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Potato Yield and Yield Components as Affected by Positive Selection During Several Generations of Seed Multiplication in Southwestern Uganda

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Abstract

Potato (*Solanum tuberosum* L.) is an important crop in Uganda but production is low. There is not a well-functioning official seed system and farmers use potato tubers from a previous harvest as seed. This study investigated how effectively the seed technology positive selection enhanced yield and underlying crop characteristics across multiple seasons, compared to the farmers' selection method. Positive selection is selecting healthy plants during crop growth for harvesting seed potato tubers to be planted in the next season. Farmers' selection involves selection of seed tubers from the bulk of the ware potato harvest. Positive selection was compared to farmers' seed selection for up to three seasons in three field trials in different locations in southwestern Uganda using seed lots from different origins. Across all experiments, seasons and seed lots, yields were higher under positive selection than under farmers' selection. The average yield increase resulting from positive selection was 12%, but yield increases were variable, ranging from -5.7% to $+36.9\%$, and in the individual experiments often not significant. These yield increases were due to higher yields per plant, and mostly higher weights per tuber, whereas the numbers of tubers per plant were not significantly different. Experimentation and yield assessment were hampered by a varying number of plants that could not be harvested because plants had to be rogued from the experimental plots because of bacterial wilt (more frequent under farmers' selection than under positive selection), plants disappeared from the experimental field and sometimes plants did not emerge. Nevertheless, adoption of positive selection should be encouraged due to a higher production and less virus infection of seed tubers in positive selected plants, resulting in a lower degeneration rate of potato seed tubers.

Keywords Multi-seasonal trials · Positive selection · Seed degeneration · Seed potatoes · Seed regeneration · Uganda · Yield increase

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Introduction

Potato (*Solanum tuberosum* L.) is one of the main staple crops for food and nutrition security in Uganda (Whitney et al. 2017), where it serves also as a cash crop for smallholder farmers (Gildemacher et al. 2009; Olanya et al. 2012). While Uganda has a large potato production area, average yields with 4.2 Mg ha⁻¹ are lower than in other East-African countries (FAO 2019) and far below the attainable yield of 25 Mg ha⁻¹ (International Potato Center 2011). One of the most important yield-defining factors in potato production is the quality of the seed tubers planted (Struik and Wiersema 1999; Haverkort and Struik 2015). Smallholder farmers in Uganda generally plant tubers from an informal source, like their own harvest, the market or a neighbour (Gildemacher et al. 2009). Tubers for seed are mostly taken from the bulk of the ware potato harvest and selected based on size and visual inspection. This method is further referred to as “farmers’ selection” or FS. These successively cycled seed tubers are often highly degenerated due to accumulation of tuber-borne pests and diseases (especially viruses and bacteria), resulting in poor yield and poor quality of the harvest (Turkensteen 1987; Salazar 1996; Struik and Wiersema 1999; Thomas-Sharma et al. 2016).

Due to the lack of a well-functioning formal seed system for purchasing high-quality and healthy seed tubers, Ugandan farmers have the following options to overcome poor seed quality. Farmers can buy quality-declared seed tubers from the Ugandan National Seed Potato Association (UNSPPA) (International Potato Center 2011). However, the availability of these tubers often does not meet the high demand (CTA 2014; Kakuhenzire et al. 2015). Moreover, many smallholder farmers cannot afford to buy these tubers. An option for improving seed tuber quality is the technique of positive selection whereby the most healthy-looking plants in a ware potato field are identified and pegged during flowering and checked for health thereafter. The tubers harvested from these most healthy-looking plants serve as seed tubers in the following growing season. With this technique the most healthy tubers are selected and a decrease in seed-borne pests and diseases can be realized (Gildemacher et al. 2011; Schulte-Geldermann et al. 2012; Okeyo et al. 2018). Another option is using the seed plot technique,¹ which seems appropriate for farmers who have a surplus of land to reserve it for improving their seed potatoes (Kakuhenzire et al. 2005; Kinyua et al. 2015). In a previous paper on the experiments described in the present paper, we confirmed that positive selection, when applied during multiple seasons (and thus for several generations of seed multiplication), could reduce the virus level in the seed potatoes compared to when applying farmers’ selection (Priegnitz et al. 2019b).

Positive selection in ware crops during one cropping cycle results in an overall yield increase of 28% (Gildemacher et al. 2011), 30% (Schulte-Geldermann et al. 2012) or 37% (Siddique et al. 2017) compared to farmers’ selection. This present study is related to the published paper by Priegnitz et al. (2019b), where in the same experiments the virus incidences were compared in seed lots from different origins and resulting from different seed selection treatments across multiple

¹ In the seed plot technology, a separate plot of potatoes is grown by the farmer for production of seed tubers. Positive selection is applied within this plot and tubers from the selected plants are used to produce the next-season seed plot, while the remaining tubers are used to grow the ware crop.

seasons. This present study focuses on the yield and yield components of those experiments and can be considered as the second part of the results of those experiments.

The objective of this study was to assess if positive selection during multiple seasons leads to an improvement in yield compared with farmers' selection and which yield components underlie this yield increase. Different sources of seed potatoes, potato cultivars and locations were included in the study which was carried out in Kabale district in southwestern Uganda, which is the most important potato cropping region of Uganda (Bonabana-Wabbi et al. 2013).

Material and Methods

Experimental Design and Starting Material

In Kabale district, the main potato production region of Uganda, three field experiments were conducted at three locations across four production seasons. The experiments had a split-plot design with three replicated blocks and with the seed potato lot as main factor and seed selection treatment as sub-factor. Relevant information of all experiments and locations is presented in Table 1. For more information please refer to Table 1 in Priegnitz et al. (2019b, Table 1). Key aspects in all experiments were that four seed selection treatments were applied: (1) positive selection (PS) in all seasons (referred to as PS-PS-PS), (2) alternating seed selection in the seasons starting with positive selection in the 1st season and followed by farmers' selection (referred to as PS-FS-PS), (3) alternating seed selection in the seasons starting with farmers' selection in the 1st season (referred to as FS-PS-FS) and (4) farmers' selection (FS) in all seasons (referred to as FS-FS-FS). In the 4th season, plants were selected according to treatment, but without replanting the produced tubers in the next season. Consequently, the selection treatment carried out in the 4th season is not reflected in the experimental code because this treatment did not influence yield and underlying components of the crop in which it was carried out.

Per experimental plot, 60 tubers were planted in 6 rows at a spacing of 70 cm between rows and 30 cm within rows; for the net plot the border plants in the outer rows were excluded, so 40 plants were used for assessment. In the PS treatments, 15 healthy-looking plants per plot were selected during crop growth and harvested separately; this accounts for plants from 37.5% of all seed tubers planted in the net plot. Seed tuber selection was done by farmers by selecting medium-sized seed tubers from these PS plants after storage at planting time. Under the local conditions, the harvest of 15 plants was needed to achieve enough medium-sized seed tubers for the next planting season. In the FS plots, plants were not selected during crop growth, but medium-sized seed tubers were selected by farmers at planting time from the stored tuber bulk of the former harvest. In a few cases in the 3rd and 4th season, there were not enough medium-sized seed potatoes and smaller-sized seed potatoes had to be planted in some plots (Table 1). For each of the four selection treatments, tubers from the replicated plots were combined before selecting the seed tubers.

Table 1 Information on the three experimental sites in Kabale district (adjusted from Priegnitz et al. (2019b), Table 1)

	Experiment 1	Experiment 2	Experiment 3
Location	Karengyere	Kachwekano	Hamurwa
Elevation	2433 m asl	2246 m asl	2220 m asl
Fertilization	45 kg N/ha	45 kg N/ha	45 kg N/ha
Seed lots (seed source and cultivar)	3G KAZARDI/cv. Victoria 3G KAZARDI/cv. Katchpot 1	3G KAZARDI/cv. Victoria 3G KAZARDI/cv. Katchpot 1	4G UNSPPA/cv. Victoria Local market/cv. Victoria 5G farm-saved/cv. Rwangume
Selection treatments	PS-PS-PS PS-FS-PS FS-PS-FS FS-FS-FS	PS-PS-PS PS-FS-PS FS-PS-FS FS-FS-FS	PS-PS-PS PS-FS-PS FS-PS-FS FS-FS-FS
Storage (all seasons)	DLS on wooden shelves	Wooden shed (dark) on wooden shelves	DLS on wooden shelves
Selection of seed tubers	Before planting	Before planting	Before planting
1st season: 2013—LRS			
Planting date	03 October 2013	04 October 2013	05 October 2013
Seed tuber size ^a	Medium	Medium	Medium
Total rainfall in the growing period (mm)	83.5 (excl. 2013)	107.4	Not available
Haulm destruction date	21 January 2014 (110 DAP)	23 January 2014 (111 DAP)	21 January 2014 (108 DAP)
Harvest date	29 January 2014 (118 DAP)	30 January 2014 (118 DAP)	31 January 2014 (118 DAP)
2nd season: 2014—SRS			
Planting date	07 April 2014 (69 DAH)	06 April 2014 (67 DAH)	08 April 2014 (68 DAH)
Seed tuber size ^a	Medium	Medium	Medium
Total rainfall in the growing period (mm)	183.6	61.2	Not available
Haulm destruction date	17 July 2014 (100 DAP)	19 July 2014 (103 DAP)	21 July 2014 (103 DAP)
Harvest date	28 July 2014 (111 DAP)	29 July 2014 (113 DAP)	30 July 2014 (112 DAP)
3rd season: 2014—LRS			
Planting date	10 October 2014 (75 DAH)	09 October 2014 (73 DAH)	11 October 2014 (74 DAH)
Seed tuber size ^a	Cv. Victoria: medium Cv. Katchpot 1: small for one plot of PS-FS-PS and FS-PS-FS, and mix of small and medium in PS-PS-PS; otherwise, medium	Cv. Victoria: medium Cv. Katchpot 1: small size for one plot of PS-PS-PS, FS-PS-FS and FS-FS-FS; otherwise, medium	4G UNSPPA/ cv. Victoria: small size for one plot of PS-PS-PS and FS-PS-FS; otherwise, medium Local market/ cv. Victoria: mix of small and medium in one plot of PS-PS-PS and FS-PS-FS; otherwise, medium 5G farm-saved seed/ cv. Rwangume: mix of small and medium in one plot of PS-PS-PS, and small in one plot of PS-PS-PS and FS-PS-FS; otherwise, medium
Total rainfall in the growing period (mm)	250.4	197.5	Not available

Table 1 (continued)

	Experiment 1	Experiment 2	Experiment 3
Haulm destruction date	28 January 2015 (110 DAP)	27 January 2015 (110 DAP)	26 January 2015(107 DAP)
Harvest date	03February 2015 (116 DAP)	02 February 2015 (116 DAP)	04 February 2015 (116 DAP)
4th season: 2015—SRS			
Planting date	16 April 2015 (73 DAH)	14 April 2015 (72 DAH)	15 April 2015 (71 DAH)
Seed tuber size ^a	Cv. Victoria: small for one plot of PS-PS-PS; otherwise, medium Cv. Katchpot 1: small for one plot of PS-FS-PS; otherwise, medium	Cv. Victoria: small for one plot of PS-PS-PS, PS-FS-PS and FS-FS-FS each; otherwise, medium Cv. Katchpot 1: mix of small and medium in one plot of PS-PS-PS, and small in one plot of PS-FS-PS; otherwise, medium	Medium
Total rainfall in the growing period (mm)	227.8	156.2	Not available
Haulm destruction date	21 July 2015 (96 DAP)	23 July 2015 (100 DAP)	23 July 2015 (99 DAP)
Harvest date	04 July 2015 (110 DAP)	06 August 2015 (114 DAP)	07 August 2015 (114 DAP)

DAH days after harvest, DAP days after planting, DLS diffuse light storage, LRS long rainy season, FS farmers' selection, PS positive selection, SRS short rainy season

^a Medium size, 30–60 mm; small size, 5–30 mm; the selection treatment in italics refers to the planted seed

Haulm Removal, Tuber Harvest and Tuber Storage

The haulm was manually removed between 96 and 111 days after planting (DAP) and tubers were harvested between 111 and 118 DAP (Table 1).

