Effect of temperature on sweet potato virus disease symptom expression

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DOI: https://doi.org/10.5897/AJAR2017.12442

ABSTRACT

The incidence and severity of sweetpotato virus disease (SPVD) was reported to be highly variable under different agroecological zones in Uganda, a situation that could be partly attributable to differences in temperature. This raised a need for understanding the effect of temperature on the biology of SPVD causative agents which ultimately influences disease development and symptom expression that undermines productivity among sweet potato cultivars. This study was carried out at Makerere University Agricultural Research Institute, Kabanyolo (MUARIK). Initially clean sweet potato cultivars were inoculated with two viruses namely Sweet potato chlorotic stunt virus (SPCSV) and Sweet potato feathery mottle virus (SPFMV) that cause SPVD when co-infecting sweet potato and established at two temperature environments; field and glasshouse, followed by a weekly interval monitoring of the plants for symptom expression and growth response. Temperature differences significantly ($p<0.001$) influenced SPVD severity and the growth response of different sweet potato cultivars. Overall, the plants under field conditions where temperature was lower produced higher SPVD severity than under glasshouse where higher temperatures were recorded. SPVD severity for most of the cultivars was higher in the field than under glasshouse. Cultivar (cv.) Ejumula displayed the highest severity levels followed by cvs. Tanzania and Beauregard. Conversely, New Kawogo, Dimbuka and Naspot 1 showed none to mild severities particularly under the glasshouse conditions. Therefore temperature influenced the development of SPVD; low temperatures of 20 to 29°C produced more disease severities than high temperatures of 30 to 39oC. It is suggested that reasonably high temperatures under a controlled environment should be incorporated in any sweet potato seed production system for possible elimination of SPVD.

Key words: Temperature, disease symptom expression, viruses, Ipomea batatas, growth response.

INTRODUCTION

Sweet potato (*Ipomoea batatas*, family Convolvulaceae) is of great importance to Uganda and other African countries such as Rwanda and Burundi because of its various food and feed uses (Kpaka et al., 2013). The sweet potato (orange-fleshed varieties) also plays a key role in alleviating vitamins A, B and E deficiencies, which are rampant among children in Sub-Saharan Africa at more than 40 and 21.1% (127 million) of pre-

school children and 5.6% (7.3 million) of pregnant women worldwide (HarvestPlus, 2012; Kpaka et al., 2013). According Kpaka et al. (2013), Uganda is the biggest producer of sweet potato in Africa but its low average yield of 4.58 t/ha (compared to experimental yield estimates of 25 t/ha) makes it impossible to satisfy the country's production demand. Major constraints such as pests and diseases explain the crop's current low yields (Kpaka et al., 2013; Sanginga and Mbabu, 2015). The most serious pest is the sweet potato weevil. The other pests include aphids (*Myzus persicae*), whiteflies (*Bemisia tabaci*), mites and caterpillars (Sanginga and Mbabu, 2015). The diseases which undermine the crop's productivity are mainly viral and some of these viruses are sweet potato chlorotic stunt virus (SPCSV) and sweet potato feathery mottle virus (SPFMV); vectored by whiteflies and aphids, respectively (Wasswa, 2012). The two viruses synergize to produce sweet potato virus disease (SPVD) (Gibson et al., 2014). SPVD is the most important disease of the crop that threatens sweet potato in the tropics (Kpaka et al., 2013). It causes yield losses of up to 95%; there are no reports of immune cultivars (Adikini et al., 2016; Gibson et al., 2014; Sanginga and Mbabu, 2015). However, there exist good levels of SPVD resistance among the commonly grown sweet potato varieties in high infection areas (Kpaka et al., 2013). It is notable that some of the locally adapted cultivars like New Kawogo are more SPVD resistant than others (Gibson et al., 2014; Wasswa, 2012). Environmental conditions also seriously influence the productivity of sweet potato and these include temperature extremes (15 to 35°C for sweet potato growth), humidity and rainfall patterns and intensity, among other factors (Gibson et al., 2014; HarvestPlus, 2012). This study was focused on gaining an insight into the effect of temperature on the development of SPVD and growth of sweet potato.

Viruses that infect and replicate well in their hosts tend to decrease the survival of the hosts by affecting their growth and development (Gibson et al., 2014). In addition, the incidence and severity of pathogens is strongly influenced by the interaction of temperature, vectors, hosts, and pathogen genetics (Adikini et al., 2016; Mwanga et al., 2016). From one environment to another, climatic aspects namely rainfall patterns and intensity, relative humidity, wind speed and direction, and temperature tend to differ and fluctuate none equivocally (Mwanga et al., 2016; Sabaghnia et al., 2012).

Such changes influence the epidemiology of plant diseases and may also affect disease expression (Gibson et al., 2014; Wasswa, 2012). Previous studies reported that some areas such as central Uganda had higher SPVD incidences and severities than for instance the eastern region (Adikini et al., 2016). The two regions differ in average ambient temperature, among other climatic aspects; with the eastern being hotter than the central region. It has been suggested that high temperature favours recovery from SPVD (Adikini et al., 2016; Gibson et al., 2014). There are increasing reports on rise of SPVD outbreaks in traditionally disease free agro-ecologies in Uganda. The new epidemics could be associated with changes in climatic conditions especially temperature and humidity. The temperature range in which the sweet potato crop can grow is reportedly 15 to 35°C but most pathogens also thrive in the same temperature range (HarvestPlus, 2012; Seidl Johnson et al., 2014). An optimum temperature for the satisfactory sweet

potato crop productivity and its recovery from the SPVD is not established (Gibson et al., 2014). There is also limited knowledge on the relationship between sweet potato growth response among cultivars and SPVD development at different temperatures. The main objective of this study was to generate knowledge about the effect of temperature on SPVD development. The specific objectives of this study were: (i) To determine the effect of temperature on the expression of sweet potato virus disease symptoms, and (ii) To characterize the growth and physiological response of sweet potato cultivars at different temperatures. Results from this study are expected to contribute towards improvement of sweet potato crop productivity through exploitation of high temperatures in controlled environments (such as the screen house) for SPVD management.

MATERIALS AND METHODS

Plant materials

Six sweet potato cultivars used in this study were collected from MUARIK and Namulonge (NaCRRI) research stations located in Wakiso district in Uganda. The cultivars selected for use in this study were based on their diverse attributes (Table 1). Different sweet potato cultivars were used in this study so as to ensure inclusion of genotypes of various attributes such as high yield, SPVD tolerance or resistance, nutritional value and farmer preference. Some varieties are more readily infected by SPVD than others even when exposed to similar amounts of inoculums. New Kawogo is reportedly more resistant to SPVD than other cultivars (Gasura and Mukasa, 2010; Mwanga *et al*., 2016). Beauregard is an orange – fleshed variety rich in beta carotene, a precursor for vitamin A; and is highly preferred in some countries like Australia (HarvestPlus, 2012). In the selection process, consideration was put to ensure the inclusion of orange and non-orange fleshed cultivars. These were New Kawogo, Dimuka, NASPOT 1, Beauregard, Ejumula and Tanzania. During the cultivar samples collection, only vines were obtained from the research stations since they are the locally common sweet potato propagation materials. Each of these cultivars were then delivered on the experimental site and established in an SPVD vector proof screen house.

Table 1. List of attributes of sweet potato cultivars used in the study.

Cultivar	Origin of parent	Desirable/undesirable traits
New Kawogo	Uganda (landrace)	High dry matter content, white fleshed, resistant to SPVD, susceptible to *A. bataticola* blight
Dimbuka	Uganda (landrace)	High dry matter content, white flesh of storage roots, tolerant to SPVD
Ejumula	Uganda (landrace)	High dry matter content, orange flesh of storage roots, highly susceptible to SPVD
Tanzania	Uganda (landrace)	High dry matter, sweet taste, tolerant to SPVD
NASPOT 1	Uganda (bred clone)	High dry matter, orange flesh of storage roots, high root yield, *Alternalia bataticola* blight
Beauregard	CIP/Peru	Low dry matter content, orange flesh of storage roots, good root shape, susceptible to SPVD

Extracted and modified from Gasura and Mukasa (2010) and Mwanga et al. (2016).

