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Effects of *Sweet Potato Feathery Mottle Virus* and *Sweet Potato Chlorotic Stunt Virus* on the Yield of SweetPotato in Uganda

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Abstract

Sweet potato feathery mottle virus (SPFMV) and *Sweet potato chlorotic stunt virus* (SPCSV) are the most common viruses infecting sweetpotato in Uganda. Field plots planted with graft inoculated plants of virus-free cultivars Beauregard, Dimbuka, Ejumula, Kabode and NASPOT 1 were used to assess the effect of SPFMV and SPCSV on yield and quality of sweetpotatoes in two agro-ecologies. SPFMV spreads rapidly to control plots at Makerere University Agricultural Research Institute Kabanyolo (MUARIK), and these plots had similar yields to those singly infected with SPFMV but at the National Semi Arid Resource Research Institute (NaSARRI) where SPFMV spreads slowly, plots infected with SPFMV yielded 40% less than the control. Recovery from SPFMV appeared to be more frequent at NaSARRI than at MUARIK. Infection by SPCSV alone resulted in yield losses of 14–52%, while mixed infections of SPFMV+SPCSV resulted in yield losses in both locations of 60–95% depending on the cultivar. SPCSV and mixed infections of SPFMV+SPCSV also reduced the number of roots formed as well as the diameter of the roots, resulting in a greater length to diameter ratio compared to the healthy control. This study, therefore, confirms that both SPFMV and SPCSV, both singly and when mixed, can reduce yield, the extent depending on the cultivar. To mitigate the effect of these viruses, farmers should use clean planting materials of resistant varieties.

Introduction

Sweetpotato is a vegetatively propagated crop, and systemic pathogens like viruses can persist and spread over successive crop cycles (Bryan et al. 2003). Over 30 viruses belonging to potyvirus, crinivirus, carlavirus, cucumovirus, ipomovirus, badnavirus and begomovirus have been reported to infect sweetpotatoes worldwide (Mukasa et al. 2006; Untiveros et al. 2007; Valverde et al. 2007; Clark et al. 2012). Of these, only six have been reported in Uganda, namely *Sweet potato feathery mottle virus* (SPFMV), *Sweet potato chlorotic stunt virus* (SPCSV), *Sweet potato chlorotic flecks virus* (SPCFV), *Sweet potato collusive virus* (SPCV), *Sweet potato mild mottle virus* (SPMMV) and *Sweet potato leaf curl Uganda virus* (SPLCUV) (Gibson et al. 1998; Mukasa et al. 2003; Aritua et al. 2007; Wasswa et al. 2011). SPFMV and SPCSV are the most prevalent and when they co-infect, result in severe symptoms described as sweetpotato virus disease (SPVD) (Gibson et al. 1998; Karyeija et al. 2000; Mukasa et al. 2006) causing up to 90% yield losses (Mukiibi 1977; Karyeija et al. 1998; Aritua et al. 2000).

Due to the severe yield losses caused by SPVD, most research in Africa including Uganda has concentrated on this, neglecting the occurrence as single infection with SPFMV and SPCSV. Plants affected by SPVD are easily recognizable by farmers due to the severe symptoms and may be controlled by combination of removal and not selecting them as planting material

for the next crop (Aritua et al. 1999). On the other hand, the impact of individual viruses which are usually symptomless and are therefore difficult for farmers to control has not been well studied. In addition, no field study has so far been carried out in Uganda to determine the effect of single virus infections on yield of sweetpotatoes. Studies in other countries on the effect of SPFMV on yield of sweetpotato cultivars are contradictory. Some studies have reported no effects on yield of storage roots and vines in comparison with healthy plants (Milgram et al. 1996; Clark and Hoy 2006), and other studies have reported SPFMV-infected plants producing better yield than the healthy control (Gutierrez et al. 2003), while others have reported yield reduction of up to 46% (Gibson et al. 1997; Mukasa 2004; Njeru et al. 2004; Domola et al. 2008). Due to this contradictory evidence, there is a need to further investigate the effect of SPFMV on Ugandan sweetpotato cultivars to design an effective management system in Uganda.

Also, single infection of SPCSV may produce clear symptoms in some cultivars, but farmers can confuse its symptoms with purpling of mature leaves due to nutrient deficiencies in the soil or plant maturity (Gibson et al. 1997; Mukasa et al. 2003). As a result, cuttings from such plants are used for subsequent propagation. Data on effects of single infection of SPCSV under field conditions in Uganda are also limited. However, SPCSV alone has been reported to cause a 30% yield reduction in cv Costanero, in Peru (Untiveros et al. 2007). In Uganda, a yield reduction of 50% in cv Tanzania under screenhouse conditions was reported although the yield performances of both healthy plants and infected ones were poor (Gibson et al. 1998; Mukasa et al. 2006). Virus expression and its effect in plants is influenced by the environment, and hence, there is a need to determine the effect of virus under field conditions in contrasting agro-ecologies.

Continued use of symptomless but infected cuttings by farmers in Uganda could also be a reason why the potential average yield has not been achieved. This study therefore aimed to determine the effects of single infection of SPFMV or SPCSV and their combination on the yield of four sweetpotato cultivars grown in Uganda under field conditions of two agro-ecologies.

Materials and Methods

Virus testing

Three leaf samples (leaf disc of ~1 cm diameter) per plant were picked from the top, middle and bottom part of the plants and ground in a polyvinyl bag using appropriate enzyme-linked immunosorbent assay (ELISA) extraction buffer (1 ml buffer per leaf disc). The leaf samples were tested either using NCM ELISA or DAS and TAS ELISA. Nitrocellulose membrane ELISA was carried out following the protocol obtained from CIP Lima, Peru to detect the presence of any of the ten viruses, that is SPFMV, SPMMV, *Sweet potato latent virus* (SPLV), SPCFV, *Sweet potato mild speckling virus* (SPMSV), C-6 virus, SPCSV, SPCV, *Sweet potato virus G* (SPVG) and *Cucumber mosaic virus* (CMV) for which antibodies were available. The presence of virus was judged on the visual intensity of the colour change on the membrane. Additional tests using DAS and TAS ELISA were specifically carried out to detect and estimate the virus titre for SPFMV or SPCSV, respectively, using protocol by Clark and Adams (1977). The DAS-ELISA kit (containing coating antibody immunoglobulin G (IgG) and detecting antibody IgG-AP) against SPFMV and TAS ELISA kit containing (primary antibody, rabbit IgG, secondary mouse monoclonal antibody MAb and detection antibody, rabbit anti-mouse IgG-AP) against SPCSV and respective positive controls were from Leibniz-Institut DSMZ-Deutsche sammlung von Mikroorganismen und Zellkuturen GmbH, Germany. The p-nitrophenyl phosphate substrate and microplates used were from Sigma Chemical Co. The absorbance was measured at 405 nm after one and half hours using a Bio-Rad microplate reader (model 680).