In the net plots receiving FS in a given season, tubers were harvested from all plants to determine tuber yield; in the plots receiving PS, tubers from the non-selected and the selected plants were harvested separately but the yields of the two fractions were summed to derive the yield per plot. During storage, the individual replicates of one treatment were combined and stored separately from the tubers of the other treatments.

Tubers were stored on wooden shelves either in a dark wooden shed (Experiment 2) or in a diffused light store (Experiments 1 and 3); the layer of tubers was sprinkled with insecticide a.i. Malathion 57% and covered with kikuyu grass (*Pennisetum clandestinum*) and couch grass (*Digitaria abyssinica*). Storage duration of the tubers until planting was between 67 and 75 days (Table 1).

Weather Data

Daily weather data can be found in Priegnitz et al. (2019b). For Experiment 2, weather data were derived from the internet platform [awhere \(awhere.com\)](http://awhere.com); for Experiment 1, rain data were manually recorded at the KAZARDI station in Karengyere. No reliable weather data were available for Experiment 3.

Measurement of Agronomic Characteristics

Plant Numbers

The *number of emerged plants* in the net plot was recorded 35–36 DAP in the 1st season (2013–LRS), and during leaf sampling (24–30 DAP) in the 2nd, 3rd and 4th season (2014–SRS, 2014–LRS, 2015–SRS; Priegnitz et al. 2019b). The purpose of leaf sampling was to check for virus infection of the seed tubers. Details on infection by individual viruses in those seed tubers can be found in Priegnitz et al. (2019b). Plant *establishment* (especially to assess if no unaccounted loss appeared) was checked during PS pegging time (63–73 DAP). Plots were also inspected for bacterial wilt (*Ralstonia solanacearum*) every 10 days, and when infected, plants (including their tubers) were removed and their number was counted (*rogued plants*). At harvest, the *numbers of harvested plants* were recorded. In some cases, the number of plants at harvest was lower than the number of emerged plants minus the rogued plants, which might be attributed to thefts from the field. We defined these missing plants as “*unaccounted loss*”. In Tables 2, 3 and 4 the numbers of *plants emerged, rogued, lost and harvested* are presented as the actual plant number and as percentage of the original number of seed tubers (planting positions) planted. In Table 5 and Fig. 1, numbers of plants are presented as percentage.

Number of Tubers, Tuber Yield, Number of Stems and Ground Cover

To establish number and yield of tubers resulting from the selection treatments in the previous year(s), data of all plants per net plot (including selected and non-selected plants in PS plots) were considered. At harvest, each plant was harvested separately and for each plant the total number of tubers was recorded. The average *number of tubers per harvested plant* in the net plot was derived from the sum of the individually harvested plants divided by the number of the harvested plants. The harvested *number of tubers per square metre* was derived from the total number of tubers harvested per plot divided by the plot area. The *weight per individual tuber* was the total tuber fresh weight in the net plot divided by the total number of harvested tubers in the plot. The average *yield per plant* was calculated by dividing the total tuber fresh yield per plot by the number of harvested plants in the plot. The *total tuber fresh yield* was the total tuber fresh yield per plot recalculated into $Mg\ ha^{-1}$ from the planted area of the plot. Tubers of each plot were graded into *three size categories*: large (> 60 mm), medium (30–60 mm) and small (5–30 mm) and the weight in each category was assessed.

Canopy development in all plots was measured as *ground cover (%)* every 10 days and estimated by using a wooden frame of 0.70 m × 0.90 m divided into 100 equal units (which equals 100%); if one unit was filled more than half with green foliage it was counted as one percentage. The values presented represent the maximum ground cover (Supplementary Material Table 2A–4A). Main stems which emerged directly from the seed tuber were counted to assess *the number of stems* per plant.

Table 2 Effects of selection treatments, seasons and seed lots on agronomical characteristics in location Karengyere, Experiment 1 (selection treatment in *italics* refers to the seed planted in the specific season)

Treatment	Emergence	Rogued plants	Unaccounted plant loss	Harvested plants	Tubers per plant	Tubers per m ²	Weight per tuber (g)	Yield per plant (kg)	Tuber yield (Mg/ha)	
Relative change	%	%	%	%	%	%	%	%	%	
2nd season: 2014—SRS										
3G(ev. Victoria										
<i>PS-PS-PS</i>	100.0 (120/120)	+2.5 0.0 (0/120)	- 2.5 (3/120)	-1.6 97.5 (117/120)	+0.8 6.2	+10.7 28.9	+14.2 49.0	-8.1 0.304	+4.8 14.2	+7.5
<i>PS-FS-PS</i>	97.5 (117/120)	0.0 0.0 (0/120)	- 1.7 (2/120)	-0.8 95.8 (115/120)	-0.8 7.0	+25.0 32.1	+26.8 45.6	-14.4 0.318	+9.6 14.5	+9.8
<i>FS-PS-FS</i>	97.5 (117/120)	0.0 0.0 (0/120)	- 0.8 (1/120)	0.0 96.6 (116/120)	0.0 5.2	-7.1 24.1	-4.7 53.1	-0.4 0.274	-5.5 12.7	-3.7
<i>FS-FS-FS</i>	97.5 (117/120)	0.0 (0/120)	0.8 (1/120)	96.7 (116/120)	5.6	25.3	53.3	0.290	13.2	
3G(ev. Katchpot 1										
<i>PS-PS-PS</i>	75.0 (90/120)	+2.3 0.0 (0/120)	- 0.0 (0/120)	0.0 75.0 (90/120)	+2.2 4.8	+4.3 17.0	+6.9 67.7	+26.8 0.315	+26.0 11.2	+30.2
<i>PS-FS-PS</i>	68.3 (82/120)	-6.8 0.0 (0/120)	- 0.0 (0/120)	0.0 68.3 (82/120)	-6.8 3.9	-15.2 12.9	-18.8 61.9	+15.9 0.245	+2.0 8.1	-5.8
<i>FS-PS-FS</i>	81.7 (98/120)	+11.4 0.0 (0/120)	- 1.7 (2/120)	-1.6 80.0 (96/120)	+9.1 4.9	+6.5 18.9	+18.9 65.9	+23.4 0.320	+28.0 12.2	+41.8
<i>FS-FS-FS</i>	73.3 (88/120)	0.0 (0/120)	0.0 (0/120)	73.3 (88/120)	4.6	15.9	53.4	0.250	8.6	
3rd season: 2014—LRS										
3G(ev. Victoria										
<i>PS-PS-PS</i>	99.2 (119/120)	+3.4 0.0 (0/120)	- 9.2 (11/120)	-6.3 90.0 (108/120)	-2.7 5.3	+8.1 22.9	+5.5 79.4	-3.7 0.425	+3.4 18.3	+2.2
<i>PS-FS-PS</i>	98.3 (118/120)	+2.6 0.0 (0/120)	- 10.8 (13/120)	-7.7 87.5 (105/120)	-5.4 5.3	+8.1 22.3	+2.7 85.7	+3.8 0.460	+11.9 19.3	+7.8
<i>FS-PS-FS</i>	96.7 (116/120)	+0.8 0.0 (0/120)	- 10.0 (12/120)	-6.8 86.7 (104/120)	-6.3 5.4	+10.2 22.2	+2.3 91.2	+10.5 0.494	+20.1 20.3	+13.4
<i>FS-FS-FS</i>	95.8 (115/120)	0.0 (0/120)	3.3 (4/120)	92.5 (111/120)	4.9	21.7	82.5	0.411	17.9	
3G(ev. Katchpot 1										
<i>PS-PS-PS</i>	95.8 (115/120)	+1.7 0.0 (0/120)	- 0.0 (0/120)	0.0 95.8 (115/120)	+1.7 6.1	+3.4 27.9	+4.1 91.8	+0.5 0.554	+1.6 25.4	+4.1
<i>PS-FS-PS</i>	87.5 (105/120)	-7.1 0.0 (0/120)	- 0.0 (0/120)	0.0 87.5 (105/120)	-7.1 5.7	-3.4 24.0	-10.4 74.5	-18.4 0.413	-24.2 17.4	-28.7
<i>FS-PS-FS</i>	93.3 (112/120)	-0.8 0.0 (0/120)	- 0.0 (0/120)	0.0 93.3 (112/120)	-0.8 5.4	-8.4 24.2	-9.7 101.4	+11.1 0.527	-3.3 23.4	-4.1
<i>FS-FS-FS</i>	94.2 (113/120)	0.0 (0/120)	0.0 (0/120)	94.2 (113/120)	5.9	26.8	91.3	0.545	24.4	
4th season: 2015—SRS										
3G(ev. Victoria										
<i>PS-PS-PS</i>	91.7 (110/120)	-3.5 0.0 (0/120)	- 9.2 (11/120)	-8.4 82.5 (99/120)	-12.3 5.1	+6.2 20.1	-7.3 98.6	+12.9 0.494	+15.2 19.3	+0.5

Table 2 (continued)

Treatment	Emergence	Rogued plants	Unaccounted plant loss	Harvested plants	Tubers per plant	Tubers per m ²	Weight per tuber (g)	Yield per plant (kg)	Tuber yield (Mg/ha)
Relative change	%	%	%	%	%	%	%	%	%
FS-FS-FS	97.5 (117/120)	+2.6 0.0 (0/120)	- 0.0 (0/120)	+0.8 97.5 (117/120)	+3.5 5.3	+10.4 24.6	+13.3 95.7	+9.6 0.509	+18.6 23.7
FS-PS-FS	97.5 (117/120)	+2.6 0.0 (0/120)	- 1.7 (2/120)	-0.8 95.8 (115/120)	+1.7 4.8	0.0 21.8	+0.5 90.1	+3.2 0.435	+1.3 19.8
FS-FS-FS	95.0 (114/120)	0.0 (0/120)	0.8 (1/120)	94.2 (113/120)	4.8	21.7	87.3	0.429	19.2
3G/cv. Katchipot 1									
PS-PS-FS	90.0 (108/120)	-0.9 0.0 (0/120)	- 4.2 (5/120)	-3.4 85.8 (103/120)	-4.6 5.7	-16.2 23.1	-20.6 104.8	+20.8 0.696	+18.9 24.3
PS-FS-FS	73.3 (88/120)	-19.2 0.0 (0/120)	- 0.0 (0/120)	+0.8 73.3 (88/120)	-18.5 6.8	0.0 23.7	-18.5 88.0	+1.5 0.598	+2.2 20.8
FS-PS-FS	93.3 (112/120)	+2.7 0.0 (0/120)	- 0.0 (0/120)	+0.8 93.3 (112/120)	+3.7 6.7	-1.5 29.9	+2.7 84.7	+2.3 0.567	-3.1 25.2
FS-FS-FS	90.8 (109/120)	0.0 (0/120)	0.8 (1/120)	90.0 (108/120)	6.8	29.1	86.7	0.585	25.1
<i>P</i> values									
Selection Treatment (ST)	0.047	-	ns	ns	ns	ns	ns	ns	ns
Seed Lot (SL)	<0.001	-	0.003	<0.001	ns	ns	ns	ns	ns
Season (S)	ns	-	ns	ns	ns	ns	<0.001	0.002	0.004
ST × SL	ns	-	ns	ns	ns	0.005	ns	0.028	<0.001
ST × S	ns	-	ns	ns	ns	ns	ns	ns	ns
SL × S	0.001	-	0.027	<0.001	0.009	<0.001	ns	ns	ns
ST × SL × S	ns	-	ns	ns	ns	ns	ns	ns	ns

Emergence (%): plant number emerged/tuber number planted; Rogued plants because of bacterial wilt (%); plant number removed/tuber number planted; Unaccounted plant loss (%) missing number of plants/tuber number planted; Harvested plants (%): plant number harvested/tuber number planted; Tubers per plant (# per harvested plant): Tuber number per m²; # m⁻² planted area; Weight per tuber: g/tuber; Yield per plant: kg tuber fresh weight/harvested plant = plant number; Yield: Mg ha⁻¹ planted area,