Experimental design

Six sweet potato cultivars were collected for use in the field and glasshouse experiment at MUARIK. The samples were indexed for sweet potato viruses namely SPCSV and SPFMV using an indicator plant *Ipomoea setosa*. Vines in each cultivar found to be free from the said viruses were then multiplied under the vector proof screen house in order to raise a sufficient number of planting materials for the experiments. Five plants per cultivar for each temperature regime were graft inoculated with scions known for presence of SPCSV and SPFMV. Single isolates of SPCSV and SPFMV which were confirmed earlier using PCR technique by Wasswa et al. (2012)and kept in a vector-proof screen house at MUARIK were used from two respective plants of a common cultivar Ejumula. Before use in this study, indexing for verification was carried out by grafting on *I. setosa*. The plants were multiplied and bud grafting in which the scions were the infectious material was used. The inoculated plants were observed in two environments namely the field and an insect proof glasshouse at MUARIK. Plants which were inoculated were potted one week before planting of the controls. The controls were the non-inoculated plants planted on the day of inoculation. The plants were planted in pots of uniform size, with a soil volume of 3,234 cm^3. One plant was planted per pot. In the field, watering was done only when it had not rained for a period of four consecutive days to avoid desiccation. In the glasshouse, plants were watered regularly after every two days, in the morning hours to ensure that the soil remained saturated.

Data collection and analysis

Data collection on SPVD severity (on a most symptomatic leaf where applicable) and sweet potato plant growth response in the field and glasshouse was done at a 1 - week interval for 10 weeks, starting at 2 weeks after inoculation. The foliage of each plant was the observational unit. Disease expression was monitored based on visual virus symptoms. Disease incidence was recorded by counting the number of plants showing symptoms, and expressing it as a percentage. SPVD severity was recorded at a scale of 1 to 5 as modified from Gasura and Mukasa (2010), where: 1 = no apparent symptoms; 2 = $<^1/_{10}$ of the leaves/leaf surface has symptoms; 3 = $^1/_{10}$ to $^3/_{10}$ of the leaves/leaf surface shows symptoms; 4 = $^3/_{10}$ to $^1/_2$ of the leaves/leaf surface shows symptoms; and 5 = $>^1/_2$ of the leaves/leaf surface has symptoms (Figure 1). Field mercury thermometers were used to take record of daily temperature as it fluctuated both in the field and glasshouse, from which average weekly temperatures were computed for correlation with SPVD symptom expression. An analysis of variance (ANOVA) was carried out using GenStat 13^{th} edition, at a 5% level of significance. Average temperature was recorded as the average of the maximum and minimum temperature of the day and at 8:00 am and 1:00 pm.

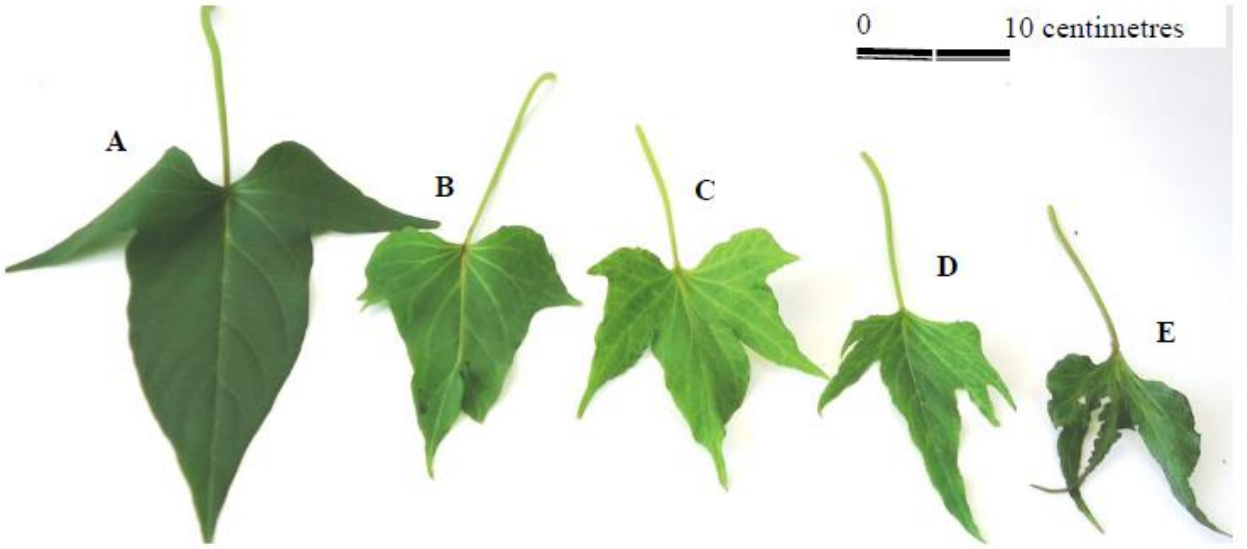

Figure 1. SPVD symptoms severity scoring at a scale of 1 to 5; where 1 (A) = no apparent symptoms, 2 (B) = <1/10 of the leaves/leaf surface has symptoms, 3 (C) = 1/10 to 3/10 of the leaves/leaf surface shows symptoms, 4 (D) = 3/10 to 1/2 of the leaves/leaf surface shows symptoms and 5 (E) = >1/2 of the leaves/leaf surface has symptoms.

he data on growth parameters of length of internodes, stem length, number of auxiliary shoots, number of leaves and tuber yield was collected from the field and glasshouse. The length of internodes and stem length was recorded in centimetres (cm). Tuber yield was obtained at 14 weeks after planting by harvesting the plants in pots, washing the tubers off the soil and thereafter weighing. Yield data were recorded in grams per pot (g/pot), which was the same as grams per plant since each pot was planted with a single vine of uniform length, 10 cm. Means and probability values were generated by subjecting the internode length, stem length, number of auxiliary shoots, number of leaves and tuber yield data to ANOVA at 5% significance level. Field 1, Glasshouse 1, Field 2 and Glasshouse 2 were used to denote SPVD non-inoculated plants in field, SPVD non-inoculated plants in glasshouse, plants inoculated with SPVD viruses in field and plants inoculated with SPVD viruses in glasshouse, respectively the results section.

RESULTS

SPVD severity and temperature fluctuations

There was a significant difference ($p<0.001$) in SPVD symptom expression between the glasshouse and field environments. Less severity score averages were recorded in the glasshouse (2.397) than in the field (2.89). Overall, sweet potato cultivar Dimbuka in the glasshouse was the least severely affected whereas the highest SPVD scores were observed on Beauregard in the field. In the field, New Kawogo showed the lowest mean disease score (1.8) followed by Naspot 1, Dimbuka, Ejumula, Tanzania, and Beauregard with the highest disease core of 3.86 (Figure 2). In the glasshouse, Dimbuka displayed the lowest score (1.66) followed by Naspot 1, New Kawogo, Tanzania, Ejumula, and Beauregard with the highest score (3.18). Across the two environments,

New Kawogo had the lowest SPVD score (1.89) followed by Dimbuka and Naspot 1 at score 2.18, Ejumula, Tanzania and Beauregard with the highest score (3.52). As field temperature increased, glasshouse temperature increased. Similarly, as the field temperature decreased, the glasshouse temperature generally decreased in a corresponding manner. In the field, considering results during a period of three to ten weeks after planting, the lowest SPVD scores were obtained at different mean weekly temperatures. For instance New Kawogo showed its lowest disease score at 26.0°C (week 10); Dimbuka and Naspot 1 at 28.9°C (week 4), 25.4°C (week 7), and 25.4°C (week 8) though Naspot 1 showed a low score also at 21.3°C (week 5); Beauregard and Ejumula at 25.4°C (week 7); and Tanzania at 28.9°C (week 4). On a weekly interval, SPVD symptom scores generally varied from one cultivar to another as temperature also varied. For New Kawogo, it was observed that symptom development did not change systematically with plant age unlike the rest of the cultivars where severity scores generally increased with plant age, with Tanzania showing the clearest forward trend (Table 2).

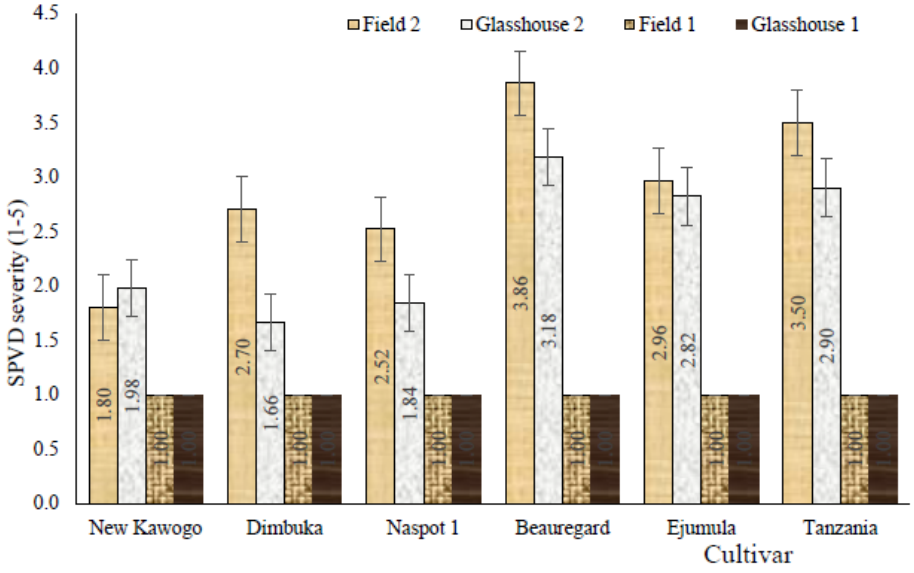

Figure 2. SPVD severities of different cultivars under the two environments of field and glasshouse averaged for the 10 weeks of the experiment.