Source of virus inoculum

Isolates of SPFMV and SPCSV were sourced from farmers' fields at Namulonge, Wakiso district. Cuttings were collected and graft inoculated onto the nearly universal indicator plant, *Ipomoea setosa,* and left to grow to allow symptoms to express. The symptomatic plants were tested using nitro-cellulose membrane (NCM) ELISA for ten viruses for which the antibodies were available and those reacting positively for SPFMV and for SPCSV alone were selected and retested using DAS or TAS ELISA, respectively. SPCSV was maintained in cv Kampala white, SPFMV was maintained in cv Resisto, and mixed SPFMV + SPCSV was maintained in cultivar Ejumula in a screenhouse at MUARIK. The screenhouse was sprayed every 2 weeks with imidacloprid to kill aphids and whiteflies. The virus presence in these cultivars was continually checked by grafting to *I. setosa* plant and by serology using DAS or TAS ELISA.

Sources of healthy planting material

Symptomless sweetpotato cuttings of cvs. Beauregard, Dimbuka, NASPOT 1 and Ejumula were collected from sweetpotato fields at the National Crops Resource Research Institute (NaCRRI), Namulonge in Wakiso district, while cv. Kabode was obtained from farmers' fields in Soroti district. They were grafted on plants of *I. setosa*. The grafted plants were monitored for the absence of virus symptoms for 5 weeks. Their virus-free status was further confirmed using NCM ELISA. Scions that tested negative for viruses here referred to as healthy scion were multiplied in plastic pots containing sterilized mixture of soil, sand and animal manure in equal proportions and left to grow in an insect proof screenhouse at Makerere University Agricultural Research Institute Kabanyolo (MUARIK) in Wakiso district. The numbers of cuttings for field planting were increased through repeated two node cuttings. To ensure sustained availability of virus-free planting material, some of the materials were multiplied *in vitro* at MUARIK.

Generation and multiplication of planting materials infected with viruses

Virus-indexed sweetpotato cuttings of cvs Dimbuka, Ejumula, Kabode, NASPOT 1 and Beauregard of 30 cm length were potted and left to grow for 2 weeks in a screenhouse at MUARIK. Each cultivar was planted in 15 pots making a total of 75. The plants were divided into three groups, each having five cuttings per cultivar. One group was graft inoculated with SPFMV, another was graft inoculated with SPCSV, and third was graft inoculated with SPFMV+ SPCSV. These were left to grow while monitoring for symptoms. After 1 month, infection was confirmed using DAS (for SPFMV) and TAS ELISA (for SPCSV) and the cuttings were multiplied through making repeated two node cuttings to obtain enough planting material for the field experiment. The multiplied planting material was further tested by grafting on *I. setosa* to confirm their infection status before planting in the field.

Field experiment

Four field trials were conducted at MUARIK and at the National Semi Arid Resource Research Institute (NaSARRI) located in Serere district in eastern Uganda. In the first trial, the yield of SPFMV-infected sweetpotato was compared to that of virus-indexed material at both MUARIK and NaSARRI. In this trial, a split plot randomized block design was used in which the SPFMV-infected plants and healthy controls acted as the main plot (to minimize virus spread), while the cultivars acted as the subplots. Five cultivars, namely Kabode, NASPOT 1, Ejumula, Dimbuka and Beauregard, were evaluated. The experiment was replicated three times with each experimental block laid in an area of 5 by 10 m. Each treatment was planted in five mounds per plot, and each mound was made at spacing of 1 by 1 m and planted with three vine cuttings. In the second trial, a similar design was used except that an additional treatment of SPFMV-infected cuttings from the 1st trial was included in the 2nd trial in order to evaluate the cumulative exposure to virus infection on yield. Also in the 2nd trial, cv Beauregard was dropped and the remaining four cultivars were used in the study using the same design as above.

In the 3rd and 4th field trials, SPFMV, SPCSV and the combination of SPFMV+ SPCSV were evaluated. A randomized split plot design was used where the main blocks consisted of pathogen inoculum and the sub-blocks were the cultivars used. This was replicated three times. Four treatments all obtained from screenhouse were used, that is healthy controls, SPFMV, SPCSV and SPCSV+ SPFMV and the same cultivars except Beauregard. Systemic insecticide (imidacloprid locally known as Confidor) was applied monthly for field trials at MUARIK to control aphids and white flies. Weeding was performed 2–3 times depending on the weed intensity using a hand hoe.

Disease symptoms and yield measurement

Sweetpotato plants were monitored for virus symptom development, and severity data were collected at monthly interval beginning 1 month after planting for period of 4 months. A severity score of 1–5 was used, where 1 = plants showing no symptoms; 2 = virus symptoms just starting to appear and this can be as mild chlorotic spots on the older leaves or mild vein clearing or mild purpling at the leaf margin of mature leaf; 3 = the symptoms above enlarge and become more visible; 4 = infected plants showing severe disease symptoms including leaf purpling, leaf chlorosis and leaf shape starts to get distorted; and 5 = infected plants showing very severe virus disease symptoms including total distortion in leaf shape, stunted growth, mosaic, leaf chlorosis and sometimes complete death of infected plant (Hahn et al. 1981). Harvesting was performed 5 months after planting. At

harvest, total yield/mound, marketable yield, total root number, marketable root number, root diameter, root length and vine weights were determined. The root length and diameter were measured using a marked thread. For each sweetpotato storage root, the diameter was measured at three positions, at the neck end, the middle and the tail end and the average diameter recorded.

Evaluation of sweetpotato virus disease recovery and virus infection

Detection of viruses that could have infected sweetpotato during the growing season in the 1st and 2nd field trials was carried out using NCM ELISA. Samples were collected from symptomatic leaves or a leaf from the basal, middle and upper parts of symptomless plants. At least 15 samples (five samples per plot) per cultivar per treatment of each trial were collected and tested for 10 viruses, that is SPFMV, SPMMV, SPLV, SPCFV, SPMSV, C-6, SPCSV, SPCV, SPVG and CMV which antibodies were available. Positive control samples for each virus were provided in the NCM ELISA Kit by CIP Lima, Peru. The plants were serologically evaluated at the end of each trial before harvesting. The presence of virus was confirmed visually based on the intensity of the colour change on the membrane. Also prior to harvesting, ten symptomless cuttings per cultivar from SPFMV-infected plants were graft inoculated on *I. setosa* and monitored for any virus symptom for a period of 5 weeks. Any infected *I. setosa* plants were further tested with NCM ELISA to confirm the viruses present.

SPFMV and SPCSV accumulation in different sweetpotato cultivars in two agro-ecologies

The virus quantification was carried out on the 3rd and 4th trial to determine the virus load of SPFMV and SPCSV in the field exposed materials in two agro-ecologies. DAS and TAS ELISA were used as described previously (Gibson et al. 1998) to estimate the virus titre.

Statistical analysis

Statistical analyses were carried out using Genstat 13th Edition. Data on virus severity, storage root yield, storage root quality and vine weight were subjected to analysis of variance, and the means separated using Fisher's protected least significant difference at 5% probability level.

