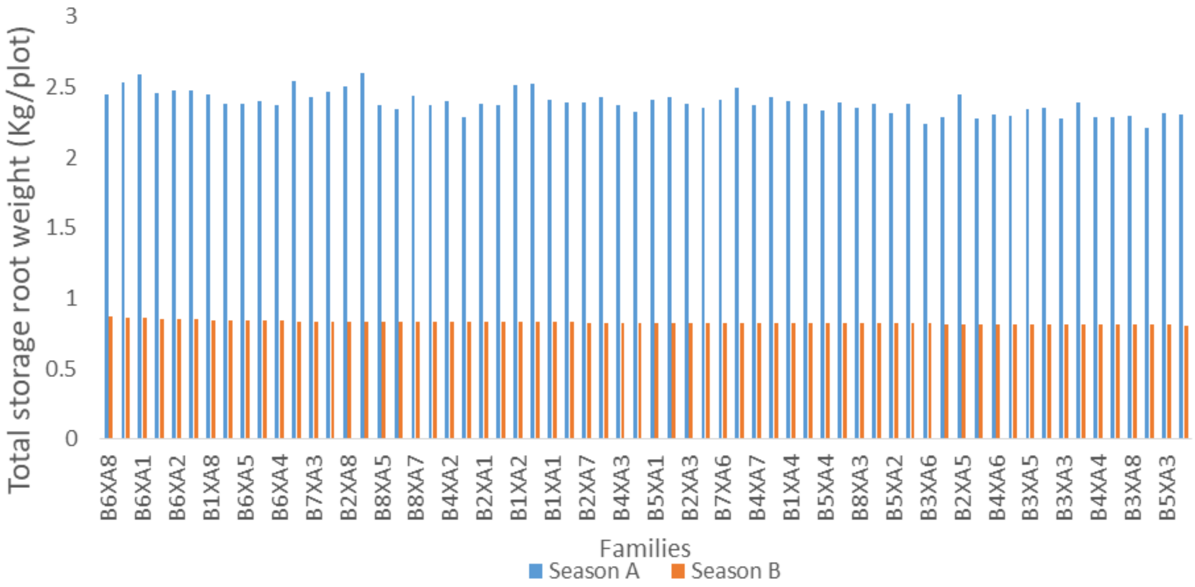

Figure 1. Mean performances of families using BLUPs for storage root weight in seasons A and B.

than for the season B. In season A, 50% of the genotypes had 2.36 kg/plot and above whilst the same percentage performed far less (0.82 kg/plot) in season B. At the same time the highest storage root weight yield was 6.87 and 2.26 kg/plot in seasons A and season B, respectively. The flesh color performance was better in season B than season A. 50% of the genotypes had a flesh color ranked at least 2 and the best genotypes for this trait scored 7 in season A, while half of the genotypes had a flesh color ranked at least at 4 and the best performance nearly reached 9 (8.51). The genotypes showed slightly better SPVD resistance status in season A than in season B. Less signs of disease were noticed in the first season where the most affected genotypes had a score of 3.88 on average as compared to the second season where the most affected genotypes had a score of 4.57 on average. The vine weight had also a better record for season A. Half of the genotypes had at least 3.92 and 3.07 kg/plot for seasons A and B, respectively. The highest performance was 10.67 kg/plot in the first season and 8.82 kg/plot in the second (Table 2).

Analysis of variance

The mean performances for the measured traits were all significantly different between families as well as within families (Figures 1 to 4). Progenies form the families B7×A1, B6×A1, B7×A5, B6×A3 and B7×A7 had the highest storage root yield with 2.6, 2.58, 2.54, 2.53 and 2.52 kg/plot, respectively (Figure 1). Genotypes belonging to the families B1×A1, B3×A1 and B1×A7 ranked the highest for flesh color with 5.6, 5.0 and 4.5, respectively (Figure 2). For SPVD resistance, progenies from B3×A6, B3×A2 and B5×A2 showed less signs of virus disease with a rank of 2.7 in average (Figure 3).

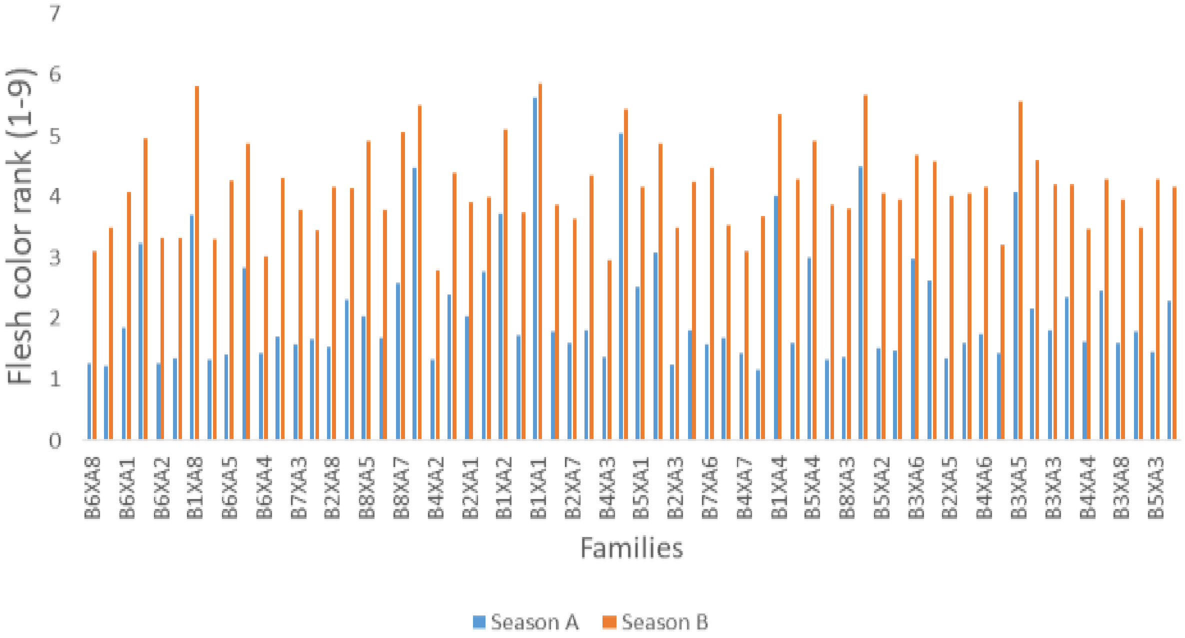

Figure 2. Mean performances of families using BLUPs for flesh color in seasons A and B.