Table 2. Mean weekly severities of SPVD for different cultivars.

Cultivar	Weeks after planting										
	1	2	3	4	5	6	7	8	9	10	Mean
New Kawogo	1.0	1.0	1.9	2.1	2.5	2.5	2.6	2.1	1.7	1.5	1.89a
Dimbuka	1.0	2.0	2.2	2.5	2.3	2.5	2.3	2.2	2.4	2.4	2.18b
Naspot 1	1.2	1.9	1.9	2.0	2.1	2.7	2.5	2.2	2.5	2.8	2.18b
Ejumula	1.7	1.8	3.1	3.2	3.3	3.0	2.7	3.0	3.4	3.7	2.89c
Tanzania	1.3	1.4	2.5	3.2	3.3	3.5	3.7	4.2	4.2	4.7	3.20d
Beauregard	1.3	2.9	3.6	3.8	3.8	3.8	3.5	4.0	4.2	4.3	3.52e
Mean	1.25	1.83	2.53	2.80	2.88	3.00	2.88	2.95	3.07	3.23	2.643
s.e.d.	0.147	0.192	0.306	0.289	0.261	0.339	0.361	0.29	0.339	0.286	0.144
l.s.d (α = 5%)	0.296	0.385	0.614	0.580	0.526	0.682	0.725	0.580	0.682	0.575	0.283
CV %	26.3	23.4	27.0	23.1	20.3	25.3	28.0	21.9	24.7	19.8	38.5
F.pr.	<0.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001

Values followed by the same letter are not significantly different at 5% level of significance.

SPVD symptoms on cv. Tanzania in the field increased gradually from week 1 to week 10, irrespective of temperature fluctuations (Figure 3). A slightly similar trend was observed in the glasshouse but the rate of symptom development increased less steadily and to a lower maximum than in the field. In the glasshouse, the lowest SPVD scores after three weeks were obtained at 30.0°C (week 9), 30.0°C (week 9), 34.2°C (week 8), 34.2°C (week 7), 34.2°C (week 7) and 28.3°C (week 5) for New Kawogo, Dimbuka, Naspot 1, Beauregard, Ejumula and Tanzania respectively. The highest scores were observed at 28.3oC (week 5), 34.1oC (week 4), 34.0oC (week 4), 34.1oC (week 4), 28.3°C (week 5) and 33.3°C (week 10) for New Kawogo, Dimbuka, Naspot 1, Beauregard, Ejumula and Tanzania, respectively. SPVD scores for New Kawogo increased from

week 1 to 5, remained constant up to week 7 and then it declined. A similar trend was observed for Dimbuka and Naspot 1. Generally, SPVD scores increased with plant age for Beauregard, Ejumula and Tanzania.

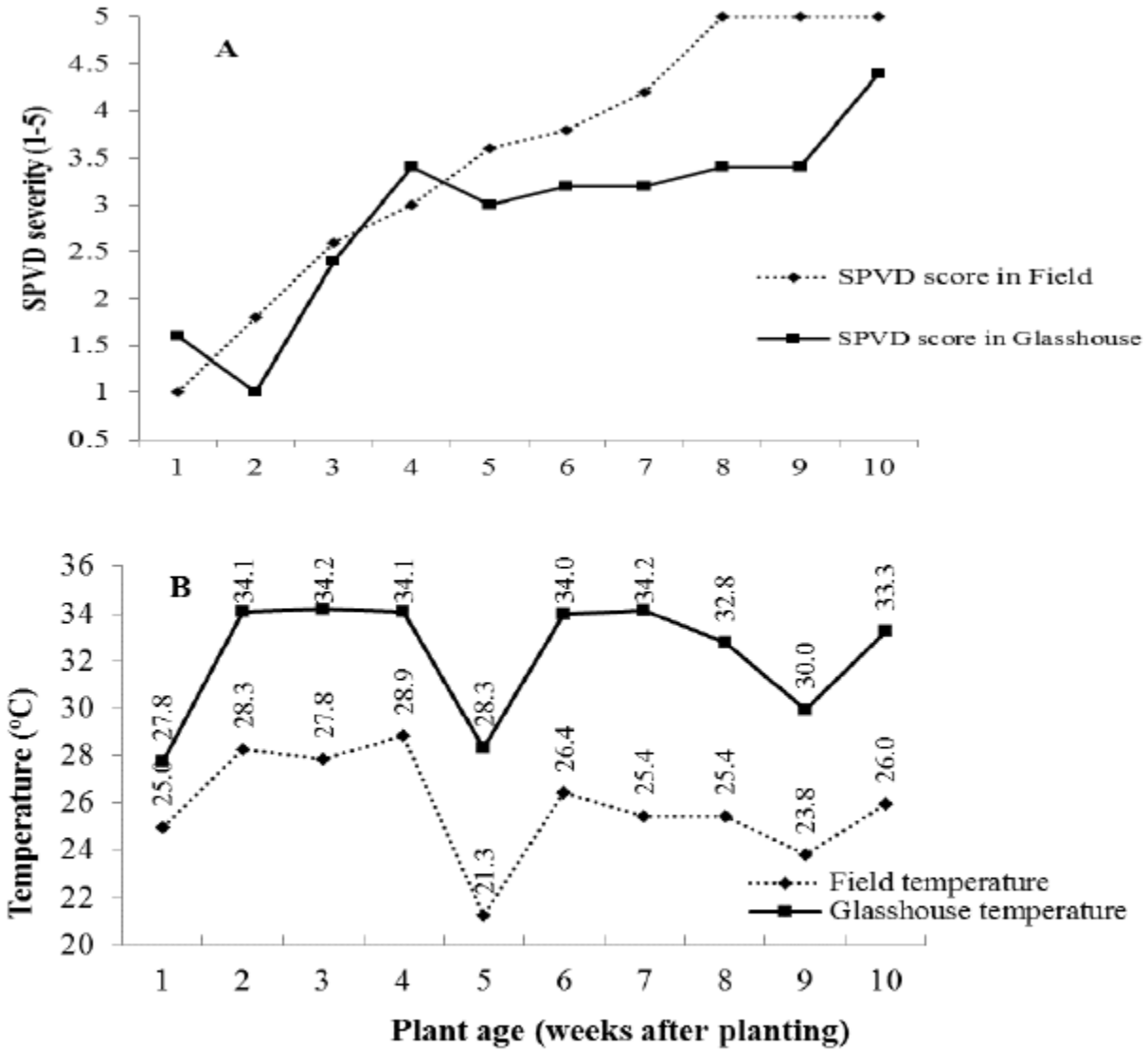

Figure 3. A comparative graph of changes in severity for cultivar Tanzania and weekly changes in temperature under the two environments. ***A*** = Changes in disease severity of cultivar Tanzania; ***B*** = Changes in temperature during the period of the experiment.

In the case of New Kawogo in the field, as plant age increased, SPVD severity increased less slightly from a score of 1 (no symptoms) at the first and second week to 2 ($<^1/_{10}$ of the leaves or leaf surface had symptoms), thereafter remained unchanged from week 3 up to week 6, beyond which the scores oscillated between 2.10 and 2.25, and declined to 1.5 at week 10. In the glasshouse, SPVD symptoms developed increasingly from the first week at score 1 to 3 at week 5, remained constant up to week 7 and then reduced decreasingly up to the 10th week (Figure 4).