Results

Symptom expression due to single or mixed infection by SPFMV and SPCSV under field conditions

Analysis of variance for disease severity indicated a significant ($P \leq 0.05$) cultivar, virus and interaction between cultivar by virus effect on disease severity at both MUARIK and NaSARRI. Severity was observed to increase with time of field exposure in all the cultivars tested in both locations (Fig. 1). Dual infection of SPFMV and SPCSV caused the most severe symptoms in all the cultivars in both locations including vein chlorosis, purple spots on the leaf, mosaic, distorted leaf shape and stunted plant growth (Fig. 2 h, i, j and k). This is followed by single infection of SPCSV (Fig. 1) in which the common symptoms were chlorotic spots, purple/reddish spots on mature leaves and leaf chlorosis (Fig. 2d–g). Disease severity due to SPFMV alone was generally low in all cultivars in both locations. The symptom expression due to SPFMV was characterized by mild chlorotic spots and mild vein clearing in some cultivars (Fig. 2a–c). Virus-indexed healthy control materials at MUARIK displayed greater disease severity scores than SPFMV-infected plants (Fig. 1 a, c, e and g). At NaSARRI, all the control plants had the least disease severity compared to virus-infected ones for all the tested cultivars (Fig. 1 b, d, f and h). Among the cultivars tested, irrespective of the virus status, Ejumula was the most severely affected, followed by Dimbuka and least in Kabode and NASPOT 1. For cultivar NASPOT 1 and Dimbuka, disease severity was high at 3 months after which, there was decline in severity in plants singly infected by SPFMV or SPCSV in both locations.

Reversion from virus infection and detection of other viruses

Among the ten viruses tested using NCM ELISA, only SPCSV and SPFMV were detected in both locations. The remaining eight viruses were negative in all the samples tested. SPCSV followed by SPFMV was more prevalent at MUARIK while in NaSARRI, the incidences of both viruses were low. At NaSARRI, most of the cultivars showed reversion from SPFMV infection, initially infected plants mostly testing negative by ELISA and graft inoculation to *I. setosa* at the end of the trial (Table 1). The reversion from SPFMV was also evident at MUARIK where some of the cultivars initially infected with SPFMV did not develop SPVD symptoms when infected with SPCSV under natural conditions. Instead, symptoms of SPCSV alone were

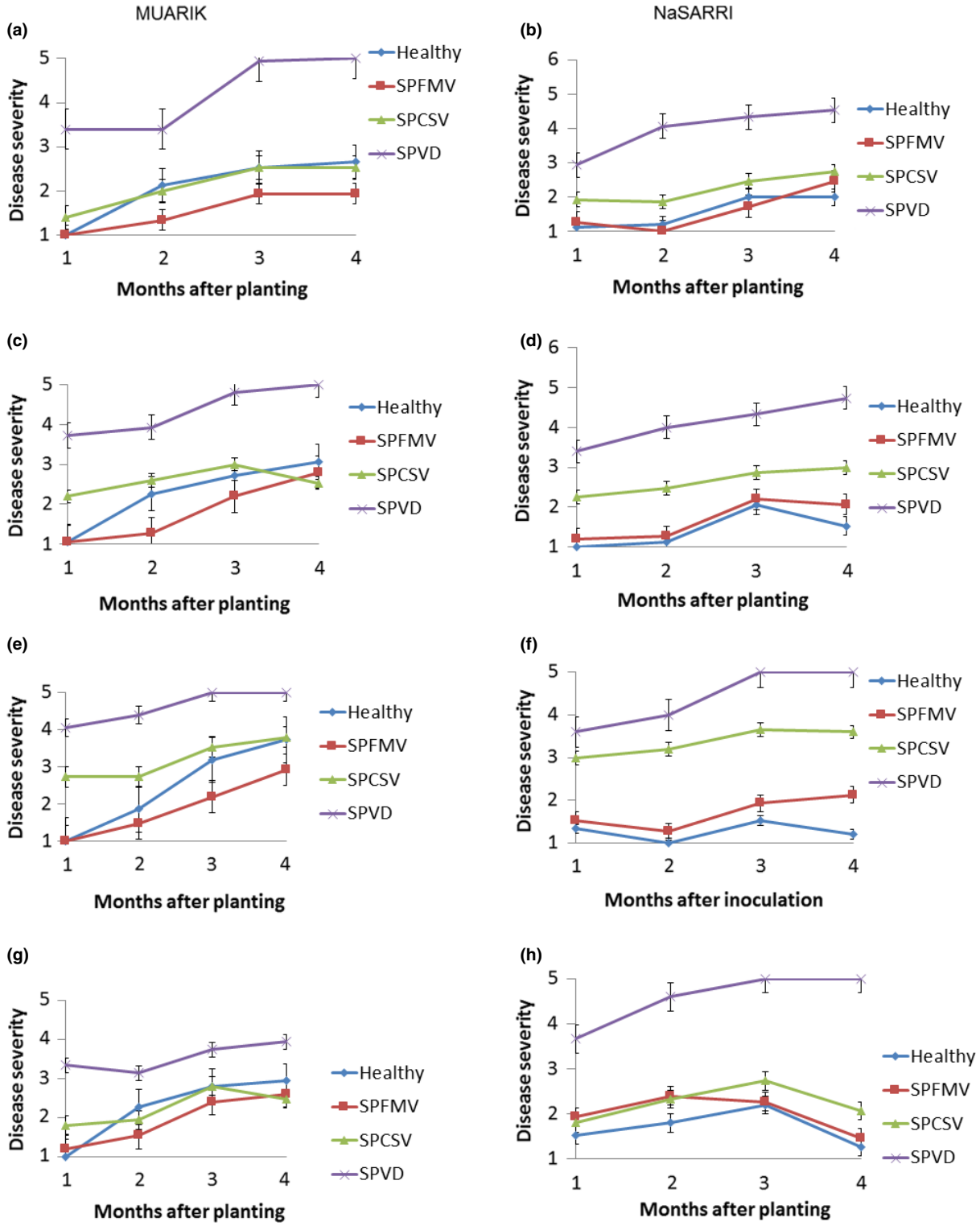

Fig. 1 Disease severity curve showing response of sweetpotato cultivars to virus infection in two agro-ecologies. (a) Disease severity curve for Kabode at MUARIK; (b) disease severity curve for Kabode at NaSARRI; (c) disease severity curve for Naspot 1 at MUARIK; (d) disease severity curve for NASPOT 1 at NaSARRI; (e) disease severity curve for Ejumula at MUARIK; (f) disease severity curve for Ejumula at NaSARRI; (g) disease severity curve for Dimbuka at MUARIK; and (h) disease severity curve for Dimbuka at NaSARRI. The disease severities plotted are the means of disease severity in the 3rd and 4th field trial.