PS positive selection FS farmers selection, ns non-significant, P ≥ 0.05

“-” indicates P value could not be obtained because of 0%

Table 3 Effects of selection treatments, seasons and seed lots on agronomical characteristics in location Kachwekano, Experiment 2 (selection treatment in *italics* refers to the seed planted in the specific season)

Treatment	Emergence		Rogued plants		Unaccounted plant loss		Harvested plants		Tubers per plant		Tubers per m ²		Weight per tuber (g)		Yield per plant (kg)		Tuber yield (Mg/ha)		
	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%	
2nd season: 2014—SRS																			
3G/ev. Victoria																			
<i>PS-PS-PS</i>	99.2 (119/120)	+ 3.4	1.7 (2/120)	- 7.2	0.0 (0/120)	- 1.7	97.5 (117/120)	+ 13.6	6.3	+ 6.7	29.2	+ 20.6	51.8	- 5.6	0.325	+ 0.6	15.1	+ 14.3	
<i>PS-FS-PS</i>	99.2 (119/120)	+ 3.4	0.8 (1/120)	- 8.2	0.8 (1/120)	- 0.8	97.5 (117/120)	+ 13.6	7.1	+ 20.3	33.2	+ 37.2	45.9	- 16.4	0.326	+ 0.9	15.2	+ 15.1	
<i>FS-PS-FS</i>	94.2 (113/120)	- 1.7	8.8 (10/120)	0.0	0.0 (0/120)	- 1.7	85.8 (103/120)	0.0	6.1	+ 3.4	24.8	+ 2.5	61.0	+ 11.1	0.371	+ 14.8	15.1	+ 14.3	
<i>FS-FS-FS</i>	95.8 (115/120)		8.7 (10/120)		1.7 (2/120)		85.8 (103/120)		5.9		24.2		54.9		0.323		13.2		
3G/ev. Katchipot 1																			
<i>PS-PS-PS</i>	80.8 (97/120)	+ 21.2	1.1 (1/120)	+ 0.8	0.8 (1/120)	+ 0.8	79.2 (95/120)	+ 18.7	5.7	+ 16.3	21.5	+ 36.1	45.9	- 3.7	0.262	+ 11.5	9.9	+ 32.0	
<i>PS-FS-PS</i>	82.5 (99/120)	+ 23.7	0.0 (0/120)	0.0	3.3 (3/120)	+ 2.5	79.2 (95/120)	+ 18.7	6.2	+ 26.5	23.4	+ 48.1	51.8	+ 8.5	0.323	+ 37.4	12.2	+ 62.7	
<i>FS-PS-FS</i>	67.5 (81/120)	+ 1.2	0.0 (0/120)	0.0	0.0 (0/120)	0.0	67.5 (81/120)	+ 1.2	4.7	- 4.1	14.9	- 5.7	63.8	+ 33.7	0.310	+ 31.9	9.6	+ 28.0	
<i>FS-FS-FS</i>	66.7 (80/120)		0.0 (0/120)		0.0 (0/120)		66.7 (80/120)		4.9		15.8		47.7		0.235		7.5		
3rd season: 2014—LRS																			
3G/ev. Victoria																			
<i>PS-PS-PS</i>	100.0 (120/120)	+ 2.5	4.2 (5/120)	0.0	5.0 (6/120)	- 0.8	90.8 (109/120)	+ 3.8	4.9	+ 13.9	21.3	+ 17.7	70.9	+ 14.7	0.353	+ 32.7	15.2	+ 36.9	
<i>PS-FS-PS</i>	98.3 (118/120)	+ 0.8	2.5 (3/120)	- 1.7	0.0 (0/120)	- 6.1	95.5 (115/120)	+ 9.5	4.8	+ 11.6	21.8	+ 20.4	71.0	+ 14.8	0.339	+ 27.4	15.5	+ 39.6	
<i>FS-PS-FS</i>	99.2 (119/120)	+ 1.7	8.4 (10/120)	+ 4.3	5.0 (6/120)	- 0.8	85.8 (103/120)	- 1.9	4.9	+ 13.9	20.2	+ 11.6	68.8	+ 11.3	0.336	+ 26.3	13.8	+ 24.3	
<i>FS-FS-FS</i>	97.5 (117/120)		4.2 (5/120)		5.8 (7/120)		87.5 (105/40)		4.3		18.1		61.8		0.266		11.1		
3G/ev. Katchipot 1																			
<i>PS-PS-PS</i>	93.3 (112/120)	+ 10.9	0.0 (0/120)	- 1.6	0.0 (0/120)	0.0	93.3 (112/120)	+ 13.1	4.9	- 3.9	22.0	+ 10.0	77.8	+ 4.4	0.383	+ 2.4	16.9	+ 14.2	
<i>PS-FS-PS</i>	95.8 (115/120)	+ 13.8	2.5 (3/120)	+ 0.8	0.0 (0/120)	0.0	93.3 (112/120)	+ 13.1	5.2	+ 1.9	23.3	+ 16.5	63.2	- 15.2	0.328	- 12.3	14.6	- 1.3	
<i>FS-PS-FS</i>	90.8 (109/120)	+ 7.9	2.7 (3/120)	+ 0.8	0.0 (0/120)	0.0	88.3 (106/120)	+ 7.1	4.6	- 9.8	19.5	- 2.5	75.5	+ 1.3	0.342	- 8.5	14.4	- 2.7	
<i>FS-FS-FS</i>	84.2 (101/120)		1.9 (2/120)		0.0 (0/120)		82.5 (99/120)		5.1		20.0		74.5		0.374		14.8		

Table 3 (continued)

Treatment	Emergence	Rogued plants	Unaccounted plant loss	Harvested plants	Tubers per plant	Tubers per m ²	Tubers per tuber (g)	Yield per plant (kg)	Tuber yield (Mg/ha)										
Relative change	%	%	%	%	%	%	%	%	%										
4th season: 2015—SRS																			
3G/cv. Victoria																			
PS-PS-PS	99.2 (119/120)	+5.3	1.7 (2/120)	-13.4	0.0 (0/120)	0.0	97.5 (117/120)	+20.6	4.6	-2.1	21.4	+15.7	88.9	+12.8	0.398	+7.2	18.5	+29.3	
PS-FS-PS	98.3 (118/120)	+4.4	10.9 (13/120)	-2.9	0.0 (0/120)	0.0	87.5 (105/120)	+8.2	4.4	-6.4	18.6	+0.5	90.1	+14.3	0.390	+5.1	16.4	+14.7	
FS-PS-FS	97.5 (117/120)	+3.5	4.3 (5/120)	-10.5	0.0 (0/120)	0.0	93.3 (112/120)	+15.4	5.4	+14.8	23.9	+29.2	70.2	-10.9	0.376	+1.3	16.7	+16.7	
FS-FS-FS	94.2 (113/120)		14.1 (16/120)		0.0 (0/120)		80.8 (97/120)		4.7		18.5		78.8		0.371		14.3		
3G/cv. Katchpot 1																			
PS-PS-PS	68.3 (82/120)	-4.6	1.7 (2/120)	-0.8	0.0 (0/120)	0.0	66.7 (80/120)	-3.6	5.7	-9.5	18.5	-11.4	62.0	+26.2	0.345	+11.3	10.9	+6.8	
PS-FS-PS	79.2 (95/120)	+10.4	0.0 (0/120)	-2.5	0.0 (0/120)	0.0	79.2 (95/120)	+14.4	5.9	-6.3	22.6	+8.1	61.5	+25.2	0.366	+18.1	14.0	+37.2	
FS-PS-FS	70.0 (84/120)	-2.3	1.7 (2/120)	-0.8	0.0 (0/120)	0.0	68.3 (82/120)	-1.2	6.5	+3.1	21.0	+0.5	56.3	+14.6	0.359	+15.8	11.7	+14.7	
FS-FS-FS	71.7 (86/120)		2.5 (3/120)		0.0 (0/120)		69.2 (83/120)		6.3		20.9		49.1		0.310		10.2		
<i>P</i> values																			
Selection Treatment (ST)	<0.001	0.014	ns	<0.001	ns	0.002	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	<0.001
Seed Lot (SL)	<0.001	<0.001	0.043	<0.001	ns	0.033	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	<0.001
Season (S)	0.015	ns	ns	0.032	ns	ns	0.009	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
ST × SL	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
ST × S	ns	ns	ns	ns	ns	0.028	ns	0.012	0.004	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
SL × S	ns	ns	0.022	0.003	0.035	0.010	0.016	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	0.044
ST × SL × S	ns	0.020	ns	0.043	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

Emergence (%): plant number emerged/tuber number planted; Rogued plants because of bacterial wilt (%): plant number removed/tuber number planted; Unaccounted plant loss (%): missing number of plants/tuber number planted; Harvested plants (%): plant number harvested/tuber number planted; Tubers per plant: # per harvested plant; Tuber number per m²: # m⁻² planted area; Weight per tuber: g/tuber; Yield per plant: kg tuber fresh weight/harvested plant = plant number; Yield: Mg ha⁻¹ planted area
 PS positive selection, FS farmers selection, ns non-significant, P ≥ 0.05
 “.” indicates P value could not be obtained because of 0%

Table 4 Effects of selection treatments, seasons and seed lots on agronomical characteristics in location Hawurma, Experiment 3 (selection treatment in *italics* refers to the seed planted in the specific season)

Treatment	Emergence		Rogued plants		Unaccounted plant loss		Harvested plants		Tubers per plant		Tubers per m ²		Weight per tuber (g)		Yield per plant (kg)		Tuber yield (Mg/ha)		
	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%	
2nd season: 2014—SRS																			
4G UNSPPA/cv. Victoria																			
<i>PS-PS-PS</i>	94.2 (113/120)	-1.7	5.4 (6/120)	0.0	0.0 (0/120)	-2.5	89.2 (107/120)	+0.9	9.0	+1.9	38.7	+16.6	30.5	-12.1	0.259	+0.7	11.1	+1.8	
<i>PS-FS-PS</i>	92.5 (111/120)	-3.4	5.4 (6/120)	0.0	5.0 (6/120)	-2.5	82.5 (99/120)	-6.6	8.0	+1.2	31.4	-5.4	34.8	+0.28	0.253	-1.5	9.9	-9.2	
<i>PS-PS-FS</i>	93.3 (112/120)	-2.6	4.3 (5/120)	-0.8	6.7 (8/120)	-4.2	82.5 (99/120)	-6.6	8.6	+8.8	33.7	+1.5	32.3	-6.9	0.249	-3.1	9.7	-11.0	
<i>FS-PS-FS</i>	95.8 (115/120)		5.2 (6/120)		2.5 (3/120)		88.3 (106/120)		7.9		33.2		34.7		0.257		10.9		
Market/cv. Victoria																			
<i>PS-PS-PS</i>	95.0 (114/120)	-3.4	4.5 (5/120)	-2.7	0.0 (0/120)	-12.1	90.8 (109/120)	+12.3	7.8	+4.0	33.9	+18.9	33.3	+11.0	0.257	+19.5	11.3	+34.5	
<i>PS-FS-PS</i>	94.2 (113/120)	-4.2	5.2 (6/120)	-1.8	1.7 (2/120)	-10.2	87.5 (105/120)	+8.2	8.8	+17.3	36.9	+29.4	34.1	+13.7	0.295	+37.2	12.5	+48.8	
<i>FS-PS-FS</i>	92.5 (111/120)	-5.9	1.8 (2/120)	-5.3	1.7 (2/120)	-10.2	89.2 (107/120)	+10.3	8.2	+9.3	34.5	+21.1	37.3	+24.3	0.287	+33.5	12.4	+47.6	
<i>FS-FS-FS</i>	98.3 (118/120)		6.8 (8/120)		10.8 (13/120)		80.8 (97/120)		7.5		28.5		30.0		0.215		8.4		
5G fám-saved/cv. Rwangume																			
<i>PS-PS-PS</i>	96.7 (116/120)	0.0	0.8 (1/120)	-2.5	4.2 (5/120)	+3.4	91.7 (110/120)	-0.9	15.7	+9.0	68.5	+7.7	12.2	-5.4	0.190	+2.7	8.3	+1.2	
<i>PS-FS-PS</i>	99.2 (119/120)	+2.6	0.0 (0/040)	-3.4	2.5 (3/120)	+1.7	96.7 (116/120)	+4.5	15.0	+4.2	69.1	+8.6	12.0	-6.9	0.179	-3.2	8.2	0.0	
<i>FS-PS-FS</i>	95.0 (114/120)	+1.7	3.5 (4/120)	-0.0	0.0 (0/120)	-0.8	91.7 (110/120)	-0.9	13.4	+6.9	58.8	-7.5	12.4	-3.8	0.173	-6.5	7.7	-6.1	
<i>FS-FS-FS</i>	96.7 (116/120)		3.4 (4/120)		0.8 (1/120)		92.5 (111/120)		14.4		63.6		12.9		0.185		8.2		
3rd season: 2014—LRS																			
4G UNSPPA/cv. Victoria																			
<i>PS-PS-PS</i>	92.5 (111/120)	-3.4	4.5 (5/120)	-2.5	1.7 (2/120)	-0.8	86.7 (104/120)	-7.1	5.2	-7.1	21.3	-15.1	102.2	+15.8	0.527	+7.3	21.8	-0.9	
<i>PS-FS-PS</i>	91.7 (110/120)	-4.3	1.9 (2/120)	0.0	0.0 (0/120)	-0.8	90.0 (108/120)	-3.5	5.5	-1.8	23.6	-5.9	83.1	-5.8	0.450	-8.3	19.5	-11.3	
<i>FS-PS-FS</i>	98.3 (118/120)	+2.6	2.6 (3/120)	-0.8	0.0 (0/120)	-0.8	95.8 (115/120)	+2.6	4.5	-19.6	20.6	-17.9	101.5	+15.1	0.453	-7.7	20.7	-5.9	
<i>FS-FS-FS</i>	95.8 (115/120)		1.8 (2/120)		0.8 (1/120)		93.3 (112/120)		5.6		25.1		88.2		0.491		22		
Market/cv. Victoria																			
<i>PS-PS-PS</i>	94.2 (113/120)	0.0	0.8 (1/120)	-0.8	0.8 (1/120)	+0.8	92.5 (111/120)	0.0	6.1	+15.1	26.9	+14.9	93.6	+5.0	0.567	+18.1	25.2	+16.1	
<i>PS-FS-PS</i>	93.3 (112/120)	-0.8	8.9 (10/120)	+6.7	0.0 (0/120)	0.0	85.0 (102/120)	-8.1	6.6	+24.5	26.8	+14.5	80.5	-9.6	0.529	+10.2	21.4	-1.4	