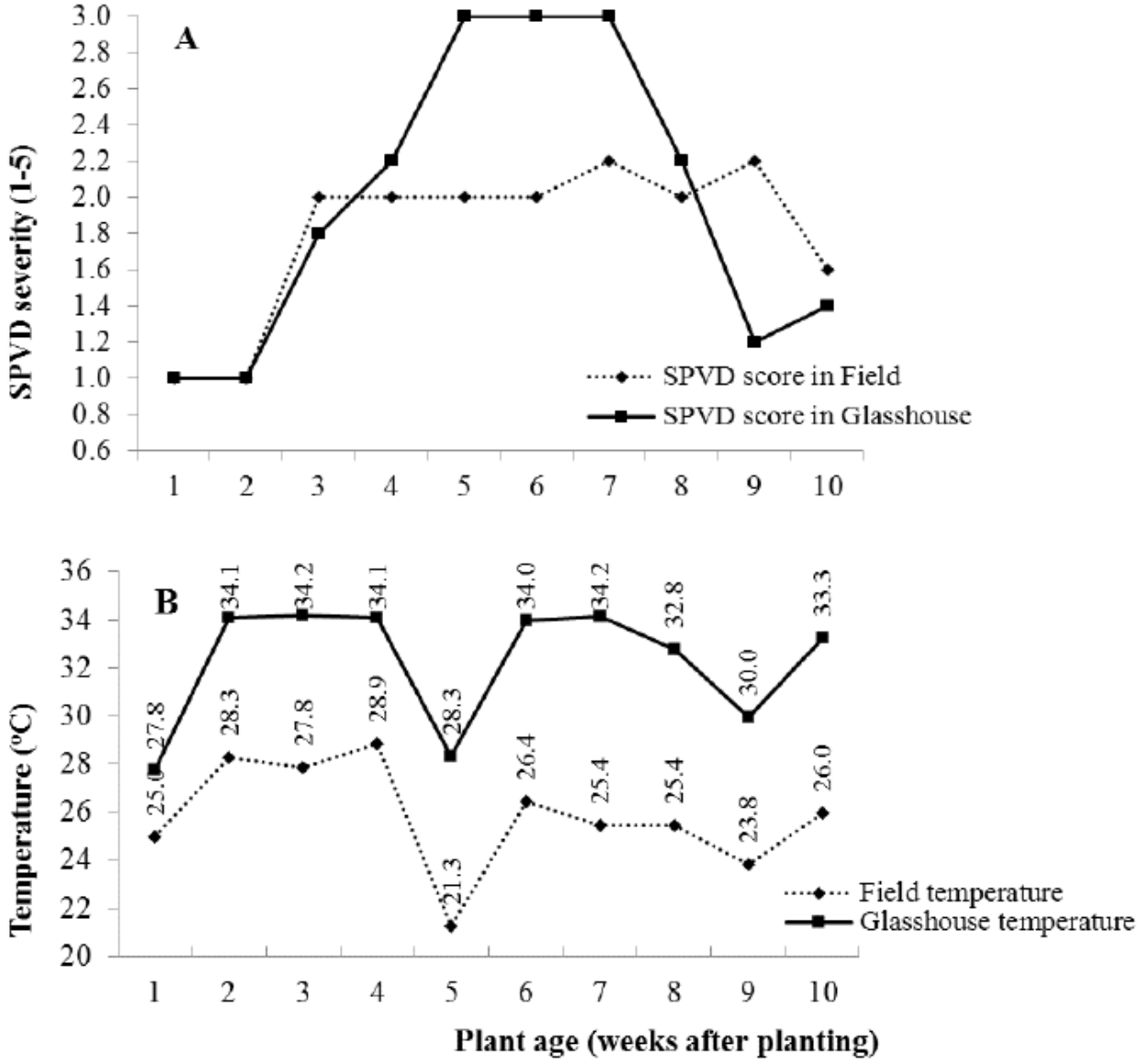

Figure 4. A comparative graph of changes in severity for cultivar New Kawogo over time.

Growth response

Length of internode per plant (cm)

There was a significant difference ($p<0.001$) in internode length between the two environments at a 5% significance level, with the highest mean for non-inoculated plants in glasshouse (3.23 cm) followed by inoculated plants in glasshouse, non-inoculated plants in field, and inoculated plants in field had the shortest internodes (1.91 cm) (Table 3). Significant still was the difference

($p<0.001$) in internode length among different cultivars. Generally, longer internodes were observed among non-inoculated plants than in presence of SPVD. Apart from New Kawogo cultivar whose plants had longest internodes in absence of SPVD in the field, the rest of the cultivars had highest internode lengths in absence of the disease in glasshouse. Plants with shortest internodes for New Kawogo were observed in presence of SPVD in glasshouse whereas for the remaining cultivars, shortest internodes are recorded from inoculated plants in the field. Across environments, Beauregard had the highest internode length (4.51 cm) followed by New Kawogo, Dimbuka, Naspot 1, Tanzania, and Ejumula with the shortest internodes (1.80 cm). Beauregard had the highest internode length across environments and SPVD treatments while Ejumula produced the shortest internodes in the field on SPVD inoculated plants.

Table 3. Mean internode length of sweet potato cultivars under the two environments.

Cultivars	Environment				Mean	s.e.d	l.s.d	c.v %	F.pr.
	Field 1	GH 1	Field 2	GH 2					
New Kawogo	2.54	2.46	2.43	2.08	2.38	0.145	0.286	31.0	0.019
Dimbuka	2.36	2.85	1.76	2.51	2.37	0.243	0.480	51.4	<0.001
Naspot 1	1.96	2.83	1.74	2.51	2.26	0.192	0.379	42.5	<0.001
Beauregard	3.91	5.75	2.96	5.44	4.51	0.493	0.973	54.6	<0.001
Ejumula	1.51	2.50	1.07	2.11	1.80	0.143	0.281	39.7	<0.001
Tanzania	1.75	2.97	1.52	2.64	2.22	0.168	0.331	37.8	<0.001
Mean	**2.34c**	**3.23a**	**1.91d**	**2.88b**	**2.59**	**0.107**	**0.209**	**50.4**	**<0.001**
s.e.d	**0.140**	**0.305**	**0.232**	**0.296**	**0.131**	**0.261**			
l.s.d.(α =5%)	**0.389**	**0.600**	**0.457**	**0.582**	**0.256**		**0.513**		
c.v %	**42.3**	**47.2**	**60.7**	**51.3**	**50.4**			**50.4**	
F.pr.	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**				**<0.001**

Values followed by the same letter are not significantly different at 5% level of significance.

On a weekly interval, internode lengths generally increased at a decreasing rate for all the cultivars. Cv. Beauregard, however, stood out with the longest internodes (Figure 5).The longest internodes were obtained in the glasshouse. Beauregard achieved the longest internodes among SPVD free plants in the glasshouse followed by SPVD inoculated plants in glasshouse, SPVD free plants in field and the shortest internodes were recorded from SPVD inoculated plants in the field (Figure 6).

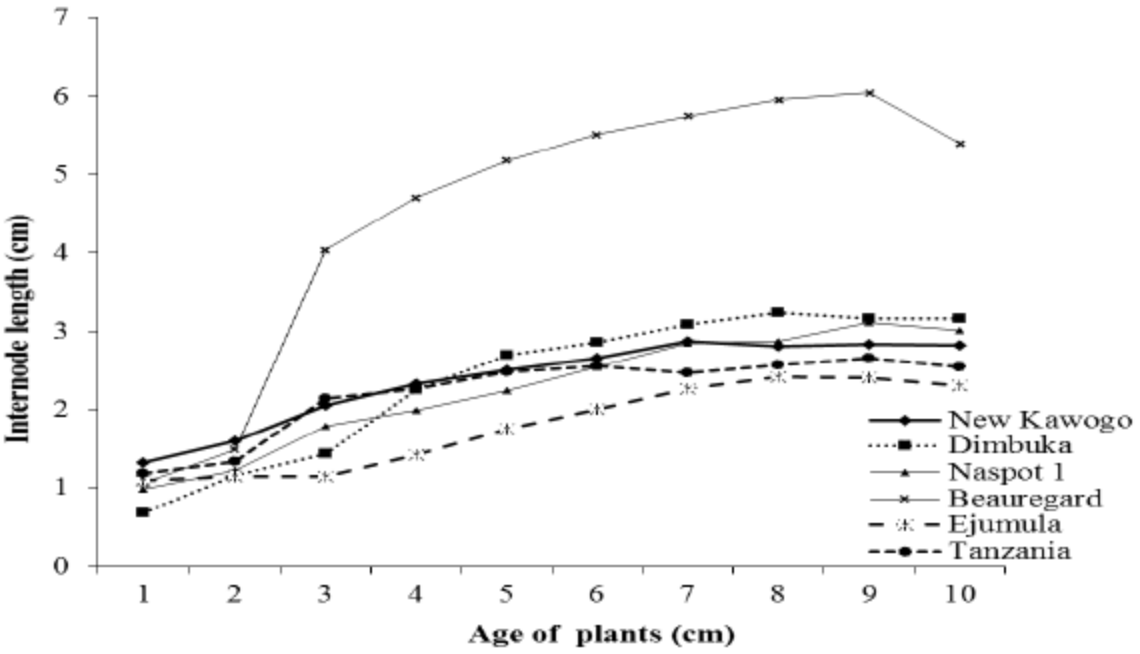

Figure 5. Variation of internode length among cultivars over time.