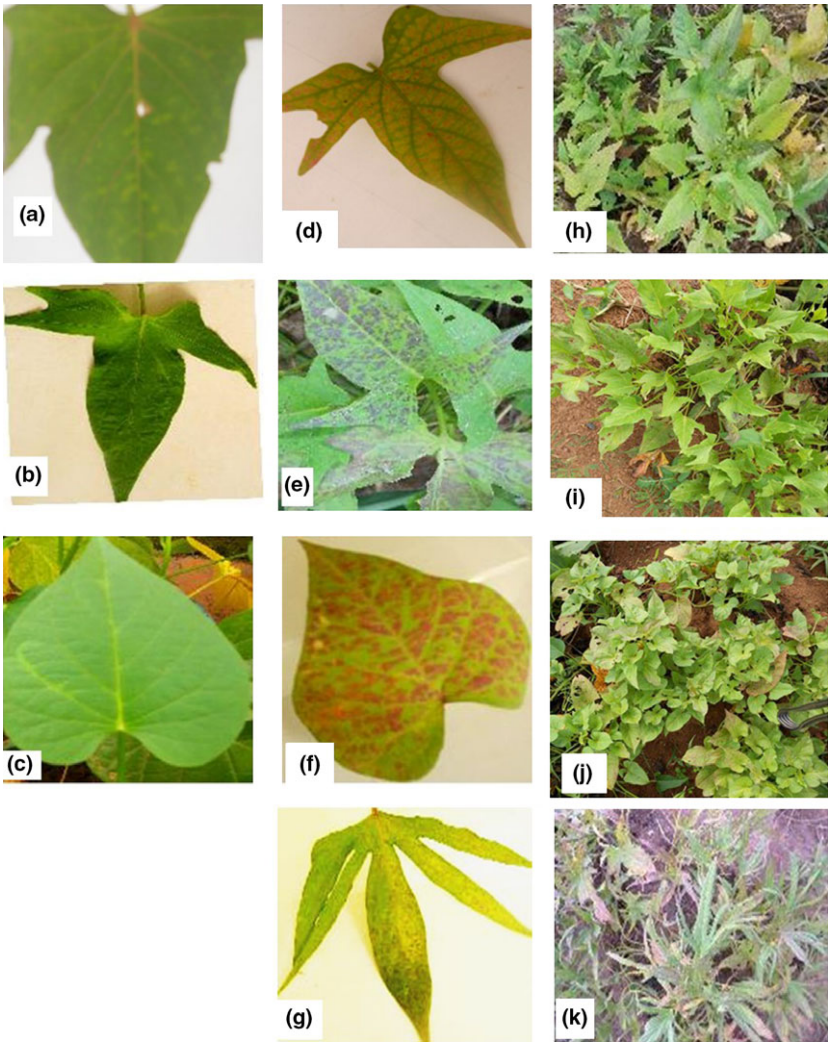

Fig. 2 *Symptoms expressed by sweetpotato cultivars when infected with SPFMV, SPCSV and combination of SPFMV+SPCSV. (a) Mild chlorotic spots on NASPOT1 due to SPFMV, (b) mild vein clearing on Ejumula due to SPFMV, (c) mild vein clearing on Dimbuka due to SPFMV, (d) purple spot on NASPOT1 due to SPCSV, (e) purple spot on Ejumula due to SPCSV, (f) purple spot on Dimbuka due to SPCSV, (g) chlorotic spot on cultivar Kabode due to SPCSV, (h) SPVD symptom on NASPOT1, (i) SPVD symptom on Ejumula, (j) SPVD symptom on Dimbuka and (k) SPVD symptom on Kabode, respectively.*

expressed, and plants tested negative by ELISA for SPFMV and positive for SPCSV (Table 1).

Virus accumulation in different sweetpotato cultivars in two agro-ecologies

Results from DAS and TAS ELISA indicated greater virus accumulation in plants grown at MUARIK than that at NaSARRI irrespective of the type of virus (Fig. 3). Higher absorbance values were observed in plants with mixed infections than those with single infection in both locations and in all the cultivars tested (Fig. 3). Also plants singly infected by SPCSV accumulated more viral antigen and never showed recovery as most of them tested positive unlike those plants infected by SPFMV alone in which most of them tested negative. The results also showed high spread of SPCSV within the fields as most of the samples from healthy control and those previously infected by SPFMV tested positive for SPCSV. The spread was greater at MUARIK than NaSARRI with samples from MUARIK having high absorbance values except in the case of SPVD (Fig. 3).

Effect of SPFMV on the yield of sweetpotato cultivars in two agro-ecologies

The yield and number of storage roots produced by sweetpotato varied depending on the cultivars, virus status, season of growth and location. Between locations, more yield and higher storage root number were observed in MUARIK than NaSARRI. Because of high variation observed between location and seasons, each yield data set for each season and location was analysed individually and the results presented as below.

Table 1 Reversion from SPFMV infection and detection of new virus infection under field condition at MUARIK and NaSARRI

Cultivar	Virus Status	Number of plant samples	Positive samples at MUARIK (%)			Positive samples at NaSARRI (%)		
			SPFMV	SPCSV	SPVD	SPFMV	SPCSV	SPVD
NASPOT 1	Healthy control	30	46.7	93.3	46.7	0.0	20.0	0.0
	SPFMV[1]	30	33.3	60.0	23.3	20.0	6.6	0.0
	SPFMV[2]	15	60.0	80.0	33.3	0.0	26.7	0.0
Dimbuka	Healthy control	30	13.3	93.3	13.3	0.0	3.3	0.0
	SPFMV[1]	30	20.0	40.0	20.0	26.7	0.0	0.0
	SPFMV[2]	15	66.7	86.7	33.3	6.0	6.7	0.0
Ejumula	Healthy control	30	86.7	100.0	86.7	0.0	13.3	0.0
	SPFMV[1]	30	100.0	80.0	80.0	53.3	20.0	6.7
	SPFMV[2]	15	100.0	100.0	100.0	13.3	26.7	3.3
Kabode	Healthy control	30	13.3	100.0	0.0	0.0	16.7	0.0
	SPFMV[1]	30	26.7	86.7	26.7	6.0	10.0	0.0
	SPFMV[2]	15	26.7	100.0	26.7	0.0	0.0	0.0
Beauregard	Healthy control	15	100.0	100.0	100.0	100.0	100.0	100.0
	SPFMV[1]	15	100.0	100.0	100.0	100.0	100.0	100.0

[1]SPFMV-infected cutting obtained from screenhouse and grown in the field for the first time.
[2]SPFMV-infected cuttings obtained from 1st trial and grown in the field for the 2nd time. SPVD = is combination of SPFMV + SPCSV.

For the 1st field trial at MUARIK, there was no significant yield difference between SPFMV-infected plants and healthy control plants of all the cultivars tested except Dimbuka. However, cvs, Kabode and NASPOT 1 infected with SPFMV had slightly more yield than the healthy control, while the healthy controls of Ejumula and Beauregard had slightly better yields than those of SPFMV-infected plants (Table 2). The total and marketable number of storage root for healthy and SPFMV-infected plants within each cultivar was not different. Among the cultivars tested, Dimbuka had the greatest number of storage roots, followed by Ejumula, NASPOT 1, Kabode and least in Beauregard. For NaSARRI trial, significantly higher total and marketable yield effect was observed between healthy control plants and SPFMV-infected plants of cultivars NASPOT 1, Dimbuka and Beauregard. For cultivar Kabode and Ejumula, there was no difference on the yield between healthy control and SPFMV-infected plants (Table 2). The yield loss due to SPFMV in this location ranged from 14% to 67% depending on the cultivar. The number of storage roots was greatest in Dimbuka followed by NASPOT 1, then Kabode, Ejumula and least in Beauregard. The storage root numbers within cultivar were not different (Table 2).