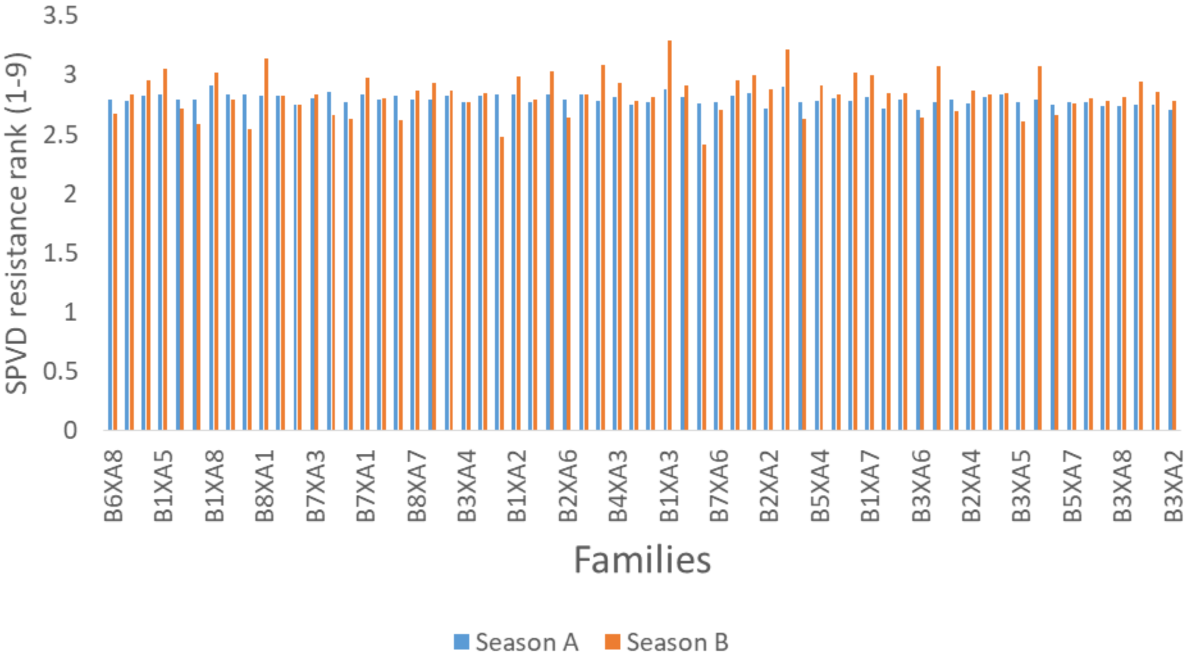

Figure 3. Mean performances of families using BLUPs for SPVD resistance in seasons A and B.

Genotypes from B2×A5, B5×A1, B8×A7 and B2×A8 had the highest vine weight (4.64-4.48 kg/plot) (Figure 4 and Table 3).

The parent’s storage root yield ranged between 2.31 and 4.63 kg/plot of which the highest were Naspot 11 and Ejumula (4.63 and 3.21 kg/plot, respectively), and the lowest was Magabali. Parent A1 (Ejumula) had the highest flesh color rank followed by parent B7 (New Kawogo) and parent B6 (Naspot 11) had the lowest score. Parent B3 (Naspot 5) was the most resistant to

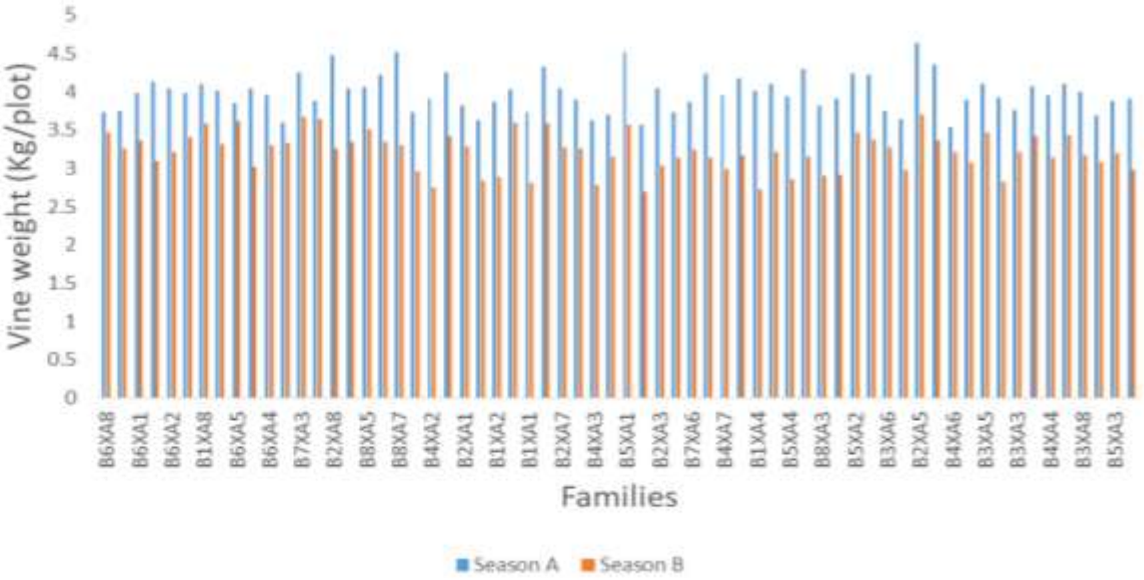

Figure 4. Mean performances of families using BLUPs for vine weight in seasons A and B.