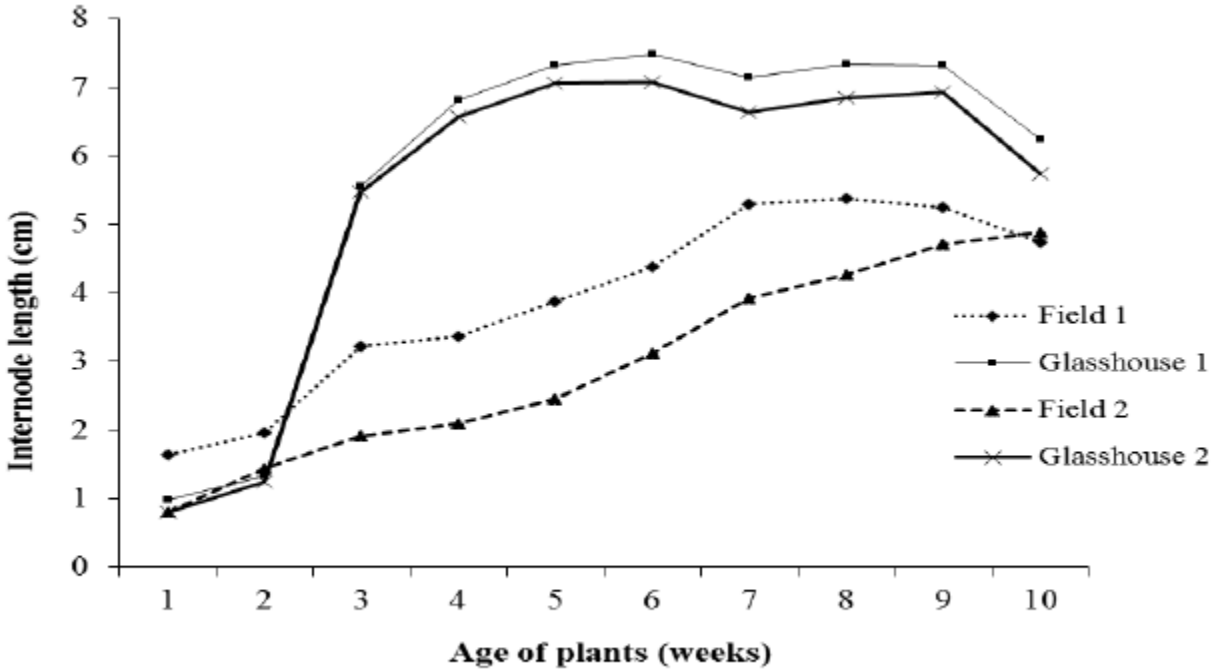

Figure 6. Variation of internode length of Beauregard plants under the two environments.

Stem length per plant (cm)

The difference ins tem length was significant ($p<0.001$) between the two environments, with a higher mean in the glasshouse on non-inoculated plants (55.1 cm) followed by glasshouse on SPVD inoculated plants, field on non-inoculated plants, and the shortest plants were obtained in the field in presence of SPVD (19.6 cm) (Table 4). The difference among cultivars was also significant ($p<0.001$). Similar to the trend of internode lengths, apart from New Kawogo which had its longest plants in field in absence of SPVD, the rest of cultivars registered their highest stem lengths in glasshouse in absence of the disease. Unlike in the trend of internode lengths, the shortest plants for all the six cultivars were observed in the field in presence of SPVD. Across environments, Beauregard had the tallest plants (83.2 cm) followed by New Kawogo, Tanzania, Dimbuka, Naspot 1, and Ejumula had the shortest plants (24.4 cm) (Figure 7). An in-depth description of stem length variation was based on Beauregard; and it further illustrated that the longest plants were observed in the glasshouse where temperatures were higher than in the field (Figure 8). SPVD free plants were longer than infected plants. Beauregard both inoculated and non-inoculated produced the longest plants in glasshouse while the shortest plants were observed in the field among SPVD inoculated plants, with the Ejumula being the shortest.

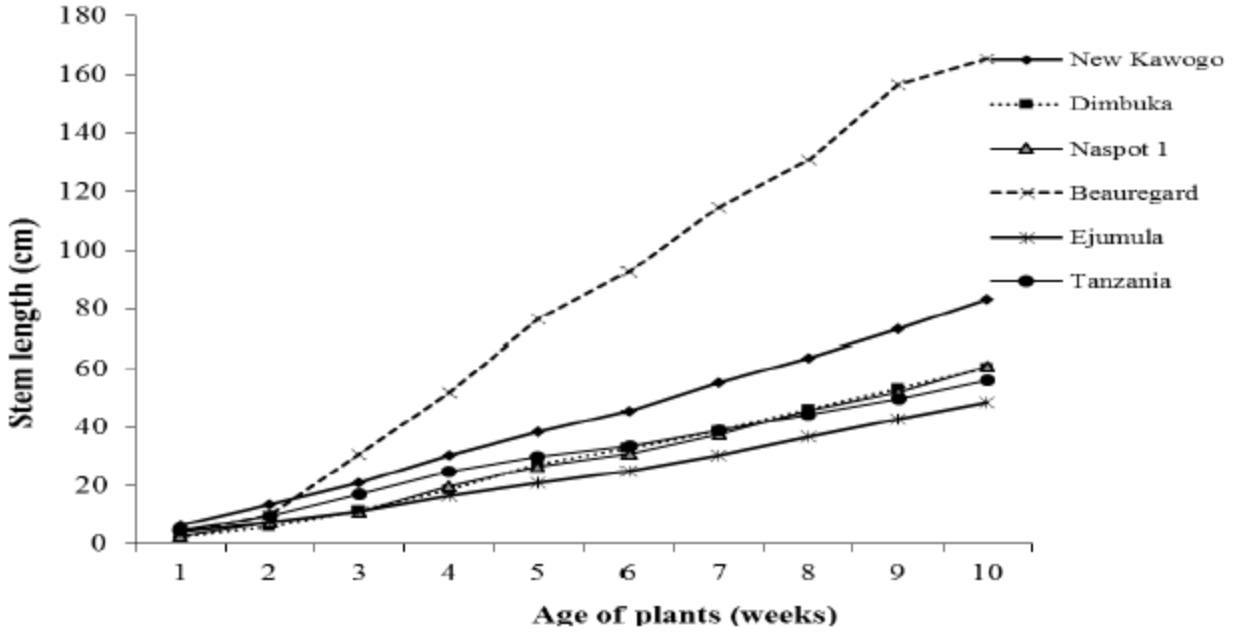

Figure 7. Variation of stem length among cultivars over time.

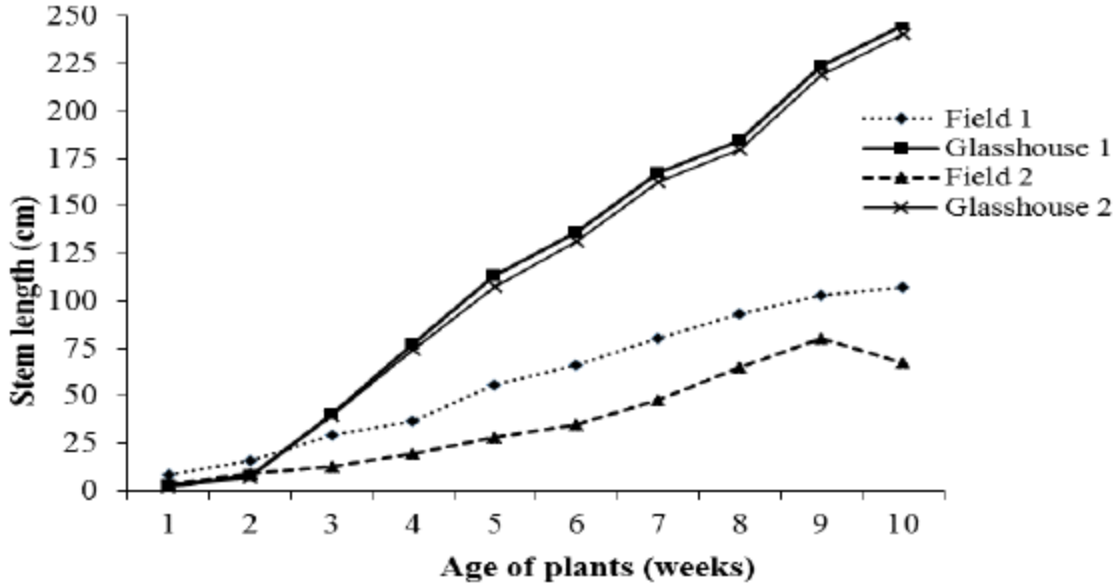

Figure 8. Variation of stem length of Beauregard plants under the two environments.