Table 4 (continued)

Treatment	Emergence	Rogued plants	Unaccounted plant loss	Harvested plants	Tubers per plant	Tubers per m ²	Weight per tuber (g)	Yield per plant (kg)	Tuber yield (Mg/ha)										
Relative change	%	%	%	%	%	%	%	%	%										
FS-PS-FS	97.5 (117/120)	+3.5	4.1 (5/120)	+2.5	0.0 (0/120)	0.0	93.3 (112/120)	+0.9	5.1	-3.8	22.7	-2.9	105.1	+17.9	0.540	+12.5	24.1	+11.1	
FS-FS-FS	94.2 (113/120)		1.8 (2/120)		0.0 (0/120)		92.5 (111/120)		5.3		23.4		89.1		0.480		21.7		
5G farm-saved/cv. Rwangume																			
PS-PS-PS	90.0 (108/120)	-7.7	0.8 (1/120)	-1.7	3.3 (4/120)	+3.3	85.8 (103/120)	-9.6	9.8	-4.8	40.2	-15.9	58.1	+13.7	0.567	+4.8	23.1	-5.7	
PS-FS-PS	95.0 (114/120)	-2.5	0.8 (1/120)	-1.7	0.0 (0/120)	0.0	94.2 (113/120)	-0.8	8.5	-17.5	38.4	-19.6	52.3	+2.3	0.452	-16.4	20.4	-16.7	
FS-PS-FS	96.7 (116/120)	-0.8	1.7 (2/120)	-0.8	2.5 (3/120)	+2.5	92.5 (111/120)	-2.6	10.1	-1.9	44.7	-6.5	47.3	-7.4	0.480	-11.3	21.2	-13.5	
FS-FS-FS	97.5 (117/120)		2.5 (3/120)		0.0 (0/120)		95.0 (114/120)		10.3		47.8		51.1		0.541		24.5		
4th season: 2015—SRS																			
4G UNSPPA/cv. Victoria																			
PS-PS-PS	100.0 (120/40)	+2.5	5.8 (7/120)	-6.6	8.3 (10/120)	-3.5	85.8 (103/120)	+6.2	5.2	+1.9	21.4	+8.6	62.4	+6.7	0.325	+6.9	13.2	+12.8	
PS-FS-PS	100.0 (120/120)	+2.5	8.3 (10/120)	-3.7	5.0 (6/120)	0.0	86.7 (104/120)	+7.2	5.3	+3.9	21.7	+10.1	61.4	+4.9	0.329	+8.2	13.3	+13.6	
FS-PS-FS	99.2 (119/120)	+1.7	5.0 (6/120)	-7.5	0.0 (0/120)	-5.2	94.2 (113/120)	+16.5	5.3	+3.9	23.8	+20.8	60.6	+3.6	0.313	+2.9	14.1	+20.5	
FS-FS-FS	97.5 (117/120)		11.9 (14/120)		5.0 (6/120)		80.8 (97/120)		5.1		19.7		58.5		0.304		11.7		
Market/cv. Victoria																			
PS-PS-PS	96.7 (116/120)	+3.5	9.5 (11/120)	0.0	4.2 (5/120)	-8.4	83.3 (100/120)	+14.9	5.0	-10.7	19.9	+1.0	65.1	+14.0	0.326	+3.2	13.0	+19.3	
PS-FS-PS	98.3 (118/120)	+5.3	28.7 (34/120)	+21.1	15.8 (19/120)	+4.7	54.2 (65/120)	-25.3	5.9	+5.3	15.4	-21.8	44.3	-22.4	0.263	-16.7	7.0	-35.7	
FS-PS-FS	96.7 (116/120)	+3.5	8.6 (10/120)	-0.9	5.0 (6/120)	-7.5	83.3 (100/120)	+14.9	4.5	-19.6	17.8	-9.6	58.9	+3.1	0.264	-16.4	10.5	-3.7	
FS-FS-FS	93.3 (112/120)		9.7 (11/120)		11.6 (14/120)		72.5 (87/120)		5.6		19.7		57.1		0.316		10.9		
5G farm-saved/cv. Rwangume																			
PS-PS-PS	96.7 (116/120)	-2.5	0.8 (1/120)	-2.5	9.2 (11/120)	+6.8	86.7 (104/120)	-7.1	9.4	-3.1	38.9	-10.7	49.9	+8.0	0.464	+5.7	19.2	-1.5	
PS-FS-PS	97.5 (117/120)	-1.7	3.3 (4/120)	0.0	6.7 (8/120)	+4.2	87.5 (105/120)	-6.2	10.7	+10.3	44.4	+1.8	38.1	-17.5	0.405	-7.7	16.9	-13.3	
FS-PS-FS	96.7 (116/120)	-2.5	11.1 (13/120)	+7.7	2.5 (3/120)	0.0	83.3 (100/120)	-10.7	9.9	+2.1	39.3	-9.8	46.4	+0.4	0.457	+4.1	18.0	-7.7	
FS-FS-FS	99.2 (119/120)		3.4 (4/120)		2.5 (3/120)		93.3 (112/120)		9.7		43.6		46.2		0.439		19.5		
<i>P</i> values																			
Selection Treatment (ST)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Seed lot (SL)	ns	0.011	ns	ns	ns	ns	ns	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	ns	ns	ns	ns	ns
Season (S)	0.028	0.008	ns	ns	ns	ns	0.043	0.005	0.005	0.002	0.002	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

Table 4 (continued)

Treatment	Emergence	Rogued plants	Unaccounted plant loss	Harvested plants	Tubers per plant	Tubers per m ²	Weight per tuber (g)	Yield per plant (kg)	Tuber yield (Mg/ha)
	%	%	%	%	%	%	%	%	%
ST × SL	ns	0.003	ns	0.005	ns	ns	ns	ns	ns
ST × S	0.042	ns	ns	ns	ns	ns	ns	ns	ns
SL × S	ns	ns	ns	ns	ns	ns	0.033	0.040	ns
ST × SL × S	ns	ns	ns	ns	ns	ns	ns	ns	ns

Emergence (%): plant number emerged/tuber number planted; Rogued plants because of bacterial wilt (%): plant number removed/tuber number planted; Unaccounted plant loss (%): missing number of plants/tuber number planted; Harvested plants (%): plant number harvested/tuber number planted; Tubers per plant: # per harvested plant; Tuber number per m²: # m⁻² planted area; Weight per tuber: g/tuber; Yield per plant: kg tuber fresh weight/harvested plant = plant number; Yield: Mg ha⁻¹ planted area

PS positive selection, FS farmers selection, ns non-significant, P ≥ 0.05

“..” indicates P value could not be obtained because of 0%

Table 5 Effects of selection treatments in different seed lots on agronomical characteristics in the three experiments. Average values across seasons

Variate and Selection treatment	Experiment 1, Karengere		Experiment 2, Kachwekano		Experiment 3, Hamurwa		Average
	3G/cv. Victoria	3G/cv. Katchpot I	3G/cv. Victoria	3G/cv. Katchpot I	4G UNSPPA/cv. Victoria	Market/cv. Victoria	
Fresh tuber yield (Mg/ha)							
PS-PS-PS	17.3 abc	20.3 c	16.3	12.6	14.4 b	16.5	16.9
PS-FS-PS	19.2 bc	15.4 a	15.7	13.6	14.6 b	13.7	15.2
FS-PS-FS	17.6 abc	20.3 c	18.9	11.9	13.5 b	15.6	15.4
FS-FS-FS	16.8 ab	19.4 bc	18.1	10.8	11.8 a	13.7	17.4
<i>P</i> value	< 0.001	ns	ns	< 0.001	ns	ns	ns
Yield per plant (kg/plant)							
PS-PS-PS	0.408 ab	0.489 d	0.359	0.330	0.344	0.384	0.407
PS-FS-PS	0.429 bcd	0.419 abc	0.352	0.339	0.345	0.362	0.345
FS-PS-FS	0.401 ab	0.471 bd	0.361	0.337	0.349	0.364	0.370
FS-FS-FS	0.377 a	0.460 bcd	0.320	0.307	0.313	0.337	0.388
<i>P</i> value	0.028	ns	ns	ns	ns	ns	ns
Weight per tuber (g/tuber)							
PS-PS-PS	75.7	88.1	70.5	61.9	66.2	64.0	40.1
PS-FS-PS	75.7	74.8	69.0	58.8	63.9	53.0	34.1
FS-PS-FS	78.1	84.0	66.6	65.2	65.9	67.1	35.4
FS-FS-FS	74.4	77.1	65.2	57.1	61.1	58.7	36.7
<i>P</i> value	ns	ns	ns	ns	ns	ns	0.041
Tuber number (#/m ²)							
PS-PS-PS	23.9 bc	22.7 ab	23.9	20.7	22.3 bc	26.9	49.2
PS-FS-PS	26.4 c	20.2 a	23.3	23.1	23.8 c	26.4	50.6
FS-PS-FS	22.7 ab	24.3 bc	23.5	18.5	20.7 ab	25.0	47.6

Table 5 (continued)