Table 3. Combined analysis of variance using Kruskal-Wallis test for four agronomic traits of the F1 progenies in season A.

Source	Df	Chi square			
		TSRW	Flesh color	SPVDR	Vine weight
Family	63	185.68***	352.41***	138.17***	122.48***

Df: Degrees of freedom, ***: data significant at P ≤ 0.001

Table 4. Combined analysis of variance using Kruskal-Wallis test for four agronomic traits of the F1 progenies in season B.

Source	Df	Chi square			
		TSRW	Flesh color	SPVDR	Vine weight
Family	63	182.56***	518.66***	206.15***	200.35***

Df: Degrees of freedom, ***: data significant at P ≤ 0.001.

SPVD and parent A1 the most susceptible. Parent B6 had the highest vine yield with 5.57 kg/plot.

The mean performances for all the measured traits were significantly different and progenies performed better in season A than in season B. Progenies from B6×A8, B6×A3, B6×A1 and B1×A5 had the highest storage root production with, respectively 0.87 kg/plot for the for the first family and 0.86 kg/plot for the three last. Genotypes belonging to the family B1×A1 ranked the highest for flesh color followed by those from B1×A8, B1×A7 and B3×A5, respectively. Families B7×A8, B7×A4, B6×A5, and B6×A6 showed the best resistance status to SPVD while progenies from B2×A5, B7×A3 and B6×A7 had the best vine production (Table 4).

The parents' storage root yield ranged between 1.59 and 0.74 kg/plot with Naspot 11 having the highest yield followed by Naspot 10 O (0.85 kg/plot). Ejumula had the highest rank for flesh color with and Naspot 11 the lowest. Naspot 11 had the best resistance status along with New Kawogo while having also the highest vine production with Mugande and Magabali.

Consistency of family performance across seasons

For storage root yield, families B6×A1 and B6×A3 were

Table 5. Mid-parent heterosis for the 30 best progenies based on the mean performances of the families on total storage root weight in both seasons.

Season A TSRW			Season B TSRW		
Clone ID	**Family**	**MPH (%)**	**Clone ID**	**Family**	**MPH (%)**
MDP139	B1×A2	33.48	MDP320	B1×A8	24.28
MDP131	B1×A2	32.80	MDP216	B1×A5	21.24
MDP110	B1×A2	30.62	MDP237	B1×A5	21.10
MDP525	B2×A8	58.04	MDP318	B1×A8	17.66
MDP524	B2×A8	49.70	MDP317	B1×A8	17.64
MDP523	B2×A8	26.58	MDP224	B1×A5	17.50
MDP513	B2×A8	20.00	MDP228	B1×A5	16.85
MDP507	B2×A8	19.24	MDP238	B1×A5	15.42
MDP1253	B7×A1	29.24	MDP311	B1×A8	14.50
MDP1247	B7×A1	27.24	MDP319	B1×A8	14.13
MDP1302	B7×A5	58.90	MDP321	B1×A8	13.66
MDP1297b	B7×A5	54.39	MDP310	B1×A8	13.36
MDP1293c	B7×A5	37.48	MDP239	B1×A5	12.97
MDP1303	B7×A5	37.37	MDP316	B1×A8	12.81
MDP1297	B7×A5	34.11	MDP328a	B1×A8	11.16
MDP1294	B7×A5	22.11	MDP314	B1×A8	10.14
MDP1296	B7×A5	18.11	MDP221	B1×A5	9.94
MDP1303a	B7×A5	16.07	MDP313	B1×A8	9.62
MDP1354	B7×A7	34.09	MDP329a	B1×A8	8.75
MDP1354	B7×A7	34.09	MDP307	B1×A8	7.71
MDP1328	B7×A7	25.15	MDP330a	B1×A8	7.12
MDP1328	B7×A7	25.15	MDP303	B1×A8	6.83
MDP1339	B7×A7	22.56	MDP220	B1×A5	6.77
MDP1339	B7×A7	22.56	MDP323a	B1×A8	6.21
MDP1346	B7×A7	19.55	MDP315	B1×A8	5.81
MDP1346	B7×A7	19.55	MDP331a	B1×A8	5.46
MDP1332	B7×A7	17.14	MDP322a	B1×A8	5.27
MDP1332	B7×A7	17.14	MDP312	B1×A8	4.98
MDP1352	B7×A7	16.41	MDP226	B1×A5	4.91
MDP1352	B7×A7	16.41	MDP322	B1×A8	4.85

TSRW: total storage root weight, MPH: mid-parent heterosis

consistently ranked among the best seven (~10%) in both seasons. Families B1×A1, B3×A5, B1×A6, B3×A1, B1×A4 and B1×A7 were consistent between the seasons for flesh color. No family was consistent between the seasons for SPVD while families B2×A5 and B2×A6 were the only consistent across the two seasons for vine weight.

Heterosis

Heterosis for total storage root weight

All the families were ranked based on their performances for the measured traits in each season and the seven best families (~10%) were chosen to calculate the mid-parent heterosis of the progenies. The progenies were thereafter ranked and the 30-best shown in Tables 5 to 8.

Clones MDP139, MDP131 and MDP110 (all belonging to B1×A2 family), showed the highest mid parent heterosis with 33.48, 32.80 and 30.62%, respectively on storage root weight in the season A. B1×A2 family had 3 progenies, while B2×A8, B7×A1, B7×A5 and B7×A7 had, respectively 5, 2, 8, and 12 progenies out of the 30 heterotic crosses. Clones MDP320, MDP216 and MDP237 had the best heterosis in season B with respectively 24.28, 21.24 and 21.10%. The 30 best progenies were shared only among two families namely

Table 6. Mid-parent heterosis for the 30 best progenies based the mean performances of the families on flesh color in both seasons.