Overall, across environments and inoculation levels, stem length for all cultivars increased at constant rates throughout the time of the experiment. Cv. Beauregard had the highest rate of increase in stem length followed by New Kawogo. Tanzania, Naspot 1 and Dimbuka have similar curve trends. Cv. Ejumula's stem length was the shortest, having the lowest increase rate.

Number of shoots per plant

The highest shooting tendency was observed in the glasshouse on non-inoculated plants while the lowest number of shoots was recorded in the field on SPVD inoculated plants. The figure shows that Ejumula (both non- and inoculated in glasshouse) was leading followed by New Kawogo (both non- and inoculated in glasshouse) while Beauregard had the lowest number of shoots. The number of shoots differed significantly ($p<0.001$) between the two environments, with a higher mean number on non-inoculated plants in glasshouse (10.07) followed by inoculated plants in glasshouse, non-inoculated plants in field, and SPVD inoculated plants in the field had the lowest number of shoots (0.7) for non-inoculated plants (Table 5). Sweet potato cultivars also significantly differed ($p<0.001$) in the number of shoots produced. All the cultivars produced their highest numbers of shoots on non-inoculated plants grown in glasshouse while the least numbers of internodes were produced on SPVD inoculated plants in field. By the 10th week across environments and inoculation levels, Ejumula had the highest shooting tendency followed by New Kawogo, Dimbuka, Tanzania, Naspot 1 and Beauregard with the least number of shoots (Figure 9). Using the case of Ejumula, the highest shooting tendency was observed in the glasshouse in absence of SPVD followed by inoculated plants in the glasshouse, SPVD non-inoculated plants in the field and plants and SPVD inoculated plants in the field had the lowest shooting tendency (Figure 10).

Table 5. Mean number of shoots of sweet potato cultivars under the two environments.

Cultivars	Environment				Mean	s.e.d	l.s.d	c.v %	F.pr.
	Field 1	GH 1	Field 2	GH 2					
New Kawogo	5.8	12.2	1.0	11.3	7.58	1.008	1.988	68.2	<0.001
Dimbuka	3.5	10.4	0.3	9.5	5.92	0.900	1.776	76.0	<0.001
Naspot 1	2.8	8.9	0.8	7.9	5.14	1.021	2.014	99.5	<0.001
Beauregard	1.6	5.9	1.4	4.9	3.48	1.730	3.412	56.6	<0.001
Ejumula	4.6	13.4	0.4	12.5	7.71	0.973	1.918	63.1	<0.001
Tanzania	7.9	9.6	0.2	8.8	6.63	0.781	1.539	58.9	<0.001
Mean	**4.37**	**10.07**	**0.70**	**9.15**	**6.07**	**0.37**	**0.727**	**74.7**	**<0.001**
s.e.d	**0.633**	**1.225**	**0.253**	**1.151**	**0.454**	**0.907**			
l.s.d.(α =5%)	**1.245**	**2.412**	**0.498**	**2.266**	**0.890**		**1.78**		
c.v %	**72.4**	**60.8**	**179.9**	**62.9**	**74.7**			**74.7**	
F.pr.	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**				**<0.001**

Values followed by the same letter are not significantly different at 5% level of significance. Field 1 = SPVD non-inoculated plants in field; Glasshouse (GH) 1 = SPVD non-inoculated plants in glasshouse; Field 2 = plants inoculated with SPVD viruses and grown in field; and Glasshouse (GH) 2 = plants inoculated with SPVD viruses and grown in glasshouse.

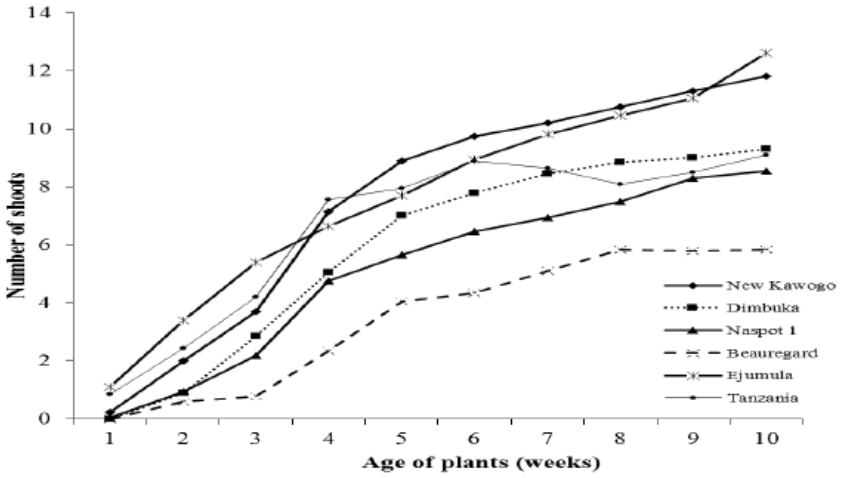

Figure 9. Variation of number of lateral shoots among cultivars over time.

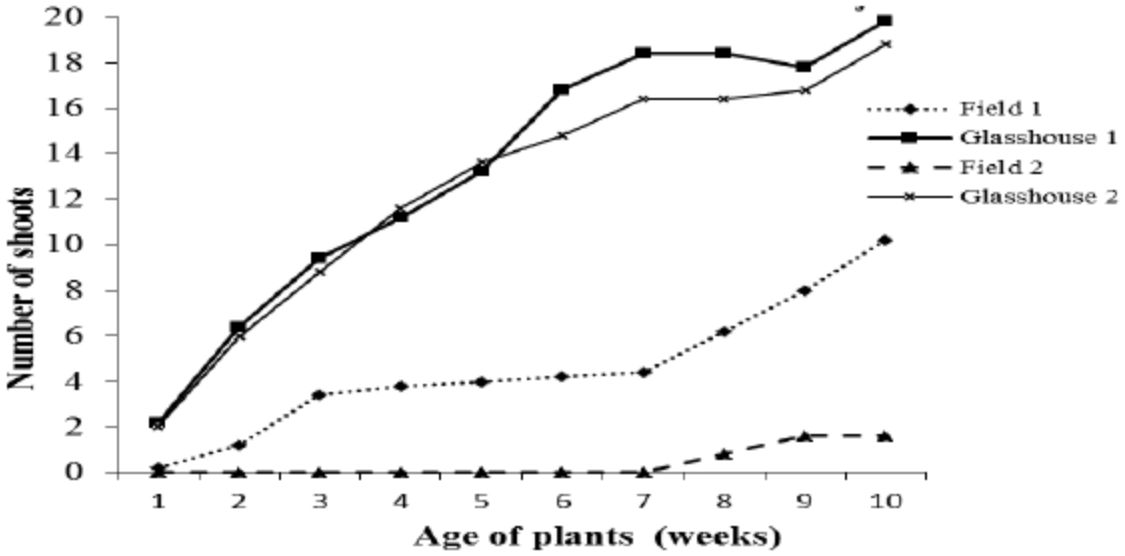

Figure 10. Variation of number of shoots of Ejumula plants under the two environments.

Number of leaves

There was a significant difference ($p<0.001$) in number of leaves between the two environments, with the highest mean leaf number in glasshouse on non-inoculated plants (21.82) followed by SPVD inoculated plants in glasshouse, non-inoculated plants in filed, and SPVD inoculated plants in the field produced the lowest number of leaves (10.37) (Table 6). The difference among cultivars was also significant ($p<0.001$). For all the six cultivars, their highest mean number of leaves were observed on non-inoculated plants grown in glasshouse while their lowest leaf numbers were recorded on SPVD inoculated plants grown in the field (Figure 11). Across environments, New Kawogo produced the highest mean number of leaves (21.45) followed by Beauregard, Ejumula, Tanzania, Naspot 1 and Dimbuka with the lowest number of leaves (14.30). The highest foliage number was observed on the SPVD non-inoculated New Kawogo in the glasshouse followed by SPVD inoculated New Kawogo in the glasshouse, and the lowest number on inoculated Ejumula in the field. By the 10th week, New Kawogo had the highest number of leaves followed by Beauregard, Ejumula, Tanzania, Naspot 1 and Dimbuka with the least leaf number (Figure 11). The highest foliage production was observed on SPVD free plants in glasshouse in which temperatures were higher than in the field; followed by diseased plants in the glasshouse, SPVD non-inoculated plants in field and the lowest foliage production was recorded on diseased plants in the field (Figure 12).

Table 6. Mean number of leaves of sweet potato cultivars under the two environments.