Cumulative effects of SPFMV on the yield of sweetpotato in two agro-ecologies

The cumulative effect of SPFMV was conducted by planting a 2nd field trial using SPFMV-infected cuttings from the first field trial along with the newly infected SPFMV materials obtained from a screenhouse and virus-indexed material as healthy control at MUARIK and NaSARRI, respectively. Significant differences were detected among cultivars, vine source and interaction between cultivars and vine source in both locations for total yield, marketable yield, total number of storage root and marketable number of storage roots (Table 3). In both locations, the yield of healthy control was greater than the SPFMV-infected ones (Table 3). For the MUARIK trial, the newly SPFMV-infected materials from the screenhouse had more total and marketable yield and storage root number than the SPFMV-infected materials obtained from 1st field trial. The total yield loss due to SPFMV-infected material from screenhouse ranged between 0% and 23.8% while the total yield loss due to SPFMV-infected materials obtained from the 1st field trial ranged between 14% and 26.1% (Table 3). The exception was in cv, Kabode, in which the field exposed material had slightly more yield than screenhouse-infected materials although statistically not different from the healthy control. For the NaSARRI trial, SPFMV-infected materials from the 1st field trial yielded more than the screenhouse-infected materials planted in the field for the first time in all the cultivars except Dimbuka. The total yield loss of screenhouse-infected materials ranged between 33% and 42% while that of field exposed material ranged between 26% and 48% (Table 3). The total root numbers within

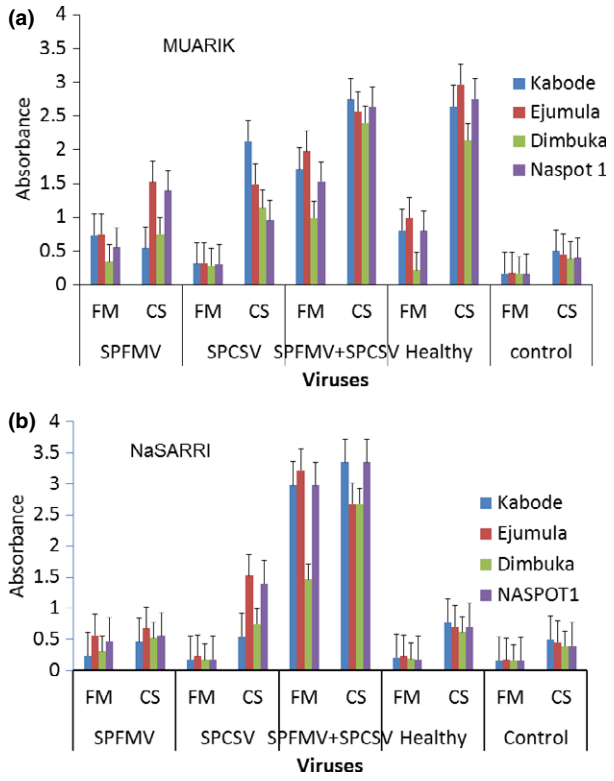

Fig. 3 *Absorbance values from detection of SPFMV antigens by DAS-ELISA and SPCSV antigen by TAS ELISA in leaves of four sweetpotato cultivars 5 months after planting in two agro-ecologies. (a) Absorbance value for samples from MUARIK and (b) absorbance value for samples from NaSARRI. All samples were tested for the two viruses. Each data point corresponds to the A_{405} values from 30 different plant samples per cultivar in two experiments. Bars represent standard error of means.*

cultivars were not different, but the marketable root numbers were different for the NaSARRI trial. Dimbuka had more storage roots, followed by NASPOT 1, Ejumula and least in Kabode (Table 3).

Effects of single or mixed infection by SPFMV and SPCSV under field conditions

In general, the total yield, marketable yield, total storage root number and marketable root number were significantly influenced by seasons within location, cultivars tested, the viruses used and their interactions. Storage root yield was greater in field trial 4 than in field trial 3 in both locations. Combination of SPFMV and SPCSV severely reduced the yield, followed by the single infection of SPCSV and least in single infection by SPFMV and healthy controls.

The total and marketable yields of sweetpotato cultivars singly infected by SPFMV were less than the healthy controls in field trial 3 and 4 in both locations except for NASPOT 1 and Ejumula in trial 4 at MUARIK although these differences were not statistically significant. The total yield loss due to SPFMV ranged between 7% and 38% for all the cultivars in both locations except for NASPOT 1 and Ejumula during the 4th field trial at MUARIK where there was a yield gain of 111 and 114%, respectively. SPFMV alone did not affect the total number of storage root but reduced the marketable root number in all the cultivars in both seasons and locations except for cultivars NASPOT 1 and Ejumula in the 4th field trial where the total number of storage roots was less than the healthy control (Table 4).

Single infection by SPCSV significantly reduced the total and marketable yield and total and marketable storage number of roots as compared to healthy plant in both locations and in all the field trials (Table 4). The yield loss due to SPCSV ranged between 14% and 52% for all the cultivars tested in both locations for 3rd and 4th field trial (Table 4). The marketable yield, total storage root number and marketable storage root number were less in SPCSV-infected plants compared to the healthy control. Cultivars Ejumula and Dimbuka had the greatest total yield loss due to SPCSV during 3rd field trials in both locations, while in 4th field trial only Dimbuka had greatest yield loss at MUARIK and Ejumula at NaSARRI. Co-infection of SPFMV and SPCSV had an even larger effect on total yield, marketable yield and total and marketable storage root number. The yield loss ranged between 60% and 95% with Ejumula and Dimbuka having the greatest total yield loss in both locations in all seasons.

Effects of SPFMV and SPCSV on sweetpotato root length and diameter

Differences were detected ($P \leq 0.05$) on the length and diameter of storage roots due to cultivar and virus effect and their interaction. Both single infection and co-infection of SPFMV and SPCSV reduced the diameter of storage roots. Storage roots of plants infected by both SPFMV and SPCSV had the smallest diameter followed by that infected by SPCSV alone and then SPFMV. Healthy plants overall had storage roots with the greatest diameter and therefore less length diameter ratio (Table 4).