Variate and Selection treatment	Experiment 1, Karengyere			Experiment 2, Kachwekano			Experiment 3, Hamurwa			
	3G/cv. Victoria	3G/cv. Katchpot I	Average	3G/cv. Victoria	3G/cv. Katchpot I	Average	4G UNSPPA/cv. Victoria	Market/cv. Victoria	5G farm-saved/cv. Rwangume	Average
FS-FS-FS	22.9 ab	23.9 bc	23.5	20.3	18.9	19.6 a	26.0	23.9	51.7	33.9
<i>P</i> value	0.005		ns	ns	ns	0.002	ns			ns
Tubers per plant (#/plant)										
PS-PS-PS	5.5	5.5	5.5	5.3	5.4	5.4	6.5	6.3	11.6	8.1
PS-FS-PS	5.8	5.4	5.6	5.4	5.8	5.6	6.2	7.1	11.4	8.3
FS-PS-FS	5.1	5.7	5.4	5.5	5.3	5.4	6.1	5.9	11.2	7.7
FS-FS-FS	5.1	5.8	5.4	5.0	5.4	5.2	6.2	6.1	11.5	7.9
<i>P</i> value	ns		ns	ns		ns	ns			ns
Harvested plants %										
PS-PS-PS	90.0	85.6	87.8	95.3	79.7	87.5 b	87.2 bc	88.9 bede	88.1 bed	88.1
PS-FS-PS	93.6	76.4	85.0	93.6	83.9	88.7 b	86.4 bc	75.6 a	92.8 ce	84.9
FS-PS-FS	93.1	88.9	90.9	88.3	74.7	81.5 a	90.8 bede	88.6 bede	89.2 bede	89.5
FS-FS-FS	94.4	85.8	90.1	84.7	72.8	78.7 a	87.5 bc	81.9 ab	93.6 cde	87.7
<i>P</i> value	ns		ns	ns		< 0.001	0.005			ns
Unaccounted loss %										
PS-PS-PS	6.9	1.4	4.2	1.7	0.3	0.9	3.9	1.7	5.6	3.7
PS-FS-PS	4.2	0.0	2.1	0.3	1.1	0.7	3.3	5.8	3.1	4.1
FS-PS-FS	4.2	0.5	2.4	1.7	0.0	0.8	2.2	2.2	1.7	2.0
FS-FS-FS	1.7	0.3	0.9	2.5	0.0	1.3	2.8	7.5	1.1	3.8
<i>P</i> value	ns		ns	ns		ns	ns			ns
Bacterial wilt rogued plants %										
PS-PS-PS	0.0	0.0	0.0	2.5	0.9	1.7 a	5.2 b	4.9 b	0.9 a	3.7

Table 5 (continued)

Variate and Selection treatment	Experiment 1, Karengyere			Experiment 2, Kachwekano			Experiment 3, Hamurwa			
	3G/cv. Victoria	3G/cv. Katchpot	Average	3G/cv. Victoria	3G/cv. Katchpot	Average	4G UNSPPA/cv. Victoria	Market/cv. Victoria	5G farm-saved/cv. Rwangume	Average
PS-FS-PS	0.0	0.0	0.0	4.8	0.9	2.8 ab	5.2 b	14.3 c	1.4 a	6.9
FS-PS-FS	0.0	0.0	0.0	7.2	1.7	4.5 bc	3.9 b	4.8 b	5.5 ab	4.8
FS-FS-FS	0.0	0.0	0.0	9.0	1.8	5.4 c	6.3 b	6.1 b	3.1 ab	5.2
<i>P</i> value	-	-	-	ns		0.014	0.003			ns
Emerged plants %										
PS-PS-PS	96.9	86.9	91.9 b	99.4	80.8	90.1 b	95.6	95.3	94.4	95.1
PS-PS-PS	97.8	76.4	87.1 a	98.6	85.8	92.2 b	94.7	95.3	97.2	95.7
FS-PS-FS	97.2	89.4	93.3 b	96.9	76.1	86.5 a	96.9	95.6	96.1	96.2
FS-FS-FS	96.1	86.1	91.1 ab	95.8	74.2	85.0 a	96.4	95.3	97.8	96.5
<i>P</i> value	ns		0.047		ns	< 0.001		ns		ns

Different letters indicate significant difference between means according to LSD test at 5%
 ns not significant

0.0, no infection took place therefore no analysis was done

Italics were used in *P* values of the significant *F* ratios from ANOVA (results section)

Differences Between Selected and Non-selected Plants

Additionally, in all plots receiving positive selection in a given season (including the 4th season), the average yield per plant of the positive selected plants was calculated by dividing the total tuber fresh yield of the positive selected plants per plot by the number of the positive harvested plants in the plot, and the average yield per plant of the non-selected plants by dividing the yield of the non-selected plants in the plots receiving positive selection by the number of non-selected plants in these plots. To compare PS plants to non-selected plants in the same plot for number of tubers, the number of tubers of each harvested plant from positive selected plants and non-selected plants was assessed in all plots receiving the PS treatment.

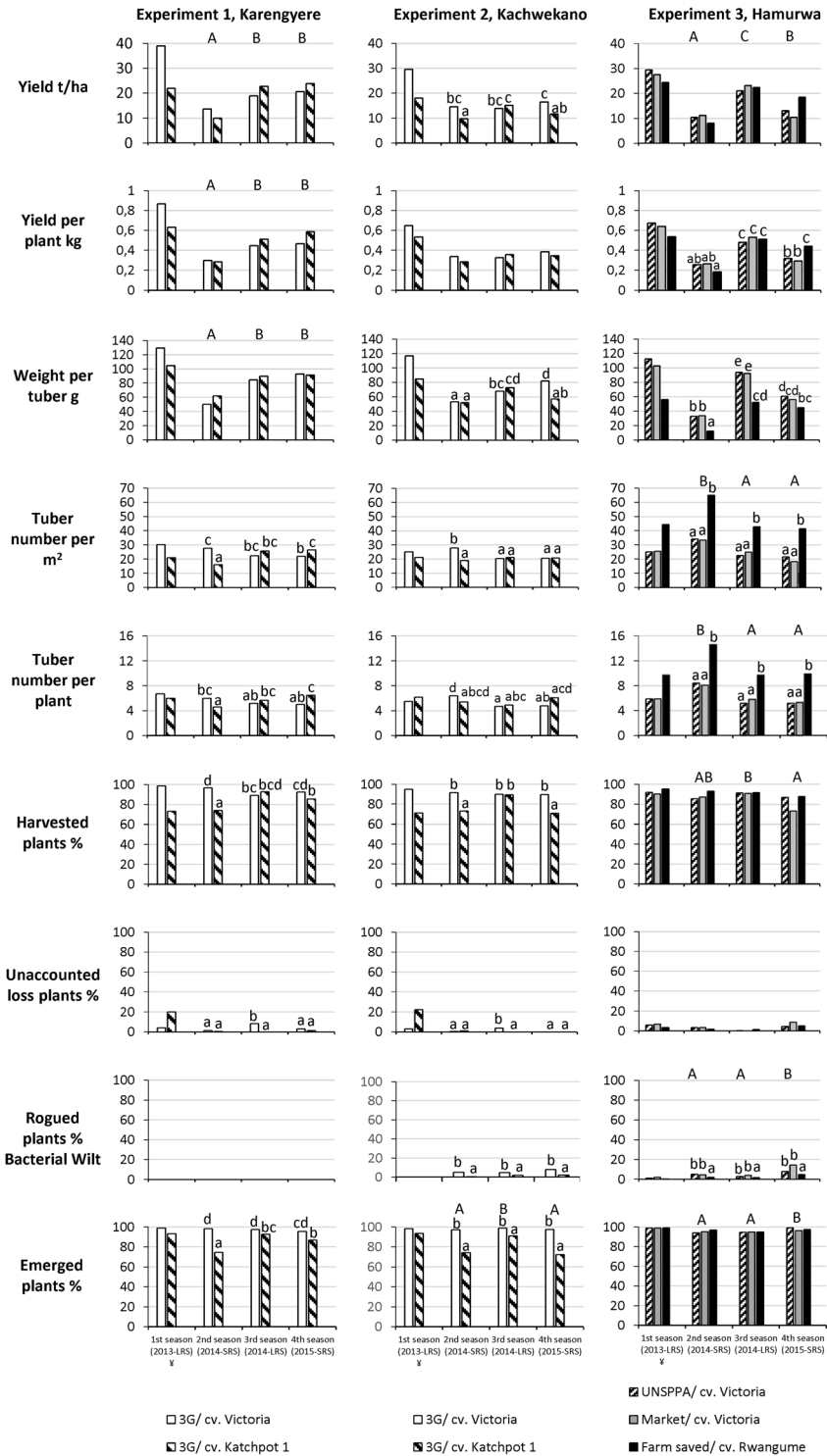
Data Analysis

Data were analysed using GenStat for Windows 18th Edition (VSN International 2016). General Analysis of Variance was used to test the effects of the factors selection treatment, seed lot and season and their interactions on the variables. The 1st season was not included in this ANOVA, because the seed planted in that season had not yet been subjected to different experimental selection treatments. Results of this 1st season are merely shown for comparison purposes. Where the P value in the ANOVA indicated significant effects or interactions ($P < 0.05$), significances of differences between means were assessed by the Fisher's LSD test at $\alpha = 0.05$. Data related to proportions (numbers of plants emerged, rogued, unaccounted loss and harvested and ground cover) were transformed before analysis. They were recalculated to proportions and angular transformations were applied (Fernandez 1992). Proportions equal to 0 or 1 were replaced by $(1/4n)$ and $[1 - (1/4n)]$ respectively, where n represents the total number of sampled plants or tubers per net plot (Fernandez 1992).

To assess differences in tuber number per plant and yield per plant between positive selected plants and non-selected plants in the same plots, boxplots were generated using data from the PS plots in all four seasons. The number of tubers and yield per plant of the positive selected plants and non-selected plants were compared and tested for significance with a paired t test.

Results

For yield and its underlying components, the full outcome of the ANOVAs and the means for the individual treatments in the three experiments are shown in Tables 2, 3 and 4; the supplementary data on yields per tuber size class, maximum ground cover and stem number per plant are shown in the supplementary material (Supplementary Tables 2A–4A). Significant three-way interactions (selection treatment \times seed lot \times season) were only found in Experiment 2 and only for the variates number of rogued plants, number of harvested plants (Table 3) and yield of large tubers (Supplementary Material Table 3A). There were some two-way interactions between selection treatment and seed lot and between selection treatment and season, whereas two-way interactions between seed lot and season were most often found (Tables 2, 3 and 4, Supplementary Tables 2A–4A). Table 5 presents the main effects of selection treatment and the



◀ **Fig. 1** Effects of season on tuber yield and yield components of different seed lots in the three experiments; average values across four selection treatments. Different letters indicate significant differences according to Fisher's protected LSD test ($\alpha = 0.05$). Capital letters reflect a significant main effect of season; lower case letters reflect a significant season \times seed lot interaction. Season 1 data are not part of the statistical analysis because the seeds planted had not yet been subjected to different selection treatments

interacting effects of selection treatment and seed lot, and Fig. 1 presents the main effects of season and the interacting effects of season and seed lot.

Effects of Selection Treatments

Fresh Tuber Yield per Hectare

In Experiment 1, the selection treatment \times seed lot interaction was significant. In cv. Victoria, the fresh tuber yield per hectare was not significantly affected by the selection treatment, whereas in cv. Katchpot 1 the yield in the PS-FS-PS treatment was lower than the yield in the other treatments, which did not differ significantly from each other (Table 5). In Experiment 2, a significant main effect of selection treatment indicated that a lower yield was obtained in the FS-FS-FS treatment than in the other treatments, which did not differ significantly from each other (Tables 3 and 5). In Experiment 3, the average yield across the seed lots was highest in the PS-PS-PS treatment, but not significantly different from the other treatments (Tables 4 and 5).

Yield per Plant

In Experiment 1, the selection treatment \times seed lot interaction was significant. In cv. Victoria, yield per plant was higher in PS-FS-PS than the FS-FS-FS treatment, with the other treatments not differing significantly from these extremes, whereas in cv. Katchpot 1, the highest yield per plant was found in the PS-PS-PS treatment, but this yield did only differ significantly from the yield per plant in the PS-FS-PS treatment (Table 5). In Experiments 2 and 3, yield per plant was not significantly affected by the selection treatment (Tables 3, 4 and 5); the average yield per plant across the seed lots was highest in the PS-PS-PS treatment (Experiment 3) and lowest in the FS-FS-FS treatment (Experiment 2), but the differences were not significant (Table 5).