Season A Flesh color			Season B Flesh color		
Clone ID	Family	MPH (%)	Clone ID	Family	MPH (%)
MDP126	B1×A2	246.9869	MDP317	B1×A8	93.88
MDP140	B1×A2	246.6692	MDP325a	B1×A8	93.78
MDP122	B1×A2	244.8855	MDP308	B1×A8	92.63
MDP124	B1×A2	244.2425	MDP313	B1×A8	92.62
MDP134	B1×A2	243.3149	MDP319	B1×A8	92.24
MDP125	B1×A2	243.0951	MDP187	B1×A4	75.94
MDP123	B1×A2	242.45	MDP330a	B1×A8	72.40
MDP128	B1×A2	239.7813	MDP315	B1×A8	71.80
MDP117	B1×A2	235.5377	MDP328a	B1×A8	71.07
MDP183	B1×A4	259.649	MDP310	B1×A8	70.98
MDP197	B1×A4	253.9032	MDP322	B1×A8	70.75
MDP190	B1×A4	240.4212	MDP311	B1×A8	70.55
MDP199	B1×A4	234.0935	MDP305	B1×A8	70.25
MDP270	B1×A6	248.9083	MDP306	B1×A8	70.04
MDP271	B1×A6	248.4737	MDP323a	B1×A8	69.97
MDP261	B1×A6	246.7578	MDP326a	B1×A8	69.04
MDP262	B1×A6	243.5808	MDP318	B1×A8	68.17
MDP269	B1×A6	241.2006	MDP269	B1×A6	65.28
MDP298	B1×A7	253.7948	MDP636	B3×A5	64.57
MDP278	B1×A7	248.2322	MDP278	B1×A7	58.60
MDP280	B1×A7	247.9483	MDP289	B1×A7	58.14
MDP294	B1×A7	240.583	MDP288	B1×A7	57.22
MDP295	B1×A7	238.3572	MDP20	B1×A1	56.93
MDP281	B1×A7	235.7962	MDP3	B1×A1	56.75
MDP301	B1×A7	235.3117	MDP31	B1×A1	56.71
MDP626	B3×A5	243.5736	MDP280	B1×A7	56.63
MDP624	B3×A5	241.9982	MDP25	B1×A1	56.59
MDP636a	B3×A5	239.726	MDP190	B1×A4	56.42
MDP647	B3×A5	237.8907	MDP35	B1×A1	56.22
MDP627	B3×A5	237.5849	MDP86	B3×A1	56.10

MPH: Mid-parent heterosis.

B1×A8 with 21 progenies and B1×A5 with 9 progenies.

Heterosis for flesh color

MDP183, MDP197 and MDP298 showed the highest heterosis for flesh color in season A with 259.64, 253.90, and 253.79%, respectively. Among the 30 best progenies, clones from B1×A2 family were 9, those from B1×A4 were 4, those from B1×A6 were 5, those from B1×A7 were 7 and those from B3×A5 were 5. In season B, the highest heterosis was recorded in B1×A8 family with clones MDP317, MDP325a and MDP308 having, respectively 93.88, 93.78 and 92.63%. Family B1×A8 had the highest number of progenies with high heterosis (16) followed by B1×A1 with 5 progenies.

Heterosis for SPVD resistance

For this trait the negative heterosis is selected to indicate the level of resistance to sweet potato virus disease. In other words, most negative values display better heterosis for this trait. In that regard, clones MDP355 and MDP362 showed the best heterosis with -13.64 and -13.61% respectively, they both belong to B2×A2 (Magabali×Naspot 1) family. Progenies from B2×A2 family were 12 and those from B5×A2 were 5. During the

Table 7. Mid-parent heterosis for the 30 best progenies based the mean performances of the families on SPVD resistance in both seasons.

Season A SPVDR			Season B SPVDR		
Clone ID	**Family**	**MPH (%)**	**Clone ID**	**Family**	**MPH (%)**
MDP355	B2×A2	-13.64	MDP1364b	B7×A8	-56.90
MDP362	B2×A2	-13.61	MDP1366c	B7×A8	-56.11
MDP880	B5×A2	-10.98	MDP1361	B7×A8	-54.84
MDP366	B2×A2	-10.46	MDP1356b	B7×A8	-52.52
MDP949	B5×A6	-10.11	MDP1789	B7×A4	-44.72
MDP370	B2×A2	-9.69	MDP815	B4×A8	-35.55
MDP893	B5×A2	-9.51	MDP1362	B7×A8	-32.09
MDP374	B2×A2	-9.40	MDP1358b	B7×A8	-30.53
MDP369	B2×A2	-9.01	MDP822	B4×A8	-30.38
MDP609	B3×A8	-8.80	MDP517	B2×A8	-29.91
MDP585	B3×A3	-8.74	MDP816	B4×A8	-27.97
MDP575	B3×A3	-8.70	MDP510	B2×A8	-27.88
MDP874	B5×A2	-8.49	MDP526	B2×A8	-27.43
MDP367	B2×A2	-8.33	MDP818	B4×A8	-26.14
MDP538	B3×A2	-8.31	MDP836i	B4×A8	-25.88
MDP360	B2×A2	-8.28	MDP824	B4×A8	-23.54
MDP357	B2×A2	-8.05	MDP646f	B3×A5	-23.28
MDP359	B2×A2	-8.05	MDP525	B2×A8	-23.22
MDP363	B2×A2	-7.77	MDP828	B4×A8	-22.34
MDP361	B2×A2	-7.76	MDP631	B3×A5	-22.13
MDP533	B3×A2	-7.61	MDP522	B2×A8	-21.91
MDP557	B3×A2	-7.40	MDP646	B3×A5	-21.86
MDP672	B3×A6	-7.36	MDP812	B4×A8	-21.83
MDP872	B5×A2	-7.27	MDP819	B4×A8	-21.52
MDP868	B5×A2	-7.26	MDP511	B2×A8	-21.39
MDP551	B3×A2	-7.06	MDP516	B2×A8	-20.68
MDP553	B3×A2	-6.73	MDP505	B2×A8	-20.66
MDP881	B5×A2	-6.72	MDP524	B2×A8	-20.54
MDP375	B2×A2	-6.69	MDP638	B3×A5	-20.14
MDP354	B2×A2	-6.64	MDP639	B3×A5	-19.75

SPVD: Sweet potato virus disease resistance, MPH: mid-parent heterosis.

season B, heterosis was better with the best performances shown by MDP1364b, MDP1366c and MDP1361 (-56.90, -56.11 and -54.84%, respectively), all belonging to B7×A8 family. NK259L was the most represented male parent, being involved in 24 out of the 30 heterotic crosses.