Discussion

Symptom expression differed with the infecting viruses and cultivars. SPFMV-infected plants produced mild symptoms in all the cultivars which later

Table 2 Mean yield and storage root number of five sweetpotato varieties grown from virus tested plants compared with plants graft inoculated with SPFMV under two agro-ecologies during the 1st field trial

		MUARIK				NaSARRI			
		Yield (Kg/m^2)		Root numbers (per mounds)		Yield (Kg/m^2)		Root numbers (per mounds)	
Cultivar	Virus status	Total	Marketable	Total	Marketable	Total	Marketable	Total	Marketable
Kabode	Healthy	2.0^a	1.8^a	6.4^a	5.2^a	1.1^a	0.8^a	3.7^a	2.2^a
	SPFMV	2.6^a	2.3^a	7.5^a	5.7^a	1.3^a	1.0^a	4.3^a	3.1^a
NASPOT 1	Healthy	3.0^a	2.6^b	9.9^a	6.1^a	2.3^a	2.1^a	5.3^a	4.9^a
	SPFMV	3.8^a	3.7^a	8.6^a	6.5^a	1.4^b	1.1^b	3.7^a	2.8^b
Ejumula	Healthy	2.1^a	1.4^a	12.4^a	4.9^a	0.7^a	0.2^a	3.1^a	0.4^a
	SPFMV	1.9^a	1.3^a	13.3^a	4.4^a	0.6^a	0.1^a	2.8^a	0.5^a
Dimbuka	Healthy	2.7^b	2.1^b	15.1^a	6.0^b	1.4^a	1.1^a	7.9^a	4.0^a
	SPFV	4.4^a	4.0^a	15.5^a	10.2^a	0.9^a	0.6^b	3.3^b	1.7^b
Beauregard	Healthy	1.2^a	0.7^a	12.3^a	3.1^a	0.6^a	0.0^a	5.3^a	0.0^a
	SPFV	0.7^a	0.2^a	5.8^b	1.1^a	0.2^b	0.0^a	1.5^b	0.0^a
SE		0.36	0.37	1.42	0.86	0.15	0.16	0.71	0.495
LSD (5%)		1.00	1.03	3.98	2.40	0.422	0.46	1.98	1.385

SE, standard errors of means; LSD, least significant difference at 5%.
Columns with the same superscript letters for individual cultivar is not significantly different.

Table 3 Mean yield and storage root number of four sweetpotato varieties grown from virus tested plants compared with virus tested plants graft inoculated with SPFMV and previously field exposed SPFMV-infected materials under two agro-ecologies during the 2nd field trial

		MUARIK				NaSARRI			
		Yield (Kg/m^2)		Root number (per mound)		Yield (Kg/m^2)		Root numbers (per mound)	
Cultivar	Virus status	Total	Marketable	Total	Marketable	Total	Marketable	Total	Marketable
Kabode	Healthy	2.1^{ab}	1.6^a	6.7^{ab}	3.6^a	1.5^a	1.5^a	5.6^a	4.7^a
	SPFMV[1]	1.6^b	1.2^a	5.0^b	2.7^a	1.0^b	0.9^b	6.7^a	4.2^a
	SPFMV[2]	2.7^a	2.1^a	8.1^a	4.5^a	1.1^{ab}	1.0^b	5.9^a	4.3^a
NASPOT 1	Healthy	2.8^a	1.7^a	4.9^a	3.3^a	2.4^a	2.3^a	9.7^a	7.9^a
	SPFMV[1]	2.5^a	1.8^a	7.7^a	3.2^a	1.4^b	1.2^b	8.4^b	5.8^b
	SPFMV[2]	2.4^a	2.1^a	6.1^a	4.1^a	1.7^b	1.5^b	8.1^b	5.7^b
Ejumula	Healthy	2.3^a	1.5^a	7.5^a	4.2^a	2.1^a	2.1^a	8.9^a	7.3^a
	SPFMV[1]	1.8^{ab}	1.4^a	9.7^a	3.2^a	1.3^b	1.1^b	7.7^a	4.5^b
	SPFMV[2]	1.5^b	0.8^b	7.5^a	2.4^a	1.5^b	1.3^b	8.1^a	5.7^{ab}
Dimbuka	Healthy	2.3^a	1.6^a	10.9^a	4.2^a	1.9^a	1.7^a	12.3^a	8.7^a
	SPFMV[1]	2.3^a	1.3^{ab}	11.5^a	3.3^{ab}	1.1^b	0.8^b	10.9^a	5.2^b
	SPFMV[2]	1.7^a	0.6^b	8.7^a	1.5^b	1.0^b	0.8^b	10.1^a	4.3^b
LSD (5%)		0.75	0.86	2.87	1.88	0.3594	0.3509	2.469	1.674

[1]SPFMV-infected cutting obtained from screenhouse and grown in the field for the first time.
[2]SPFMV-infected cuttings obtained from 1st trial and grown in the field for the 2nd time.
Columns with the same superscript letter for individual cultivar is not significantly different.

disappeared under field conditions. This suggests that these cultivars are resistant or tolerant to SPFMV infection. Such apparent tolerance may have been developed through unintentional selection by farmers (for land races) or breeders growing crops under strong disease pressure and high vector population. This finding supports reports that most Ugandan cultivars are resistant to SPFMV and when infected can revert to healthy status (Gibson et al. 1997; Mukasa et al. 2006; Wasswa 2012; Gibson and Kreuze 2015). This reversion was further confirmed when some of the previously infected plants

Table 4 Mean yield and storage root number of four sweetpotato varieties grown from virus tested plants compared with virus tested plants graft inoculated with SPFMV, SPCSV and combination of the two viruses under two agro-ecologies during the 3rd and 4th field trials

