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 \(8B \times 8A\) 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 (NaCRII) 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\(\times\)NK259L and Resisto\(\times\)Naspot 7 were the best crosses for improving total storage root while Naspot 5\(\times\)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-Saharan 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
groups separated by 18 SSR markers (David et al., 2018). 64 crosses (BxA: 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 m²), 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, \( \mu \) is the oval mean, \( g \) is the effect of the genotype, \( r \) is the effect of the ith row, \( c \) is the effect of the kth column, and \( e \) 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:

\[ \text{Mid-parent Heterosis} = \left( \frac{(F1 - MP)}{MP} \right) \times 100 \]

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):

\[ \text{GCA/SCA} = \left( \frac{2MSGCA}{(2MSGCA + MSSCA)} \right) \]

RESULTS AND DISCUSSION

Descriptive statistics on the overall population

Total storage root weight was better for the season A

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.
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        |
| 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).
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 Nasпот 11 having the highest yield followed by Nasпот 10 O (0.85 kg/plot). Ejunula had the highest rank for flesh color with and Nasпот 11 the lowest. Nasпот 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.

| 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    | 16.42   |
| MDP1253  | B7×A1    | 33.48   | 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   | MDP329   | 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   | MDP322a  | B1×A8    | 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.

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

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

| 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     | 241.45   | 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 | MDP289   | 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 on the mean performances of the families on SPVD resistance in both seasons.

| 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),...
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

| 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  | 68.44   |
| MDP1584  | B8×A8  | 65.53   | MDP421   | B2×A5  | 68.44   |
| 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.
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 B).

### 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       |
| Resist         | 0.04  | 1.89        | 0.06  | -1.1        | 240       |
| Magabali       | 0.01  | -0.56       | 0     | 0.24        | 244       |
| Huarmeyano     | -0.01 | -0.07       | 0     | 0.04        | 242       |
| Mugande        | -0.04 | -0.13       | -0.02 | 0.13        | 226       |
| Wag abolige    | -0.06 | -0.59       | 0.02  | -0.14       | 220       |
| NASPOT 5       | -0.08 | 0.51        | -0.04 | -0.02       | 240       |

### Male parent

|                | TSRW  | Flesh color | SPVDR | Vine weight | Observation |
|----------------|-------|-------------|-------|-------------|-------------|
| 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 | SPVDR | Vine weight |          |
| NASPOT 11      | 0.03  | -0.67       | -0.11 | 0.19        | 241       |
| Resist         | 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       |
| Wag abolige    | 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

|                | TSRW  | Flesh color | SPVDR | Vine weight | Observation |
|----------------|-------|-------------|-------|-------------|-------------|
| 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.
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 (Tumwegamaire et al., 2014a, b) and 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≤ 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, Resistó, 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, Resistó 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, Resistó was the best female parent in season A and B. In season B MDP317 clone, belonging to B1×A8 (Resistó×NK259L) had the highest MPH. This could be explained by the fact that dominant alleles brought by Resistó 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). Resistó 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...
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 season 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 because planting material used in season B was already infested by SPVD.

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: sweet potato virus disease resistance.

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

| Parameter | TSRW | TSRW | Flesh color | Flesh color | SPVDR | SPVDR | Vine weight | Vine weight |
|-----------|------|------|-------------|-------------|-------|-------|-------------|-------------|
|           | SA   | SB   | SA          | SB          | SA    | SB    | SA          | 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.

(Huarumeyano×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.
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 Resistio 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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