Heterosis for vine weight

Clones MDP1546, MDP1588 and MDP842 had the highest heterosis for vine weight in season A with, respectively 166.91, 91.73 and 91.02%. Huarmeyano was involved in 10 crosses as female parent out of the 30 best. Progenies from B8×A8 and B8×A7 were five in each family. MDP1774, MDP1328 and MDP322a showed the best heterosis with 141.17, 130.20 and 106.84% in season B, respectively. B7×A3 and B7×A7 were the most represented with seven progenies each.

Combining ability

The general combining ability for parents was calculated and presented in Tables 9 and 10. During season A, New Kawogo and Naspot 11 were the female parents that had the highest and positive GCA with 0.09 and 0.08, respectively, while Wagabolige and Naspot 5 showed the lowest GCA for storage root weight (-0.06 and -0.08),

Table 8. Mid-parent heterosis for the 30 best progenies based the mean performances of the families on vine weight in both seasons.

Season A Vine weight			Season B Vine weight		
Clone ID	**Family**	**MPH (%)**	**Clone ID**	**Family**	**MPH (%)**
MDP1546	B8×A7	166.91	MDP1774	B7×A3	141.17
MDP1588	B8×A8	91.73	MDP1328	B7×A7	130.20
MDP842	B5×A1	91.02	MDP322a	B1×A8	106.84
MDP415	B2×A5	87.71	MDP1354	B7×A7	102.74
MDP1570	B8×A8	81.67	MDP1335	B7×A7	99.24
MDP1556	B8×A7	80.58	MDP321	B1×A8	84.27
MDP420	B2×A5	78.67	MDP1343	B7×A7	81.84
MDP54	B2×A4	74.58	MDP318	B1×A8	78.51
MDP523	B2×A8	70.25	MDP1192	B6×A7	76.94
MDP457	B2×A6	68.84	MDP1765	B7×A3	70.82
MDP435	B2×A5	68.37	MDP1195	B6×A7	68.74
MDP1584	B8×A8	65.53	MDP421	B2×A5	68.44
MDP857	B5×A1	63.46	MDP327a	B1×A8	68.07
MDP514	B2×A8	60.81	MDP1759	B7×A3	62.42
MDP866	B5×A1	60.21	MDP1764	B7×A3	56.82
MDP1544	B8×A7	57.63	MDP313	B1×A8	56.68
MDP430	B2×A5	55.28	MDP1332	B7×A7	55.84
MDP1584a	B8×A8	47.74	MDP1780	B7×A3	51.12
MDP423	B2×A5	47.44	MDP1183	B6×A7	49.34
MDP1547	B8×A7	46.02	MDP1784	B7×A3	48.88
MDP1589	B8×A8	45.13	MDP309	B1×A8	48.05
MDP840	B5×A1	43.19	MDP1769	B7×A3	43.21
MDP52	B2×A4	43.05	MDP1341	B7×A7	42.00
MDP434	B2×A5	40.50	MDP331a	B1×A8	40.18
MDP521	B2×A8	38.69	MDP1347	B7×A7	38.90
MDP43	B2×A4	37.78	MDP438	B2×A5	34.10
MDP505	B2×A8	36.50	MDP412	B2×A5	33.70
MDP852	B5×A1	35.82	MDP1757	B7×A3	31.61
MDP68	B2×A4	35.74	MDP317	B1×A8	31.16
MDP1538	B8×A7	35.11	MDP1333	B7×A7	30.29

MPH: Mid-parent heterosis.

respectively. Ejumula had the best GCA for the same trait as male parent with 0.05. Resisto showed the highest GCA for flesh color as female parent with 1.89 and Ejumula as male parent with 0.88. Naspot 5 had the lowest GCA as female parent (-0.04), while Naspot 1 along with SPK004 had the lowest GCA with -0.01 each on male parent's group for SPVD resistance. Magabali had the best performance for vine weight as a female parent with a GCA of 0.24, whilst Ejumula and Naspot 10 O were the best male parents with -1.18 each.

During the season B Naspot 11 stood out as best female parent with a GCA of 0.03 whilst all the male parents had a GCA of 0.01 except Naspot 5/58 which had a GCA of 0 for storage root weight. Resisto still had the best GCA as female parent (1.22), while Ejumula appeared to have the highest GCA (0.37) as male parent. Magabali along with SPK004 had the lowest GCA as female and male parents with -0.05 and -0.06, respectively for SPVD resistance. Naspot 11 had the highest GCA for vine weight with 0.19 and Ejumula the highest GCA among male parents with -0.29.

The seven best SCA were all positive for total storage root in seasons A and B. B2×A8 (Magabali×Huarmeyano) cross had the highest SCA in season A while B1×A5 was the best cross in season B with 0.09 and 0.02, respectively. For flesh color SCA ranged from 1.61 to 0.51 in season A and from 0.79 to 0.45 in season B. For both seasons, B3×A5 (Naspot 5 × Naspot 7) showed the

Table 9. GCA effects of parents for the measured traits in season A.

Female parent	General combining ability Season A				Observation
	TSRW	Flesh color	SPVDR	Vine weight	
New Kawogo	0.09	-0.35	0	-0.03	218
NASPOT 11	0.08	-0.72	0.02	-0.09	241
Resisto	0.04	1.89	0.06	-0.1	240
Magabali	0.01	-0.56	0	0.24	244
Huarmeyano	-0.01	-0.07	0	0.04	244
Mugande	-0.04	-0.13	-0.02	0.13	242
Wagabolige	-0.06	-0.59	0.02	-0.14	226
NASPOT 5	-0.08	0.51	-0.04	-0.02	240
Male parent					
Ejumula	0.05	0.88	0.02	-1.18	224
NASPOT 1	0.03	-0.32	-0.01	-1.21	242
NASPOT 10 O	0.03	0	0.02	-1.18	245
NK259L	0.01	-0.3	0.01	-1.19	240
NASPOT 7	0	-0.02	0.01	-1.19	243
Dimbuka-Bukulula	0	-0.5	0.01	-1.19	241
SPK004	-0.03	0.15	-0.01	-1.21	243
NASPOT5/58	-0.07	0.22	0.01	-1.19	218

TSRW: Total storage root weight, SPVD: sweet potato virus disease resistance.