		MUARIK					NaSARRI				
		Yield (Kg/m^2)		Root numbers (per mound)		Storage root Length/ diameter	Yield (kg/m^2)		Root number (per mound)		Storage root Length/ diameter
Cultivars	Virus status	Total	Marketable	Total	Marketable	ratio	Total	Marketable	Total	Marketable	ratio
3rd Field trial											
Kabode	Healthy	1.4^{a}	1.2^{a}	6.5^{a}	4.1^{a}	1.1^{b}	1.5^{a}	1.4^{a}	4.7^{a}	4.5^{a}	0.9^{b}
	SPFMV	1.3^{a}	1.0^{ab}	5.0^{ab}	2.4^{b}	1.1^{b}	1.3^{ab}	1.3^{ab}	4.1^{ab}	3.9^{ab}	0.9^{b}
	SPCSV	0.9^{b}	0.8^{b}	4.2^{bc}	2.6^{b}	1.3^{ab}	1.1^{b}	1.1^{b}	3.5^{b}	3.0^{bc}	0.8^{b}
	SPVD	0.4^{c}	0.4^{c}	2.3^{c}	1.5^{b}	1.5^{a}	0.6^{c}	0.5^{c}	3.1^{b}	2.1^{c}	1.3^{a}
NASPOT 1	Healthy	1.6^{a}	1.3^{a}	6.1^{a}	3.9^{a}	0.8^{b}	1.9^{a}	1.9^{a}	6.2^{a}	6.1^{a}	0.8^{b}
	SPFMV	1.0^{b}	0.6^{b}	5.6^{ab}	2.3^{b}	0.9^{ab}	1.3^{b}	1.3^{b}	4.9^{a}	4.1^{b}	0.8^{b}
	SPCSV	1.1^{b}	0.8^{b}	5.7^{ab}	2.7^{b}	0.9^{ab}	1.4^{b}	1.3^{b}	5.1^{a}	4.3^{b}	0.9^{ab}
	SPVD	0.5^{c}	0.5^{b}	4.0^{c}	1.6^{b}	1.1^{a}	0.1^{c}	0.1^{c}	0.8^{b}	0.3^{c}	1.1^{a}
Ejumula	Healthy	1.6^{a}	1.2^{a}	7.5^{a}	3.9^{a}	1.2^{a}	1.5^{a}	1.4^{a}	5.7^{a}	4.8^{a}	0.9^{b}
	SPFMV	1.1^{b}	0.7^{b}	6.4^{a}	2.1^{b}	1.2^{a}	1.3^{ab}	1.3^{a}	5.1^{a}	4.4^{ab}	1.0^{b}
	SPCSV	0.8^{b}	0.4^{b}	6.3^{a}	2.0^{bc}	1.1^{a}	1.1^{b}	1.0^{b}	4.9^{a}	3.3^{b}	0.8^{b}
	SPVD	0.2^{c}	0.2^{c}	2.6^{b}	0.9^{c}	1.3^{a}	0.3^{c}	0.2^{c}	1.6^{b}	1.3^{c}	1.3^{a}
Dimbuka	Healthy	2.1^{a}	1.3^{a}	12.6^{a}	4.1^{a}	0.8^{b}	2.1^{a}	2.1^{a}	7.7^{a}	6.4^{a}	0.7^{b}
	SPFMV	1.3^{b}	0.9^{b}	6.5^{b}	2.8^{b}	0.9^{b}	1.9^{a}	1.8^{b}	7.0^{a}	6.1^{a}	0.7^{b}
	SPCSV	1.0^{b}	0.7^{b}	7.8^{b}	2.9^{b}	1.0^{ab}	1.5^{b}	1.5^{c}	6.5^{a}	4.7^{b}	0.7^{b}
	SPVD	0.1^{c}	0.0^{c}	2.1^{c}	0.5^{c}	1.2^{a}	0.1^{c}	0.0^{d}	1.2^{b}	0.1^{c}	1.4^{a}
SE		0.123	0.134	0.711	0.431	0.0763	0.098	0.1032	0.496	0.421	0.0763
LSD (5%)		0.342	0.374	1.981	1.202	0.2203	0.274	0.2877	1.381	1.172	0.2205
Field trial4											
Kabode	Healthy	3.1^{a}	3.1^{a}	6.4^{a}	6.3^{a}	1.0^{b}	1.6^{a}	1.5^{a}	6.0^{a}	5.3^{a}	1.3^{a}
	SPFMV	2.4^{b}	2.4^{b}	5.8^{a}	5.1^{ab}	1.1^{ab}	1.3^{a}	1.2^{a}	6.7^{a}	5.0^{a}	1.3^{a}
	SPCSV	1.9^{b}	1.8^{c}	5.3^{a}	3.7^{b}	1.1^{ab}	1.3^{a}	1.2^{a}	5.2^{ab}	4.1^{a}	1.3^{a}
	SPVD	0.7^{c}	0.6^{d}	3.7^{b}	1.9^{c}	1.2^{a}	0.7^{b}	0.6^{b}	4.5^{b}	2.5^{b}	1.4^{a}
NASPOT 1	Healthy	2.7^{a}	2.6^{a}	7.9^{a}	6.9^{a}	0.8^{c}	2.2^{a}	2.0^{a}	10.5^{a}	8.2^{a}	1.1^{c}
	SPFMV	3.0^{a}	2.9^{a}	7.3^{a}	6.5^{a}	0.9^{ab}	1.8^{b}	1.6^{b}	8.0^{c}	5.4^{b}	1.2^{b}
	SPCSV	2.0^{b}	1.9^{b}	7.1^{a}	5.7^{a}	1.0^{a}	1.1^{c}	1.0^{c}	5.7^{c}	4.7^{b}	1.2^{b}
	SPVD	0.4^{c}	0.3^{c}	3.0^{b}	1.5^{b}	1.0^{a}	0.1^{d}	0.0^{d}	1.3^{d}	0.0^{c}	1.4^{a}
Ejumula	Healthy	2.1^{ab}	2.1^{ab}	7.9^{a}	7.1^{a}	1.1^{a}	2.1^{a}	1.9^{a}	10.9^{a}	8.7^{a}	1.2^{a}
	SPFMV	2.4^{a}	2.3^{a}	9.5^{a}	8.7^{a}	1.2^{a}	1.4^{b}	1.1^{b}	8.0^{b}	4.9^{b}	1.2^{a}
	SPCSV	1.8^{b}	1.6^{b}	7.9^{a}	5.1^{b}	1.2^{a}	1.0^{c}	0.8^{b}	6.3^{b}	4.0^{b}	1.2^{a}
	SPVD	0.4^{c}	0.2^{c}	3.7^{b}	1.0^{c}	1.2^{a}	0.3^{d}	0.2^{c}	2.8^{c}	1.2^{c}	1.3^{a}
Dimbuka	Healthy	3.1^{a}	3.0^{a}	13.4^{a}	10.3^{a}	0.8^{b}	2.3^{a}	2.0^{a}	13.0^{a}	9.8^{a}	1.0^{a}
	SPFMV	2.5^{b}	2.3^{b}	11.5^{a}	8.3^{b}	0.9^{b}	1.4^{b}	1.2^{b}	11.6^{a}	7.7^{b}	1.1^{a}
	SPCSV	1.7^{c}	1.5^{c}	9.1^{b}	5.7^{c}	0.9^{b}	1.6^{b}	1.3^{b}	11.5^{a}	7.5^{b}	1.1^{a}
	SPVD	0.8^{d}	0.6^{d}	8.8^{b}	3.1^{d}	1.1^{a}	0.1^{c}	0.0^{c}	1.7^{b}	0.0^{c}	1.1^{a}
SE		0.20	0.21	0.79	0.58	0.0763	0.11	0.11	0.67	0.47	0.0742
LSD (5%)		0.580	0.584	2.220	1.623	0.2203	0.310	0.3168	1.872	1.323	0.2144

Columns with the same superscript letters for each cultivar are not significantly different, SPVD = plants co-infected by SPFMV and SPCSV.

from the field at NaSARRI tested negative for SPFMV using NCM ELISA and when grafted on *I. setosa*. Also reversion from SPFMV was evident at MUARIK where initially SPFMV-infected plants did not develop SPVD when infected naturally with SPCSV, instead they tested negative for SPFMV at the end of the trial. Beauregard which is a cultivar from America was very susceptible to SPFMV and SPCSV (Bryan et al. 2003; Clark and Hoy 2006), it was discarded for later trials and cannot be used by farmers in Uganda because it cannot be maintained, reaching 100% infection by both viruses within one season (Table 1).