Cultivars	Environment				Mean	s.e.d	l.s.d	c.v %	F.pr.
	Field 1	GH 1	Field 2	GH 2					
New Kawogo	21.92	25.66	14.37	23.86	21.45	2.157	4.254	51.5	<0.001
Dimbuka	14.50	18.06	8.36	16.30	14.30	1.490	2.938	52.1	<0.001
Naspot 1	14.62	20.10	8.22	18.20	15.28	1.730	3.412	56.6	<0.001
Beauregard	16.20	23.82	14.48	21.86	19.09	2.376	4.685	62.2	<0.001
Ejumula	14.88	22.56	8.18	20.60	16.55	1.642	3.238	49.6	<0.001
Tanzania	17.82	20.70	8.64	18.82	16.49	1.622	3.198	49.2	<0.001
Mean	**16.66**	**21.82**	**10.37**	**19.94**	**17.20**	**0.763**	**1.497**	**54.3**	**<0.001**
s.e.d	**1.574**	**2.272**	**1.347**	**2.124**	**0.934**	**1.869**			
l.s.d.(α =5%)	**3.098**	**4.471**	**2.651**	**4.181**	**1.833**		**3.666**		
c.v %	**47.2**	**52.1**	**64.9**	**53.3**	**54.3**			**54.3**	
F.pr.	**<0.001**	**0.014**	**<0.001**	**0.007**	**<0.001**				**0.429**

Values followed by the same letter are not significantly different at 5% level of significance. Field 1 = SPVD non-inoculated plants in field; Glasshouse (GH) 1 = SPVD non-inoculated plants in glasshouse; Field 2 = plants inoculated with SPVD viruses and grown in field; and Glasshouse (GH) 2 = plants inoculated with SPVD viruses and grown in glasshouse.

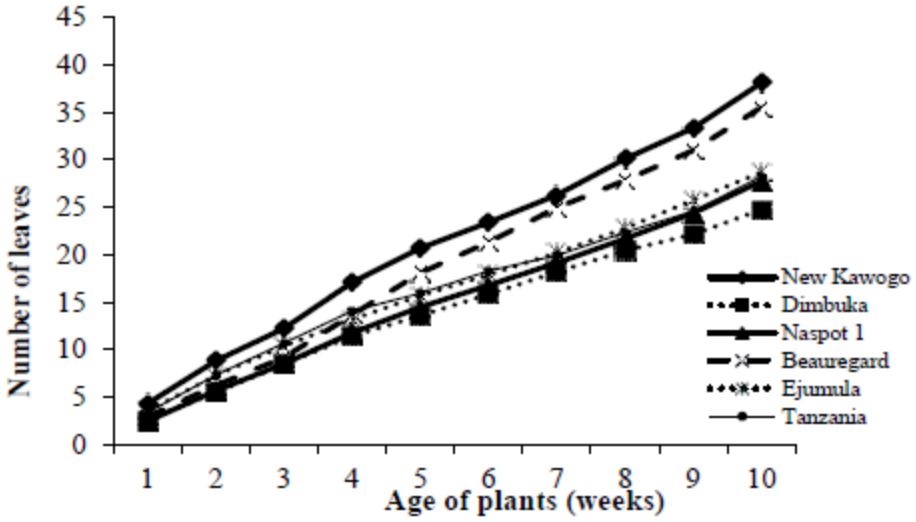

Figure 11. Variation of number of leaves among cultivars over time.

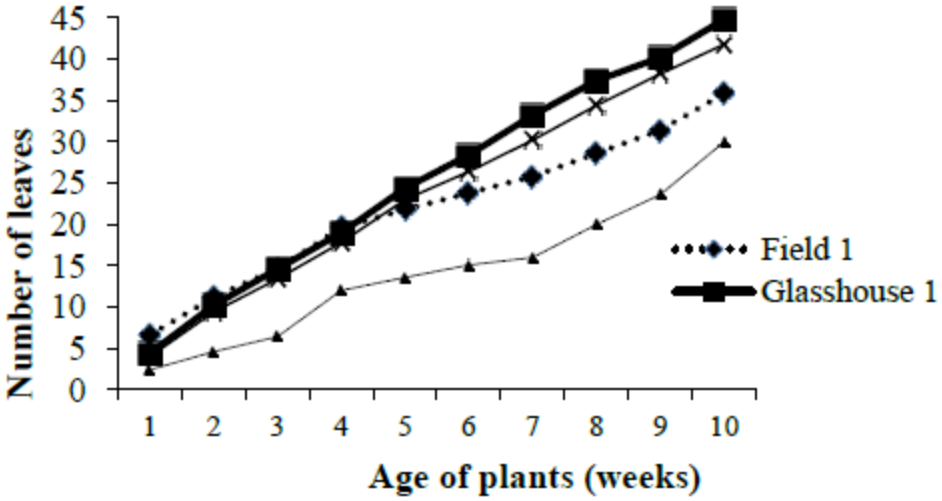

Figure 12. Variation of number of leaves of New Kawogo plants under the two environments.

Yield per plant (g)

There was a significant difference in mean yield of different environments ($p<0.001$) and different sweet-potato cultivars ($p<0.001$) (Table 7). In the case of environments and SPVD inoculations, the non-inoculated plants in the field yielded the highest (236.2 g/plant) followed by inoculated plants in the field (182.9 g/plant), non-inoculated plants in glasshouse (38.5 g/plant) and inoculated plants in the glasshouse yielded the lowest (36.6 g/plant). Across environments, New Kawogo was the best yielder (199.3 g/plant) followed by Tanzania (171.0 g/plant), Beauregard, Naspot 1, Dimbuka, and Ejumula (47.8 g/plant).

Table 7. Mean yield per plant for different cultivars under the two environments.

Cultivars	Environment				Mean	s.e.d	l.s.d	c.v %	F.pr.
	Field 1	GH 1	Field 2	GH 2					
New Kawogo	398.22	3.47	394.71	0.97	199.34a	0.150	0.318	0.1	<0.001
Dimbuka	147.00	68.18	109.27	15.68	85.03e	0.464	0.984	0.9	<0.001
Naspot 1	332.03	13.67	26.74	5.46	94.47d	0.183	0.388	0.3	<0.001
Beauregard	105.81	44.04	298.54	122.45	142.71c	0.193	0.408	0.2	<0.001
Ejumula	104.89	8.38	62.49	15.30	47.77f	0.173	0.366	0.6	<0.001
Tanzania	329.21	38.48[c]	205.55	59.77	171.92b	0.280	0.593	0.3	<0.001
Mean	**236.19[a]**	**38.48[c]**	**182.88[b]**	**36.60[d]**	**123.54**	**0.108**	**0.214**	**0.3**	**<0.001**
s.e.d	**0.383**	**0.155**	**0.170**	**0.155**	**0.132**	**0.264**			
l.s.d.(α =5%)	**0.791**	**0.320**	**0.350**	**0.320**	**0.262**		**0.523**		
c.v %	**0.3**	**0.7**	**0.1**	**0.7**	**0.3**			**0.3**	
F.pr.	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**				**<.001**

Values followed by the same letter are not significantly different at 5% level of significance. Field 1 = SPVD non-inoculated plants in field; Glasshouse (GH) 1 = SPVD non-inoculated plants in glasshouse; Field 2 = plants inoculated with SPVD viruses and grown in field; and Glasshouse (GH) 2 = plants inoculated with SPVD viruses and grown in glasshouse.

For non-inoculated plants in the field, New Kawogo was the best yielder (398.2 g/plant) followed by Naspot 1 (332.0 g/plant), Tanzania (329.2 g/plant), Dimbuka (147.0 g/plant), Beauregard and Ejumula (104.9 g/plant). In the glasshouse in absence of the disease, Tanzania was the best yielder (93.2 g/plant) followed by Dimbuka (68.2 g/plant), Beauregard (44.0 g/plant), Naspot 1, Ejumula, and New Kawogo (3.5 g/plant). In the case of inoculated plants in field, New Kawogo performed better than the rest (394.7 g/plant), followed by Beauregard, Tanzania, Dimbuka, Ejumula, and Naspot 1 (26.7 g/plant). However, Beauregard was the best yielder (122.5 g/plant) followed by Tanzania (59.8 g/plant), Dimbuka (15.7 g/plant), Ejumula, Naspot 1, and New Kawogo (1.0 g/plant), among inoculated plants in the glasshouse.

Yield performance was best in the field. Non-inoculated New Kawogo performed the best in the field and this performance was not significantly affected by inoculation with SPVD. However, the same cultivar's performance was the worst in glasshouse. Naspot 1 was the second high yielder in the field in absence of SPVD, followed by Tanzania, Dimbuka, Beauregard and Ejumula. In the glasshouse in absence of the disease, Tanzania performed the best followed by Dimbuka, Beauregard, Naspot 1, Ejumula, and the poorest yielder was New Kawogo. For SPVD inoculated plants in the field, New Kawogo performed the highest followed by Beauregard, Tanzania, Dimbuka, Ejumula, and Naspot 1. For inoculated plants under glasshouse, Beauregard performed the best followed by Tanzania, Dimbuka, Ejumula, Naspot 1, and the poorest performer was New Kawogo.