Table 10. GCA effects of parents for the measured traits in season B.

Female parent	General combining ability Season B				Observation
	TSRW	Flesh color	SPVD	Vine weight	
NASPOT 11	0.03	-0.67	-0.11	0.19	241
Resisto	0.01	1.22	0.23	-0.26	240
New Kawogo	0.01	-0.16	-0.07	0.13	218
Huarmeyano	0.01	0.32	0.15	-0.1	244
Magabali	0.01	-0.31	-0.05	0.11	244
Wagabolige	0	-0.79	0.02	-0.17	226
Mugande	0	0	-0.04	0.09	242
NASPOT 5	0	0.35	-0.11	0.04	240
Male parent					
Ejumula	0.01	0.37	0.09	-0.29	224
NASPOT 1	0.01	-0.32	0.05	-0.33	242
NASPOT 10 O	0.01	-0.08	0	-0.38	245
NK259L	0.01	-0.02	-0.12	-0.5	240
NASPOT 7	0.01	0.16	-0.07	-0.45	243
Dimbuka-Bukulula	0.01	-0.31	0.08	-0.3	241
SPK004	0.01	0.18	-0.06	-0.44	243
NASPOT5/58	0	0.06	0.06	-0.32	218

TSRW: Total storage root weight, SPVD: sweet potato virus disease resistance.

highest SCA. B4×A5 and B7×A4 had the best (lowest) SCA for SPVD resistance, respectively for seasons A and B. The seven best SCA for vine weight ranged from 1.64 to 1.47 (in season A) and from 1.12 to 0.64 (in season) with B8×A7 being the best cross in season A and B1×A8 being the best cross in season B. The GCA/SCA ratios were calculated for all traits in each season separately and shown in Table 12. The ratios were all > 0.5 for all traits in both seasons except for vine weight where it was equal to 0.5 in season A and 0.46 in season B.

Correlation tests between seasons and traits

Spearman rank tests were run to see the consistency of the performance of the progenies between the seasons.

All the correlations were significantly positive. The highest correlation was obtained for flesh color (R=0.41) followed by storage root weight (R=0.31). The lowest correlation was gotten between SPVD-SA and SPVD-SB (R=0.20).

Correlations between traits were computed using the mean performance of every clone in the two seasons for the measured traits. Storage root weight was significantly and positively correlated to other traits except for flesh color where the correlation was non-significant (Table 14). Flesh color performances were significantly correlated with SPVD performances, while a weak and significant negative correlation (-0.079) was found between flesh color and vine weight. Vine weight and SPVD status were also significantly and negatively correlated (-0.04).

DISCUSSION

Performance of F1's and parents in season A

This study was based on an unreplicated trial, which in many regards, is quite different from replicated designs. Replication along with randomization and blocking are the backbones of any experimental design (Girma and Machado, 2013), although during early breeding stages when the main focus is to rank genotypes based on their performances, it is more practical to conduct unreplicated designs. However, replication becomes mandatory in late stages of breeding programs as it increases the accuracy of estimates of cultivars differences as well as their respective performances, which is important for breeding value prediction immediately prior to commercial release (Kempton and Gleeson, 1997). In the early generations of a breeding like in our study, however, the benefits from replication are less clear because the main focus here lies on ranking genotypes rather than predicting their performances (Kempton and Gleeson, 1997). In our study yield on total storage root results can be analyzed from different angles. The population performed better in season A than season B with means of 1.68 and 0.69 Kg/plot respectively. Clearly, environmental conditions were more favorable in the first season. However, there was a consistency between seasons because the high yielding families did not differ that much across seasons. In both seasons, checks performed better than overall progenies and other parents, which is in agreement with the findings of (Mwanga et al. 2007, 2011) who recognized Naspot 11 and Ejumula as good performers for storage root yield. The frequency of the checks was maintained high to lower plot error considerably and to improve the efficiency of the ranking (Kempton and Gleeson, 1997). Because of field heterogeneity and the high number of progenies (1896), all the F1 individuals were ranked and the best 10% of the overall population was selected to infer the extend of the genetic gain of the crosses. This group had higher means than the overall population as well as the parents for all traits across seasons, indicating thus a genetic gain of some progenies over their respective parents. This not only shows that some crosses gave offsprings with added value, but also that some combinations (families) were more efficient than others. For flesh color the 10% best progenies had means superior to those of the checks in both seasons, showing a high genetic gain that was strongly statistically supported. Furthermore, Resisto was the female parent to almost all the 10% best progenies, possibly because it is an orange-flesh cultivar (Tumwegamire et al., 2014a, b) and also carries dominant alleles for this trait. The whole population showed a better resistance status to SPVD in season A than season B. This can be attributed to the buildup of viruses between season one and two of planting material. In fact, planting materials were taken from the same net-tunnels for both seasons. The best 10% offsprings performed however better in season B this could possibly be explained by their added genetic predisposition to resist to the virus. Vine weight performance was better in season A for the whole population as well as for the checks and the 10% best offsprings. This trait being genetically controlled; it appears that genotypes had a large variety of genetic makeups resulting in different vine weight yields. These present results are closely similar to the findings of Rahman et al. (2015).