Weight per Tuber

In Experiment 1, the selection treatment had no influence on weight per tuber (Table 5). In Experiment 2, there was a significant interaction between selection treatment and season (Table 3, Supplementary Table 3B); differences between selection treatments were not consistent across seasons. In the 2nd season, the FS-PS-FS treatment had a higher weight per tuber than the other treatments. In the 3rd season, differences between the selection treatments were not significant. In the 4th season, PS-PS-PS and PS-FS-PS had a higher weight per tuber than FS-PS-FS and FS-FS-FS. In Experiment 3, the selection treatment had a significant effect on weight per tuber, with

the weight per tuber being lower in the PS-FS-PS treatment than in the PS-PS-PS and FS-PS-FS treatments and FS-FS-FS not differing significantly from the other treatments.

Tuber Number per Square Metre

In Experiment 1, there was a significant selection treatment \times seed lot interaction for number of tubers per square metre. This was mainly caused by the PS-FS-PS treatment producing a relatively high number of tubers per square metre in the seed lot from cv. Victoria and a relatively low number of tubers in the seed lot from cv. Katchpot 1, whereas the other selection treatments did not differ from each other (Tables 2 and 5). In Experiment 2, the average number of tubers per square metre across the seed lots was lower in the FS-FS-FS than in the PS-PS-PS treatment (Table 5). Significant interaction of selection treatment \times season indicated a higher number of tubers per square metre in the PS-PS-PS and PS-FS-PS treatments than in the FS-PS-FS and FS-FS-FS treatments in the 2nd season (2014—SRS), whereas differences were not significant in the 3rd season and not found in the 4th season (Table 3, Supplementary Table 3B). In Experiment 3, the number of tubers per square metre was not affected by the selection treatment (Tables 4 and 5).

Tuber Number per Plant

In Experiments 1 and 3, the number of tubers per plant was not significantly affected by the selection treatment. In Experiment 2, a significant selection treatment \times season interaction indicated more tubers per plant in the 2nd season in the PS-FS-PS treatment than in the other treatments, and no differences between selection treatments in the 3rd season and 4th season (Table 3, Supplementary Material Table 3B).

Plant Numbers

In Experiment 1, there was a significant main effect of the selection treatment on the *number of emerged plants* (Table 2). Poor emergence was observed in the PS-FS-PS treatment, mainly in cv. Katchpot 1. No *bacterial wilt* occurred in this experiment; therefore, there was no plant loss due to bacterial wilt (Tables 2 and 5). No significant effects of the selection treatment could be assessed on *unaccounted loss* and the number of *harvested plants* (Tables 2 and 5), which was partly influenced by the large variation among individual plots. In some blocks, missing plants tended to occur more frequently in the PS-PS-PS plots, leading also to relatively low numbers of plants harvested in some plots.

In Experiment 2, there were significant main effects of selection treatment on the numbers of *emerged*, *rogued* and *harvested plants* (Tables 3 and 5). Across the seed lots, *plant emergence* was higher in the PS-PS-PS and PS-FS-PS treatments than in the FS-PS-FS and FS-FS-FS treatments. *Bacterial wilt* occurred across the seed lots with less in the PS-PS-PS and PS-FS-PS treatments (Tables 3 and 5). The

selection treatment had no influence on the *unaccounted loss*, which was less in this experiment than in Experiment 1. Consequently, more *plants* were *harvested* in the treatments of PS-PS-PS and PS-FS-PS, compared to FS-PS-FS and FS-FS-FS treatments (Tables 3 and 5).

In Experiment 3, emergence in general was high and the selection treatment had no clear effect on the *emergence of plants* (Tables 4 and 5): significant interaction between selection treatment and season was found but showed no meaningful differences between selection treatments in the different seasons (Supplementary Material Table 4B). There was a significant interaction between selection treatment and seed lot on the *number of rogued* and *harvested plants*; *bacterial wilt* was higher in the PS-FS-PS treatment of cv. Victoria from the market than in all other selection treatments within the two seed lots of cv. Victoria. In cv. Rwangume, the lowest incidence was found in the PS-PS-PS treatment, but effects of the selection treatment on number of rogued plants could not be assessed as significant (Tables 4 and 5). The selection treatment had no significant effect on the *unaccounted loss*, but the *unaccounted loss* tended to be most frequent in the PS-PS-PS plots for cv. Victoria from UNSPPA and cv. Rwangume (Table 4 and 5). A low *number of plants harvested* appeared in cv. Victoria from the market in the PS-FS-PS treatment (Table 5), where in the 4th season only 54% of the planted seed potatoes could be harvested (Table 4).

Differences Between Seed Lots

Fresh Tuber Yield per Hectare

In Experiment 1, a significant selection treatment \times seed lot interaction (Table 2) showed that for most selection treatments, there was no significant difference in tuber yield per hectare between the seed lots, but that in the PS-FS-PS treatment, yield of cv. Katchpot 1 was lower than that of cv. Victoria (Table 5). In experiment 2, significant seed lot \times season interaction showed that tuber yield per hectare was lower for cv. Katchpot 1 than for cv. Victoria in the 2nd and 4th seasons, whereas no significant differences in yield per hectare between seed lots were found in the 3rd season (Fig. 1). In Experiment 3, the yield per hectare was not significantly different between the three seed lots (Tables 4 and 5).

Yield per Plant

In Experiment 1, a significant selection treatment \times seed lot interaction showed a lower yield in cv. Victoria than in cv. Katchpot 1 in the FS-FS-FS and PS-PS-PS treatments, whereas the yield per plant did not differ significantly between seed lots in the other selection treatments (Table 5). In Experiment 2, seed lots did not differ in yield per plant (Table 3). In Experiment 3, the significant seed lot \times season interaction revealed that the seed lots did not differ in yield in the 2nd season and 3rd season, but that the yield of cv. Rwangume was higher than the yield of the two cv. Victoria seed lots in the 4th season (Fig. 1).

Weight per Tuber

In Experiment 1, the seed lot had no influence on the weight per tuber (Table 2). In Experiment 2, a significant interaction of seed lot and season showed a higher weight per tuber in cv. Victoria than in cv. Katchpot 1 in the 4th season, whereas there were no significant differences between seed lots in the 2nd and 3rd seasons (Fig. 1). In Experiment 3, the weight per tuber in cv. Rwangume was significantly smaller than in both seed lots of cv. Victoria in the 2nd and 3rd seasons, whereas in the 4th season, the differences between seed lots in weight per tuber were small and cv. Rwangume still had smaller tubers than cv. Victoria from UNSPPA, but cv. Victoria from the market did not differ significantly from any of the other seed lots (Fig. 1).

Number of Tubers per Square Metre

In Experiment 1, significant seed lot \times selection treatment and seed lot \times season interactions (Table 2) showed that the difference between seed lots in number of tubers per square metre depended on season and selection treatment. Cultivar Victoria produced more tubers per square metre than cv. Katchpot 1 in the PS-FS-PS treatment, whereas no differences between seed lots were found in the other selection treatments (Table 5); cv. Victoria also produced more tubers per square metre than cv. Katchpot 1 in the 2nd season, fewer tubers than cv. Katchpot 1 in the 4th season, and a comparable number of tubers per square metre in the 3rd season (Fig. 1). In Experiment 2, the significant seed lot \times season interaction showed that tuber numbers per square metre in the two seed lots differed only in the 2nd season, with more tubers in cv. Victoria than in Katchpot 1 (Fig. 1). In Experiment 3, the number of tubers in crops from the seed lot of cv. Rwangume was significantly higher than in crops from cv. Victoria (Table 4).

Number of Tubers per Plant

In Experiment 1, the significant seed lot \times season interactions showed that more tubers per plant were produced in cv. Victoria than in cv. Katchpot 1 in the 2nd season, while cv. Katchpot 1 produced more tubers than cv. Victoria in the 4th season; no significant differences between seed lots were found in the 3rd season (Fig. 1). Similar trends were visible in Experiment 2, but differences between seed lots were not significant in any of the seasons (Fig. 1). In Experiment 3, the number of tubers per plant was higher for cv. Rwangume than for the two seed lots of cv. Victoria in all seasons (Tables 4 and 5).

Plant Numbers

In Experiment 1, the significant seed lot \times season interaction showed that the *emergence of plants* was higher for cv. Victoria than for cv. Katchpot 1 in all seasons, but that the difference was most prominent in the 2nd season (Fig. 1). A significant seed lot \times season interaction showed that the *unaccounted loss* was higher in cv. Victoria than in cv. Katchpot 1 in the 3rd season, whereas the *unaccounted loss* was rather small in both cultivars in the 2nd and 4th season (Fig. 1). A significantly higher number of *plants* were *harvested* in cv. Victoria than in cv. Katchpot 1 (Fig. 1) in the 2nd and 4th season, but not in the 3rd season.

In Experiment 2, *plant emergence* was higher for cv. Victoria than for cv. Katchpot 1 (Table 2, Fig. 1). *Bacterial wilt* occurred more in cv. Victoria than in cv. Katchpot 1 (Tables 3 and 5, Fig. 1). A significant seed lot \times season interaction showed that the *unaccounted loss* was higher in cv. Victoria than in cv. Katchpot 1 in the 3rd season, whereas in the other seasons there was no difference between seed lots (Table 3). The significant three-way interaction (Table 3) showed that the number of *harvested plants* was still higher in cv. Victoria than in cv. Katchpot 1 for all selection treatments in the 2nd season, and half of the selection treatments (PS-PS-PS and FS-PS-FS) in the 4th season, whereas there were no significant differences between seed lots in harvested plants in the 3rd season and the remaining selection treatments (FS-FS-FS and PS-FS-PS) in the 4th season (Supplementary Material Table 3B).

In Experiment 3, seed lot had no effects on the *emergence of plants* or on the *unaccounted loss*, but plant losses due to *bacterial wilt* were higher in the cv. Victoria seed lots than in cv. Rwangume (Tables 4 and 5). Number of *plants harvested* did not differ among seed lots except in the PS-FS-PS treatment, where the number of *harvested plants* was lower in cv. Victoria from the market than in the other seed lots (Table 5).

Seasonal Variation

First Season Results

Results of the 1st season are included in Fig. 1 to show variation across seasons but are not included in the statistical analysis because the seed planted in the first season had not yet been subjected to the experimental selection treatments. In the 1st season, *fresh tuber yield*, *yield per plant* and *weight per tuber* were among the highest found in the four experimental seasons, in all experiments (Fig. 1). In Experiment 1, cv. Victoria was yielding almost 40 Mg ha^{-1} , double to fourfold of what was found in later seasons. For cv. Katchpot 1 in this experiment, yield in the 1st season was similar to yields in the 3rd and 4th seasons. In Experiment 2, cv. Victoria yielded 30 Mg ha^{-1} in the 1st season, while yield of cv. Katchpot 1 was only slightly higher than in the following seasons. In Experiment 3, yields of $25\text{--}30 \text{ Mg ha}^{-1}$ in the 1st season were also higher than in later seasons, but only slightly above those in the 3rd season, especially for cv. Rwangume. The data for *number of tubers per square metre* and *number of tubers per plant* in the 1st season were of a similar magnitude as the data in the later seasons, except for cv. Rwangume in Experiment 3, which peaked in *number of tubers* in the 2nd season.

In the 1st season, *plant emergence* and *number of harvested plants* were similar to those in the later seasons for seed lots of cv. Victoria in all experiments and of cv. Rwangume in Experiment 3. Emergence rate for cv. Katchpot 1 in Experiments 1 and 2 was comparably high in the 1st season and 3rd season (both LRSs) and higher than in the 2nd and 4th seasons (both SRSs). However, the *harvested plant number* for this cultivar was lower in the 1st season than in the 3rd season in both Experiments 1 and 2 because the *unaccounted loss* was high (20–23%) in the 1st season for cv. Katchpot 1. In the 1st season, there were no *rogued plants* due to bacterial wilt in Experiments 1 and 2 and no to very few *rogued plants* in Experiment 3.