Infection by SPCSV alone induced clear symptoms under field condition in all the cultivars. Typical symptoms of SPCSV observed were chlorotic spots, purpling and yellowing of middle and mature leaves similar to symptoms reported by Gibson et al. (1998).

Co-infection of SPFMV+SPCSV resulted in severe disease symptoms due to a synergistic interaction between them (Gibson et al. 1998; Untiveros et al. 2007).

The titre of both SPFMV and SPCSV was high in co-infected plants as compared to single-infected plants for all cultivars evaluated, suggesting that the symptoms observed were the result of higher accumulation of both viruses in infected plants. This is contradicting the previous finding that the titre of SPCSV in co-infected plants either declines or remains constant (Karyeija et al. 2000; Kokkinos and Clark 2006). However, their finding was based on experiments under screenhouse conditions. In this experiment, field conditions might have influenced virus replication and also other viruses such as begomoviruses which were not evaluated in this study and are known to be common in some cultivars in Uganda (Wasswa et al. 2011) could have infected the plants leading to synergistic interaction among them hence higher titre (Cuellar et al. 2015), but this requires further investigation. Also SPCSV seems to be the major virus in symptom development as most of the plants infected by SPCSV alone displayed very clear symptoms and produced high titre value indicating their accumulation in plants. On the other hand, SPFMV when infecting alone does not easily accumulate in the plant, and therefore, little or no symptoms were produced.

Effect of single infection of SPFMV on yield of sweetpotato was variable ranging from better apparent yield performance to yield loss as high as 40% depending on the agro-ecologies, seasons and cultivar tested. Yields of cultivars, NASPOT 1, Dimbuka and Kabode infected with SPFMV were greater or did not differ from controls at MUARIK trial, but in these, the healthy control became largely infected by SPFMV but also SPCSV whilst some of the infected plants reverted to healthy so infected plants may have had a lower level of virus infection than the control plants (Fig 2a). It could also be that prior infection with SPFMV conferred a specific protection against itself thus limiting its multiplication and accumulation in the infected plants. Alternatively, it could have conferred nonspecific protection against other viruses probably due to more activated RNA silencing pathway (Kreuze et al. 2005). Similar results have also been reported in Peru (Gutierrez et al. 2003) and Israel (Milgram et al. 1996). This finding justifies why these varieties are widely grown by farmers in central region with high virus disease pressure and therefore supports the use of field derived planting material of resistant or tolerant varieties to reduce the impact of the virus. However, previously field exposed material when reused in the subsequent season produced smaller yields than freshly SPFMV-infected material from the screenhouse especially in the susceptible cultivar, Ejumula. When tested using ELISA, most of the sweetpotato plants were positive for SPCSV and accumulation of this virus may have resulted in the smaller yields. This therefore discourages farmers from obtaining cuttings from their field for such a susceptible variety in areas with high virus incidence like MUARIK.

At NaSARRI, however, SPFMV negatively impacted on the yield of all cultivars tested despite less visible virus symptoms and the initially healthy control largely remain healthy in contrast to what was observed at MUARIK (Fig. 2). The lower infection rate in the healthy control may be because of few aphid vectors of SPFMV or few whitefly vectors of SPCSV so that there were few SPVD-affected plants to act as excellent sources of SPFMV.

Single infection of SPCSV significantly reduced the yield of all sweetpotato cultivars in both locations and proved clearly to be the most economically important virus in the central region of Uganda. The yield loss ranged from 14% to 52% in all the cultivars tested in the two locations. In other studies, yield losses of between 15% and 88% have been reported (Milgram et al. 1996; Gibson et al. 1998; Gutierrez et al. 2003; Njeru et al. 2004; Untiveros et al. 2007). However, the situation was worsened when SPCSV co-infected with SPFMV resulted in yield losses ranging from 60% to 95% similar to that reported earlier (Sheffield 1957; Schaefers and Terry 1976; Milgram et al. 1996; Gibson et al. 1998; Gutierrez et al. 2003). The reduced root yield in sweetpotato has been attributed to decrease in size of photosynthetic organs resulting from severe stunting and other symptoms of SPVD due to synergistic interaction (Hahn et al. 1981; Njeru et al. 2004).

In addition to yield loss, planting virus-infected cuttings also reduced the root quality in terms of the size and number of roots produced. Virus-infected plants produced roots with small diameter and therefore giving higher ratios of length/diameter as compared to the control plants. The length/diameter ratio was greatest in co-infection followed by SPCSV infection and SPFMV infection. This result is consistent with other studies, for example, Kano and Nagata (1999) found that SPFMV-infected plants produce roots with a smaller diameter than storage roots produced from healthy plants. Similarly, Bryan et al. (2003) reported that SPFMV-infected plants produce roots with greater length diameter ratio compared to healthy

control. In terms of number of storage roots produced, SPFMV-infected plants had similar number of total roots per mound with the healthy control plants. On the other hand, the total number of storage roots was significantly less in SPCSV-infected plants and plants infected by a combination of SPFMV and SPCSV compared to healthy controls.

The variation in yield and number of storage roots of the same cultivar in different locations or seasons could be due to differences in environmental factors. Sweetpotato yield is greatly influenced by the environment (Collins et al. 1987; Kanua and Floyd 1988; Bryan et al. 2003), and the widely differing environmental conditions between MUARIK and NaSARRI undoubtedly impacted the yield of controls and virus-infected plants. At MUARIK, the rainfall pattern is uniformly distributed throughout the year which favours production of sweetpotato, and thus, better yield as compared to NaSARRI in which most parts of the year remains hot and dry thus reducing the yield of sweetpotatoes. The continuous production of sweetpotato at MUARIK allows survival of pathogens and their vectors; thus, continuous disease spread leading to virus accumulation in the plant as was evidenced by the high disease severity. This was further supported by the fact that healthy controls became infected and some of the SPFMV-infected plants developed SPVD symptoms by the end of the growing season despite the use of a pesticide to control whiteflies in 3rd and 4th trial at MUARIK. This implies that pesticides may not be of use in managing virus vectors, instead more emphasis should be put in breeding and growing resistant cultivars for such areas with high vector and disease pressure. In NaSARRI, however, the hot dry spell in some months discourages sweetpotato production and this breaks the pathogen and pest cycle and may be the cause of reduced virus spread. This was further supported by the fact that no pesticides were applied, but most of the healthy controls did not develop virus symptoms and tested negative using ELISA and *I. setosa*. This therefore implies that both susceptible and resistant varieties can be grown in this area and also field multiplication of virus-indexed sweetpotato materials can be carried out in this agro-ecology provided the issue of drought is addressed.

This study has demonstrated that single infection with SPCSV and its co-infection with SPFMV are serious threats to sweetpotato production in the central region and other regions where the whitefly population is high. Here, there is a need to focus on resistant varieties and farmer selection of symptomless planting material, and virus cleaned material was, by itself, insufficient. Although SPFMV reduced yield, its effect alone was not very great as most of the Ugandan cultivars were resistant to it and could revert from single infection. Pesticide application proved not to be effective in controlling virus spread and therefore should not be used as this will increase the cost of production to little apparent benefit.

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