DISCUSSION

The lower severity of SPVD on inoculated plants in the glasshouse indicates that severity reduces at high temperature. Similarly, the higher severity of SPVD on inoculated plants in the field

indicates that severity increases at low temperature. Therefore, SPVD severity changes with a change in temperature. It also suggests that recovery tendencies of sweet potato from SPVD are more likely at higher temperatures. It also signals the potential for inability of SPCSV and / or SPFMV to reproduce, and this can lead to their elimination (Gasura and Mukasa, 2010; Gibson et al., 2014). It is however, probable that these two viruses are influenced differently by temperature. If this supposition is true, a prevailing temperature regime would significantly influence the level of disease that is expressed. A study into the effect of temperature on the roles of the individual viruses of SPVD needs to be undertaken.

Different sweet potato cultivars were differently affected by SPVD at different temperatures. This implies that different cultivars exhibit differential responses to the disease as temperatures vary and this could suit them to different agroecologies. This is very likely because agroecological zones differ in a number of climatic conditions, temperature inclusive. A very low severity of SPVD in some cultivars like New Kawogo and very high disease scores for Ejumula, Tanzania and Beauregard at both environments of the field and glasshouse confirms the existence of SPVD resistant and susceptible varieties. This is particularly in agreement with Gasura and Mukasa (2010)who reported that cv. New Kawogo was resistant to SPVD. However, observations from this study indicate that resistance or tolerance potential of sweet potato to the disease is heightened at higher temperatures. The difference in internode length between plants in the field and glasshouse, suggests that temperature has an effect in the rate of cell multiplication and expansion in the internodes, with a higher temperature increasing the process. This is because the two environments experienced different temperature ranges. SPVD was also observed to play a role in length of the internodes in that presence of the disease could have limited the rate of cell growth around the internodes. Cultivar wise, some cultivars having manifested longer internodes in the field where temperatures were always lower than in the glasshouse suggests differential agro-ecological adaptations. This implies that cv. New Kawogo does well at lower temperature agro-ecologies than these rest of the cultivars included in this study. However, the effect of SPVD on internode lengths was very conspicuous in most cultivars, for instance under same conditions of the field, the SPVD inoculated plants of cv. Ejumula produced shorter internodes than the non-inoculated plants.

High temperatures of the glasshouse caused the plants to grow taller than those in the field where there were low temperatures. SPVD also negatively affected the stem lengths of plants. This emphasizes that the disease causes dwarfing symptoms. This trend is similar as in the case of internode lengths which implies that tall cultivars also had long internodes. An example of such cultivars is Beauregard which had the longest internodes and stems. The cv. Ejumula had the lowest internode and stem length both in glasshouse and in the field. This implies that this cultivar is very severely affected by SPVD. It can be argued that SPVD in combination with high temperature conditions cause increased shooting tendency. This assertion is based on the observations in glasshouse; most clearly with cv. Ejumula in which SPVD inoculated plants consistently produced more shoots than the non-inoculated ones. The high shooting tendency

was also associated with dwarfing. For instance, whereas the longest plants were observed on cv. Beauregard, the highest number of shoots was recorded on cv. Ejumula.

High temperatures were observed to cause high vegetative growth at the expense of tuber yield. This is in agreement with the earlier observations by Wasswa (2010), Adikini et al. (2016)and Gibson et al. (2014)though most of these authors did not vary temperatures to wide ranges. Sweet potato infected with SPVD and grown under glasshouse conditions produce little or no tuber yield, and this observation concurs with that of Adikini et al. (2016). SPVD presence also influenced the number of leaves. Thus whereas the high temperatures of the glasshouse caused high vegetative growth, SPVD presence negatively affected the number of leaves per plant in all cultivars across environments. It is also evident that the vegetative growth response of different cultivars varies significantly at different environments. For the case of glasshouse conditions, cv. New Kawogo stood distinct from the rest of the cultivars in terms of very high leaf number however; this resulted into the lowest tuber yield. The cultivars having minimum leaf numbers produced a reasonable tuber yield under high temperatures of the glasshouse though in absence of SPVD. Such cultivars include Tanzania, Dimbuka and Beauregard. This suggests that different sweetpotato cultivars differently tolerate / resist temperature stresses. This tolerance or resistance has been based on tuber yielding ability because the East and Central African people grow this crop majorly for direct human food security (HarvestPlus, 2012). The development response of SPVD at temperatures higher than that in the glasshouse or lower than that in the field used in this study, is not yet well understood. This matter requires further investigation. A study on the effect of temperature on sweet potato virus load accumulation would help provide answers to this knowledge gap.

CONCLUSION

This study indicates that temperature influences the development of SPVD. Generally, as temperature increases SPVD development reduces, particularly with respect to symptom expression. Temperatures 20 to 29°C produce more disease severities than high temperatures of 30 to 39°C. Field conditions produce more disease severity than glasshouse conditions. SPVD also expresses differently among sweet potato cultivars at different temperatures. For instance, Ejumula is more severely affected by SPVD at high temperatures of the glasshouse than in the field whereas an opposite effect occurs with cv. Tanzania. New Kawogo followed by Dimbuka and Naspot 1 are more SPVD resistant, based on symptom expression, than the rest of the cultivars; Ejumula followed by Tanzania and Beauregard are the most SPVD susceptible according to this study.

Beauregard, Tanzania and Dimbuka are more tolerant to the disease when it comes to tuber yield across temperature levels of the glasshouse and field than the rest of the cultivars. New Kawogo grows more vegetatively under high temperatures but with negligible or no tuber yield. High temperatures generally cause increased vegetative growth at the expense of tuber yield. Under high temperature and the generally uniform growth conditions of the glasshouse, there exist differences in cultivar growth responses. For instance, cv. Beauregard plants grow the tallest with very limited

lateral shooting and relatively good tuber yield as compared to the rest of the cultivars. This suggests that some cultivars multiply better than other at high temperatures for delivery of vine cuttings to farmers. The development response of SPVD at a wider temperature range than that experienced during this experiment deserves further investigation. The results from this study suggest that reasonably high temperatures under a controlled environment should be incorporated in any sweet potato seed production system for possible elimination of SPVD. Further study into the effect of temperature on the SPVD is necessary.

CONFLICTS OF INTERESTS

The authors have not declared any conflict of interests.

REFERENCES

Adikini S, Mukasa SB, Mwanga ROM, Gibson RW (2016). Effects of sweet potato feathery mottle virus and sweet potato chlorotic stunt virus on the yield of sweet potato in Uganda. J. Phytopathol. 164(4):242-254.

Gasura E, Mukasa SB (2010). Prevalence and implications of sweetpotato recovery from sweet potato virus disease in Uganda. Afr. Crop Sci. J. 18(4).

Gibson RW, Wasswa P, Tufan HA (2014). The ability of cultivars of sweetpotato in East Africa to "revert" from Sweet potato feathery mottle virus infection. Virus Res. 186:130-134.

Crossref

HarvestPlus (2012). Disseminating Orange-Fleshed Sweet Potato: Findings from a HarvestPlus Project in Mozambique and Uganda. HarvestPlus, Washington DC.

Kpaka C, Gugerty M, Anderson C (2013). Sweet Potato Value Chain: Uganda. Evans School Policy analysis and Research (EPAR).

Mwanga RO, Kyalo G, Ssemakula GN, Niringiye C, Yada B, Otema MA (2016). NASPOT 12 O" and "NASPOT 13 O"Sweetpotato. HortScience 51(3):291-295.

Sabaghnia N, Karimizadeh R, Mohamadi M (2012). Genotype by environment interaction and stability analysis for grain yield of lentil genotypes. Žemdirbystė=Agriculture 99(3):305-312.

Sanginga N, Mbabu A (2015). Root and tuber crops (cassava, yam, potato and sweet potato). African Development Bank Group.

Seidl JAC, Jordan SA, Gevens AJ (2014). Novel Resistance in Heirloom Tomatoes and Effectiveness of Resistance in Hybrids to Phytophthora infestans US-22, US-23, and US-24 Clonal Lineages. Plant Dis. 98(6):761-765.

Wasswa P (2010). Optimization of in vitro techniques for cassava brown streak virus elimination from infected cassava clones in Uganda. Makerere University, Kampala.

Wasswa P (2012). Sweet potato viruses in Uganda: identification of a new virus, a mild strain of an old virus and reversion. National Resources Institute University of Greenwich, United Kingdom.