2nd to 4th Season Results

Fresh Tuber Yield per Hectare In Experiment 1, a lower yield for both seed lots was produced in the 2nd season than in the 3rd and 4th seasons (Fig. 1). In Experiment 2, the significant season \times seed lot interaction indicated the yield of cv. Victoria did not differ significantly between the 2nd, 3rd and 4th seasons while the yield of cv. Katchpot 1 was lowest in the 2nd season, highest in the 3rd season and with the 4th season not differing significantly from the 2nd and 3rd seasons (Fig. 1). In Experiment 3, lowest yields were produced in the 2nd season, while an increase was achieved in the 3rd season and a decrease obtained in the 4th season, for all seed lots (Fig. 1).

Yield per Plant In Experiment 1, yield per plant was lower in the 2nd season (Fig. 1) than in the 3rd and 4th seasons for both seed lots. In Experiment 2, season had no effect on yield per plant. In Experiment 3, the significant seed lot \times season interaction indicated that in cv. Rwangume the yield per plant was lower in the 2nd season than in the other seasons (Fig. 1), whereas in the two seed lots of cv. Victoria yields per plant were higher in the 3rd season than in the 2nd and 4th seasons (Fig. 1).

Weight per Tuber There was a seasonal effect on weight per tuber in Experiment 1 with a lower weight per tuber in the 2nd season than in the later seasons (Fig. 1). In Experiment 2, the significant seed lot \times season interaction showed that the individual tuber weights were lower in the 2nd season than in the 3rd season for both seed lots, whereas in the 4th season the weight per tuber was higher than in the 3rd season in cv. Victoria, and comparable to the weight per tuber in the 2nd season in cv. Katchpot 1 (Fig. 1). A significant selection treatment \times season interaction (Supplementary Material Table 3B) showed a significantly higher weight per tuber in the 3rd and 4th season than in the 2nd season in all selection treatments except FS-PS-FS, where the weight per tuber was relatively high in the 2nd season and did not differ significantly from that in later seasons; weights per tuber did not differ significantly between the 3rd and 4th seasons (Supplementary Material Table 3B). In Experiment 3, a significant season \times seed lot interaction showed that the weights per tuber were lowest in the 2nd season, especially for cv. Rwangume, and highest in the 3rd season, particularly for both seed lots in cv. Victoria (Fig. 1), with intermediate values in the 4th season for the cv. Victoria seed lots. In cv. Rwangume, weights per tuber did not differ significantly between the 3rd and 4th seasons.

Number of Tubers per Square Metre In Experiment 1, the significant seed lot \times season interaction (Table 2, Fig. 1) showed that in cv. Victoria, the number of tubers per square metre did not differ significantly across seasons whereas in cv. Katchpot 1 the number of tubers per square metre was lower in the 2nd season than in later seasons (Table 2, Fig. 1). In Experiment 2, the significant seed lot \times season interaction showed a higher number of tubers per square metre for cv. Victoria in the 2nd season than in later seasons, whereas in cv. Katchpot 1 the number of tubers per square metre did not differ significantly in the different seasons (Table 3, Fig. 1). In Experiment 3, the significant main effect of season showed more tubers per square metre in the 2nd season (2014–SRS) than in later seasons (Fig. 1).

Number of Tubers per Plant In Experiment 1, the significant seed lot \times season interaction showed no significant differences in number of tubers per plant between the seasons for cv. Victoria, while for cv. Katchpot 1 a higher number of tubers per plant was found in the 4th season than in the 2nd season, with the 3rd season not differing significantly from the other two (Fig. 1). In Experiment 2, significant interactions for season \times seed lot and season \times selection treatment showed higher number of tubers in the 2nd season for cv. Victoria than in later seasons, whereas there were no differences between seasons in number of tubers per plant in cv. Katchpot 1 (Fig. 1). The number of tubers per plant did not differ between seasons within the individual selection treatments except in the PS-FS-PS treatment that had more tubers per plant in the 2nd season than in later seasons (Supplementary Material Table 3B). In Experiment 3, more tubers per plant were found in the 2nd season than in later seasons for all seed lots (Fig. 1).

Plant Numbers In Experiment 1, the significant seed lot \times season interaction showed that *plant emergence* was comparably high over seasons in cv. Victoria whereas a lower *plant emergence* was found for cv. Katchpot 1 in the 2nd season than in the 3rd and 4th seasons (Table 2, Fig. 1). Season had no effect on *bacterial wilt*, because it was always absent in this experiment. A significant seed lot \times season interaction showed that the *unaccounted loss* was higher in the 3rd season for cv. Victoria than in the 2nd and 4th seasons and that there was almost no unaccounted plant loss for cv. Katchpot 1 (Table 2, Fig. 1). Consequently, in the 2nd season, a significantly smaller number of *plants* was *harvested* in cv. Katchpot 1 than in the other seasons, while for cv. Victoria the highest plant number was harvested in the 2nd season, which was similar to the plant number harvested in the 4th season.

In Experiment 2, the significant main effect of season showed higher *plant emergence* in the 3rd season than in the 2nd and 4th seasons (Fig. 1). The three-way interaction for *rogued plants* (Table 4) was due to a high seasonal incidence of bacterial wilt in cv. Victoria in the 4th season in all selection treatments, except in the PS-PS-PS treatment (Fig. 1, Supplementary Material Table 3B). The *unaccounted loss* was only substantial in the 3rd season in cv. Victoria (Fig. 1) (Tables 3 and 5). The percentages *plants harvested* for cv. Victoria did not differ significantly across seasons. For cv. Katchpot 1, the 2nd and 4th season showed a significantly smaller number of *plants harvested* than the 3rd season (Fig. 1).

In Experiment 3, *emergence of plants* across seed lots was higher in the 4th season than in the 2nd and 3rd seasons (Fig. 1). Incidence of *bacterial wilt* was also higher in the 4th season than in the 2nd and 3rd seasons (Fig. 1). The *unaccounted loss* was low in all seasons. The 4th season (2015—SRS) had the smallest number of *plants harvested* (Fig. 1).

Difference in Tuber Number and Tuber Weight per Plant Between Positive Selected Plants and Non-Selected Plants

In those experimental plots in which plants for production of PS seed were selected and other plants remained non-selected, the number of tubers per plant

was significantly higher in PS-selected plants than in the non-selected plants in the same plots in all seed lots and experiments (Fig. 2). Also, tuber yield per plant was significantly higher in PS-selected plants than in the non-selected plants, with one exception in Experiment 3 for cv. Victoria from the market, where the difference was not significant (Fig. 3). In three out of the seven seed lots, a significantly higher weight of large tubers was harvested in positive selected plants than in non-selected plants when tuber yield per plant was divided into classes of large, medium and small tubers (data not shown).

Discussion

Our goal was to understand what influence positive seed selection during multiple seasons has on potato yield when compared to farmers' seed selection and which yield components underlie the differences in yield. Experiments were done under farming conditions in southwestern Uganda and were partly handled by farmers.

Earlier research on the same experiments (Priegnitz et al. 2019b) showed that *virus incidence* in the seed lots fluctuated across seasons, but that continuous PS was able to maintain PLRV and PVX incidence at lower levels than continuous

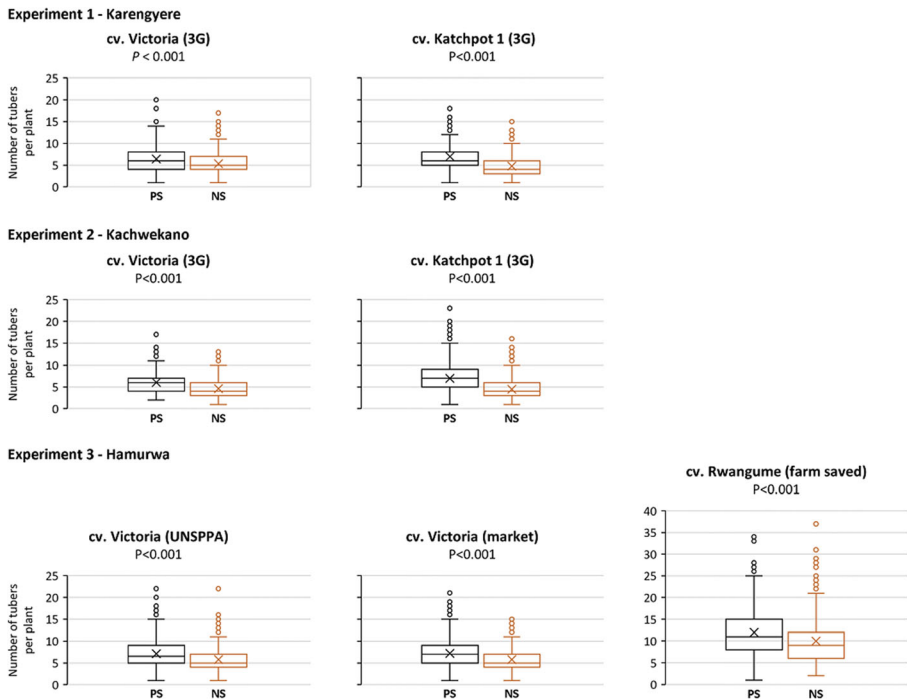
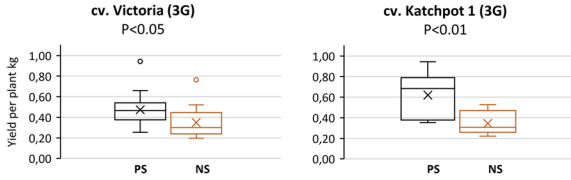
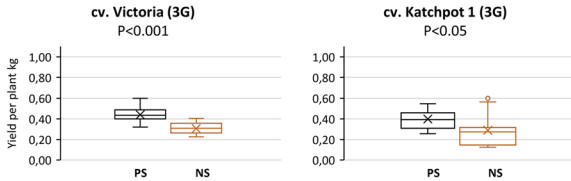


Fig. 2 Number of tubers per plant from the positive selected (PS) and non-selected (NS) plants in PS plots in all three experiments and all seasons (P value was obtained from 2-tailed t test). Boxplots show the range (rectangles from 25th to 75th percentile), mean (cross), median (line in rectangle) and minimum and maximum values in lines below and above the box; dots are outliers

Experiment 1 - Karengyere



Experiment 2 - Kachwekano



Experiment 3 - Hamurwa

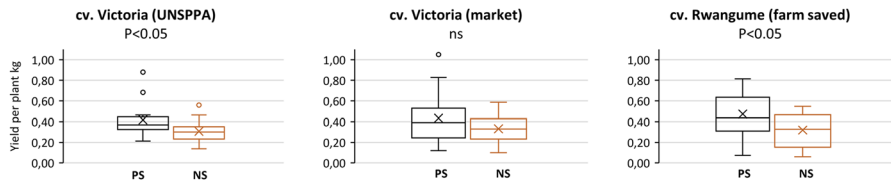


Fig. 3 Yield per plant (kg) from the positive selected (PS) and non-selected (NS) plants in PS plots in all three experiments and all seasons (P value was obtained from 2-tailed t test). Boxplots show the range (rectangles from 25th to 75th percentile), mean (cross), median (line in rectangle) and minimum and maximum values in lines below and above the box; dots are outliers

FS. PVA and PVY were only present in the seed lots at very low levels regardless of the selection treatment. PVS and PVM were present at very high levels in most seed lots, and PS was not more effective than FS in reducing their incidence. The high presence of PVS and PVM resulted in virtually no fully virus-clean plants being present in the seed lots of cv. Victoria, c. 50% clean plants on average in the seed lots of cv. Katchpot 1 and only in the seed lot of cv. Rwangume (Experiment 3) a maximum of more than 90% clean plants was found in the PS treatment in the last season. The high levels of virus present may have hindered the expression of large differences in yield.

This discussion will first focus on these differences in yield between crops under PS and FS and the yield components that underlie these differences. Thereafter potato production and productivity in the experiments under the local conditions will be discussed as well as their implications for the success of positive selection.