Analysis of variance for family performance was done using Kruskal-Wallis test (a non-parametric test) because the data were not normally distributed. Significant Chi squares for families on total storage root demonstrated genetic variation between crosses. Significant differences ($p \leq 0.001$) were also noticed between families from the Kruskal-Wallis test for all the other traits across the two seasons. These results are consistent with the findings of Rukundo et al. (2017). That study concluded that there was a significant difference between means of sweetpotato families on storage root, flesh color, vine weight and biomass though the authors used ANOVA. Therefore, this suggests that crosses were actually consistently and significantly of different breeding value and that selection can be made for taking the better progenies to the next stage of breeding.

Mid parent heterosis

Heterosis has been used in many crops to harness dominance variance through production of hybrids (Olfati et al., 2012b). The mid-parent heterosis, also relative heterosis for the seven best families (~10%) was calculated for all traits in every season. Specific parental backgrounds resulted in progeny with high MPH. In season A, for storage root weight, Resisto, Magabali and New Kawogo were the only female parent represented while Naspot 1, N259KL, Ejumula, Naspot 7 and Naspot 10 O were the male parents involved, showing that these parents can be candidates for having elite varieties for storage root. In season B on the other hand, Resisto was the only female parent for all the progenies, while the male parents were NK259L and Naspot 7. This further confirms the huge potential of using these cultivars to give high yielding progenies for storage root. In this study, the improved performances of hybrids relative to their parents can be explained by favorable allelic interactions at heterozygous loci that outperform either homozygous states or by the fact that deleterious and recessive alleles at different loci in the parental genomes are masked in the F1 hybrids thus producing a better phenotype.

For flesh color, Resisto was the best female parent in season A and B. In season B MDP317 clone, belonging to B1×A8 (Resisto×NK259L) had the highest MPH. This could be explained by the fact that dominant alleles brought by Resisto had masked the recessive alleles brought by NKL259L which is cream-flesh. This result could suggest that alleles for 'orange-fleshed root' are dominant against alleles for 'cream-fleshed root' in sweet potato. For disease resistance the best mid-parent heterosis is the negative ones because negative values show less signs of infections. In that regard MDP355 clone from B2×A2 (Magabali×Naspot 1) family showed the best heterosis in season A. Knowing that Magabali is very susceptible variety to SPVD (Mwanga et al., 2011), these findings may imply that genes responsible for SPVD resistance are homozygous and recessive in Magabali. Mid-parent heterosis for vine weight was better in seasons A than B. This can be attributed to the high buildup of virus in planting materials during season B. MDP1546 clone from B8×A7 family had the highest heterosis and Huarmeyano was the most represented female parent followed by Magabali and Mugande suggesting that these parents could be carriers of either recessive or dominant alleles for vine weight. MDP 1774 clone from B7×A3 family showed the highest heterosis in season B with New Kawogo being the most represented female parent and Naspot 10 O the most represented male parent. These findings are in agreement with previous results (Mwanga et al., 2011) where New Kawogo was described as being high biomass yielding cultivar.

GCA and SCA effects

The GCA effects of parental lines were calculated and shown in Tables 9 and 10 for seasons A and B, respectively. Though significance levels were not calculated, the values obtained were statistically strong because each parent (male or female) was observed at least 218 times.

It appeared that for total storage root, New Kawogo and Naspot 11 were the best general combiners during the first season, while Naspot 11 only had the highest GCA effect among all parental lines in season B, an indication that these parents may be used for improving storage root yield. Combining ability studies have been conducted in many crops ranging from cereals, roots to legumes, indicating that it is a crucial tool in plant breeding (Fasahat et al., 2016). In sweet potato, though some more efforts need to be done, studies on combining ability estimation are readily available (Esan and Omilani, 2018; Musembi et al., 2015; Rukundo et al., 2017). Resisto and Ejumula had the GCA effects on flesh color suggesting that these parents must be included in a breeding scheme where the target is to develop cultivars with high beta-carotene content. Naspot 5 along with NKL259L, Naspot 7 and SPK004 were the best general combiners for sweet potato disease resistance, indicating that these parents, when included in a breeding program, will produce progenies with high resistance to SPVD. For vine weight, Mugande and Naspot 11 and Magabali were the best general combiners, these parents may be carriers of dominant alleles for high vine weight yields.

SCA effects of all crosses were calculated and ranked. The seven best SCA effects for every trait in each season were chosen and shown in Table 11. SCA effects for storage root were higher in season A (due to the virus buildup in season B) and the best cross being B2×A8 (Magabali×NK259L) could be explained by additive gene effects from both parents. For flesh color B3×A5 (Naspot 5×Naspot 7) stood out as the best cross in both seasons, indicating also additive genetic actions from both parents. Crosses B4×A5 (Wagabolige×Naspot 7) and B7×A4 (New Kawogo×Naspot 10 O) showed the best SCA for SPVD in seasons A and B, respectively. It appeared also that parent A6 (SPK004) was involved in 5 out of the seven best crosses in season B, provided that SPK004 is moderately resistant (Mwanga et al., 2007), this finding could suggest that this parent carries recessive alleles for SPVD resistance. For vine weight, the best SCA were all positive, this shows that non-additive genetic events were highly pronounced in the designated crosses. SCA effects were higher in season A with B8×A7

Table 11. SCA of the best crosses for the measured traits in seasons A and B.

Season	TSRW		Flesh color		SPVDR		Vine weight	
	Crosses	SCA	Crosses	SCA	Crosses	SCA	Crosses	SCA
Season A	B2×A8	0.09	B3×A5	1.61	B4×A5	-0.07	B8×A7	1.67
	B7×A1	0.07	B3×A1	1.19	B2×A2	-0.06	B2×A5	1.60
	B6×A1	0.07	B5×A4	0.76	B1×A7	-0.06	B5×A1	1.59
	B7×A5	0.07	B7×A4	0.75	B5×A2	-0.05	B4×A8	1.57
	B6×A3	0.06	B1×A1	0.70	B7×A5	-0.04	B7×A2	1.49
	B5×A4	0.06	B2×A8	0.56	B4×A4	-0.04	B7×A3	1.48
	B1×A2	0.06	B8×A7	0.51	B1×A6	-0.04	B3×A4	1.47
Season B	B1×A5	0.02	B3×A5	0.79	B7×A4	-0.35	B1×A8	1.12
	B5×A5	0.02	B5×A4	0.67	B7×A8	-0.24	B2×A5	0.93
	B6×A8	0.01	B8×A7	0.64	B6×A6	-0.23	B8×A5	0.84
	B3×A4	0.01	B6×A5	0.59	B1×A6	-0.22	B4×A8	0.81
	B1×A8	0.01	B4×A6	0.59	B2×A6	-0.17	B6×A5	0.65
	B4×A8	0.00	B3×A1	0.48	B3×A6	-0.15	B3×A5	0.65
	B4×A2	0.00	B1×A8	0.45	B7×A6	-0.14	B7×A7	0.64

TSRW: Total storage root weight, SCA: specific combining ability, SPVDR: sweetpotato virus disease resistance.

Table 12. GCA/SCA ratios for the measured traits in seasons A and B.

Parameter	TSRW SA	TSRW SB	Flesh color SA	Flesh color SB	SPVDR SA	SPVDR SB	Vine weight SA	Vine weight SB
GCA/SCA	0.67	0.61	0.79	0.76	0.55	0.62	0.5	0.46

TSRW: Total storage root weight, SCA: specific combining ability, GCA: general combining ability, SPVDR: sweet potato virus disease resistance, SA: season A, SB: season B.

(Huarmeyano×Naspot 10 O) being the cross with the best SCA effect followed by B2×A5 (Magabali×Naspot 7). Magabali being a low yielding variety (Mwanga et al., 2007) and Naspot 7 being moderately yielding variety, this result agrees with the fact that non-additive genetic action is predominant for vine weight. Predominant genetic actions were looked at for each trait by calculating GCA/SCA ratios and the results are shown in Table 12. Ratios were greater than 0.5 for storage root, flesh color and SPVD resistance, implying predominance of additive over non-additive genetic effects. This ratio was however equal to 0.5 for vine weight in season A and to 0.46 in season B suggesting a significant role of non-additive genetic effect on this trait. These results are in strong agreement with the findings of (Rukundo et al., 2017). The same results were also obtained by Musembi et al. (2015) when studying the predominant genetic action for fresh root.

Correlation tests between traits and seasons

Spearman rank correlation tests were conducted to see the consistency in the performances of each genotype from one season to the other. The results of the tests are assigned in Table 13. All the tests were significantly positive. However, the highest correlation coefficient did not reach 0.5, showing that the environmental factor between trials was quite significant. The strongest correlation was seen in flesh color followed by total storage root (0.31). The lowest correlation was between the virus resistance in seasons A and B and this is because planting material used in season B was already infested by SPVD.

Correlation tests were also conducted between traits. Storage root was positively correlated to all other traits but only significantly with SPVD resistance and vine weight at $P \leq 0.05$ and $P \leq 0.001$, respectively. These results can be explained by two facts: the slight positive correlation found between storage root yield and SPVD resistance is explained by the fact that estimation of virus symptoms was collected from vines rather than roots and genotypes with more vigorous vines tend to produce more storage roots. Part of these results is in agreement with the conclusion of Badu (2018) who found a positive and significant correlation between storage root yield and

Table 13. Spearman rank correlation tests between same traits across the two seasons.

Correlation	TSRW-SB	Flesh color-SB	SPVDR-SB	Vine weight-SB
TSRW-SA	R=0.31***			
Flesh color-SA		R=0.41***		
SPVDR-SA			R=0.20***	
Vine weight-SA				R=0.26***

***: Signifiant P≤ 0.0001, R: Correlation coefficient, TSRW: total storage root weight, SCA: specific combining ability, GCA: general combining ability, SPVDR: sweet potato virus disease resistance, SA: season A, SB: season B.

Table 14. Pearson correlation tests of the mean performances of progenies for combined seasons.

Correlation	TSRW	Flesh color	SPVDR	Vine weight
TSRW		0.0017^{ns}	0.06*	0.16***
Flesh color			0.093***	-0.079**
SPVDR				-0.04*
Vine weight				

*,**,***, ns: Significant at P ≤ 0.05, P ≤ 0.01, P ≤ 0.001, non-significant, respectively. SPVDR: Swee tpotato virus disease resistance, TSRW: total storage root weight.

vine weight. This indicates the feasibility of improving sweet potato for better storage root yield as well as SPVD resistance. The same is also true for storage root and flesh color and vine weight. Flesh color was positively correlated with SPVD resistance at $P \leq 0.001$ and negatively correlated with vine weight at $P \leq 0.01$. And finally, there was a negative and significant correlation between SPVD resistance and vine weight at $P \leq 0.05$, probably because high virus infestations impeded establishment of vines. These findings will be insightful to sweet potato breeders as they allow them to predict in which way a given trait is going to vary if another improves or decreases.

Conclusion

The different performances between the two seasons indicated that the environmental conditions as well the quality of the planting material between seasons had a true influence on the genotypes. Analyses of variance showed that some crosses performed significantly better than others. The GCA to SCA variance ratios indicated that additive gene action was more predominant than non-additive gene action in controlling all the traits observed except for vine weight. Magabali combined well with NK259L giving the highest root yielding progenies in season A while during season B the best cross was between Resisto and Naspot 7. Thus, these parents can be incorporated in breeding programs for improving storage root yield. Naspot 5 combined with Naspot 7 to give the best SCA for flesh color in both seasons. Therefore, progenies from this cross can be promoted to have varieties with high beta-carotene content. Combining SPK004 with New Kawogo or Naspot 5 will be a good strategy for improving resistance to SPVD. The combinations of Ejumula or Naspot 10 O with Huarmeyano are the best crosses for improving vine weight. Clones that had high heterosis for every trait in one season were not necessarily the same in the other season. This meant that they were unstable across environments and could be evaluated for use in further trials with more controlled conditions. One major finding is that it is possible to breed sweet potato varieties for having higher beta-carotene content as well as being resistant to SPVD. This result is more important when knowing that most of the current orange-fleshed sweet potato cultivars we have are susceptible to SPVD.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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