Effects of Seed Selection Treatments on Tuber Yield and its Underlying Components

Preamble

Under the local farming conditions, yield levels were very variable and plot-to-plot variation was high. The alternating seed selection treatments PS-FS-PS and FS-PS-FS

added to this variation; therefore, the discussion will mainly focus on the two most contrasting seed selection treatments, continuously PS (PS-PS-PS) and continuously FS (FS-FS-FS). Figure 4 summarizes the differences between PS and FS in yield and related characteristics for all seasons, seed lots and experiments from the data in Tables 2, 3 and 4 and Supplementary Tables 2A–4A, by plotting the data of the PS treatments against those of the respective FS treatments.

Tuber Yield and Its Components

Yield differences due to seed selection treatments indeed were more difficult to achieve and smaller than expected beforehand. *Tuber yield per hectare* can be regarded as a function of the *tuber yield per plant* and the *number of plants harvested*. In all experiments (Table 5), the *average tuber yield per hectare* was higher in PS-PS-PS treatments than in FS-FS-FS treatments, but under the experimental conditions this positive effect was only significant in Experiment 2 and not that large. Also, *tuber yield per plant* seemed consistently, but not significantly, higher under PS than under FS in all experiments (Table 5).

When inspecting the size of the differences between continuous PS and FS in detail for all seed lots and individual seasons (Fig. 4), the *tuber yield per plant* was always higher under PS than under FS (Fig. 4b). Averaged over all cases, the yield per plant under PS was 9.8% higher than that under FS. The maximum difference was +32.7%, the minimum +0.6% (Table 3). For *tuber yield per hectare*, Tables 2, 3, and 4 show clearly an overall yield increase by PS; on average this yield increase was 12%. This is smaller than the yield increases of around 25–30% reported by Gildemacher et al. (2011) and Schulte-Geldermann et al. (2012). This smaller increase will be partly due to the degree to which PS was able to reduce the virus status. Due to the necessity of planting guard rows in an experimental set up, the selection pressure in the present experiments was probably lower than in other conditions (15 plants out of 40 planted tubers were selected to produce seed tubers). The maximum positive difference between crops under PS and FS was +36.9% (Table 3). However, Fig. 4a also shows that in some cases, there was no effect of PS and there were even cases where the tuber yields per hectare were lower under PS than under FS (Experiment 1, cv. Katchpot 1 in 4th season; Experiment 3, seed lot UNSPAA/cv. Victoria in 3rd and 4th seasons and farm-saved/cv. Rwangume in 4th season; Tables 2 and 4). In all these cases of lower yield per hectare, the *plant number harvested* (Tables 2, 3, 4 and 5; Fig. 4c) was lower in the PS plots than in the FS plots by an even larger percentage. This shows that the plant number harvested was a variable of considerable importance in determining the yield per hectare in this research. In Experiment 2, plant numbers harvested under PS were higher than under FS (Table 5), but across all experimental data, there was no systematic relation between the plant number harvested under FS and PS ($R^2 = 0.047$) (Fig. 4c; Table 5). We will elaborate on plant numbers below.

The higher *yield per plant* in PS than in FS treatments seemed to be more related to an increase in *weight per tuber* (Fig. 4d, Table 5), by on average 7.4%, than to differences in *number of tubers per plant* (Fig. 4e, Table 5). Under the experimental

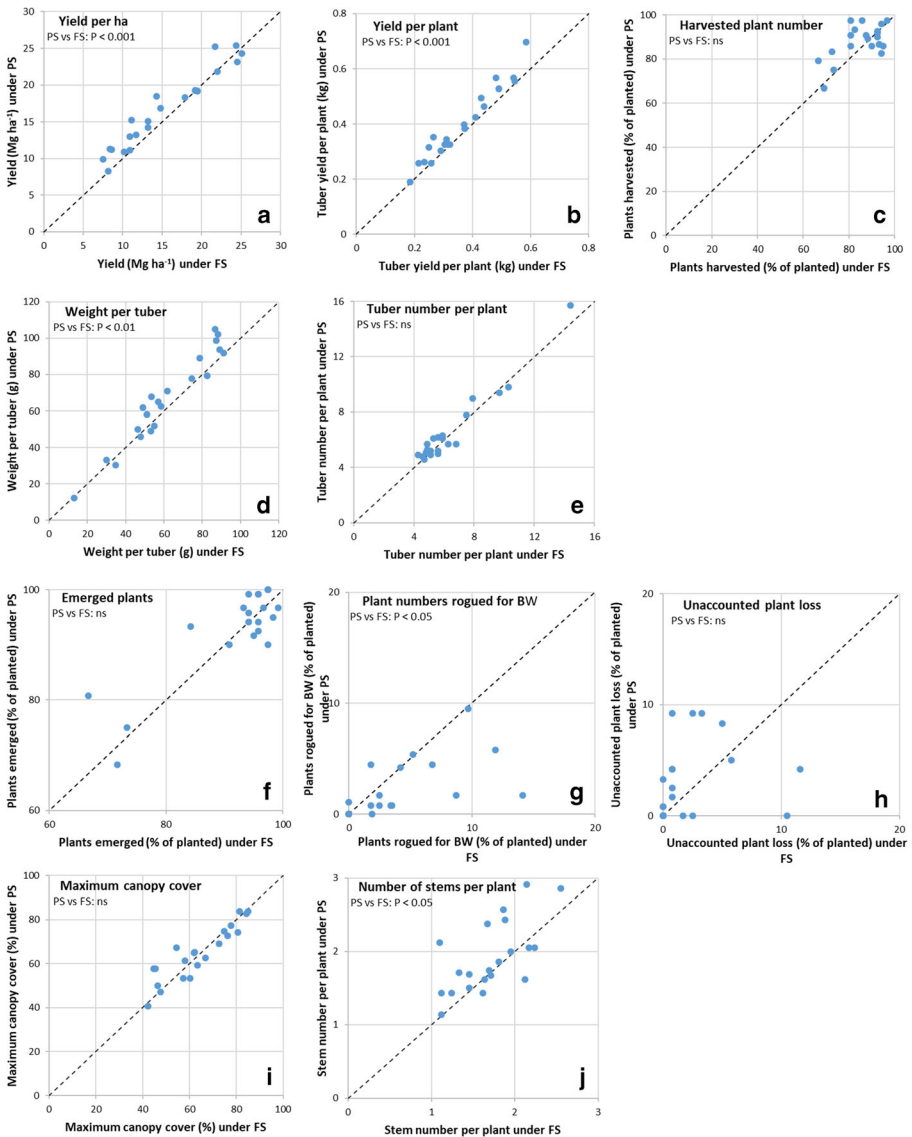


Fig. 4 Overview of differences between continuously PS and continuously FS in yields and relevant characteristics in all experiments, seasons and seed lots, based on means from Tables 2, 3 and 4 and Supplementary Tables 2A–4A. Dashed lines indicate the 1:1 line where PS would equal FS. Probabilities indicate if the differences between PS and FS were significant according to a paired, 2-sided *t* test

conditions in Uganda, the number of tubers per plant in most seed lots of cvs. Victoria and Katchpot 1 was relatively small with 5.5 tubers per plant.

Reasons for Differences in the Number of Plants Harvested

As shown above, the number of plants harvested was of considerable importance in determining the yield per hectare and there was no clear direct association between the

plant number harvested under PS or FS across experiments (Fig. 4c). The plant number harvested may therefore vary also for reasons that may or may not be related to the selection treatment. Lower number of harvested plants was caused either by a lower number of *emerged plants*, a higher *plant number rogued* because of bacterial wilt and/or more plant *losses* due to *unaccounted* reasons, like animal feeding or thefts. Plant emergence was generally variable and, surprisingly, not systematically higher under PS than under FS, except in Experiment 2 where planting PS seed resulted in a higher percentage emergence than planting FS seed (Fig. 4f). It is not clear to what extent the storage conditions might have affected these differences between experiments. In Experiment 2, the seeds were stored in darkness, in the other experiments under DLS. In Experiment 2, the higher number of emerged plants under PS than under FS (Table 5), together with a lower number of plants that had to be rogued because of bacterial wilt in plots under PS, clearly contributed to the higher number of plants harvested under PS than under FS (Table 5). The number of plants rogued because of bacterial wilt also in Experiment 3 seemed lower under PS than under FS (Table 5, Fig. 4g). The lower number of plants with bacterial wilt in plots under PS is in line with observations by Gildemacher et al. (2011). Plant losses due to bacterial wilt did not occur in Experiment 1, in Karengyere, the site at the highest altitude of the three locations.

A very important factor determining large variation in number of plants harvested was the unaccounted loss of plants (Table 5). Due to the high variation in plant numbers, the differences between PS and FS in the number of plants lost for unaccounted reasons could not be assessed as significant, but in most cases (but definitively not in all) a higher unaccounted loss appeared in PS plots than in FS plots (Fig. 4h) which again led to smaller number of plants harvested; the maximum unaccounted plant loss was 22.5% in the 1st season in cv. Katchpot 1 in Experiment 2. We expect the plots under PS showed higher losses because they may have had the most attractive plants.

Effects of Positive Selection During Multiple Seasons on Yield Levels

Most research work thus far was done on effects of PS after one season of selection (e.g. Gildemacher et al. 2011; Schulte-Geldermann et al. 2012). In the present experiments, we particularly wanted to verify if seed tuber health and the yield levels from these seed tubers could be maintained or increased when continuing the selection methods during multiple seasons.

The season itself obviously had a large effect on yield in our research (Fig. 1), but—during the seasons 2–4 when differently selected seed was compared—there were no indications that the absolute differences in yield per hectare or yield per plant between continuous PS or continuous FS increased or decreased when more rounds of selection were applied: there were no significant two-way interactions for seed selection method \times season for yield per hectare or yield per plant nor significant three-way interactions (Tables 2, 3 and 4). This is consistent with the effects of PS on the virus status (Priegnitz et al. 2019b). PS seems to be able to keep the virus incidence at a slightly lower level than continuously FS and the yield at a slightly higher level. One case of regeneration was observed, but this was not (only) due to positive selection: cv. Rwangume produced the lowest yield in the 2nd season, when the seed planted had

the highest incidence of viruses of all seasons. Cultivar Rwangume regenerated at the end of the experiments in becoming cleaner (Priegnitz et al. 2019b) and more productive in comparison to the other cultivars in this experiment, yet the PS treatment did not differ significantly from the FS treatment.

It seemed difficult to maintain the yield levels of quality-declared seed using PS only. In the 1st season, when the seed used had not yet been subjected to different selection treatments, a considerably higher yield (up to 39 Mg ha⁻¹) was achieved by planting quality-declared seed of cv. Victoria (3G seed in Experiments 1 and 2 and 4G-UNSPPA seed in Experiment 3) than in the later seasons 2–4 (Fig. 1) when the selection treatments that started in season 1 were continued. Although it cannot be excluded that this higher yield was due to favourable weather or more favourable physiological age of the seed tubers, this cultivar seemed to show clearly the importance of good seed quality in early generations for high productivity, like Schulte-Geldermann et al. (2013) and Demo et al. (2015) described. During the 1st season, plants became more infected by PLRV, PVX and PVA, resulting in a higher virus incidence of the seed tubers produced (Priegnitz et al. 2019b). The yield level of the 3G seed of cv. Katchpot 1 (Experiments 1 and 2) in the 1st season seemed to be sustained when compared to the 3rd and 4th seasons in Experiment 1 (Fig. 1), but the yield level assessed for this seed lot in the 1st season was reduced by a high percentage (c. 20%) of unaccounted loss of plants.

This suggests that under the present conditions in Uganda with high disease pressure and limited disease control, the seed quality and attainable yield of quality declared seed decrease already during the first multiplication, but that positive selection can keep production thereafter at a higher level than farmers' selection.

Effects of the Experimental Environment and Their Implications for Yield and the Success of Positive Selection

Potato Production and Productivity

Our long-term experimental yields ranged from 8.1 to 39 Mg ha⁻¹ with an average of 18.5 Mg ha⁻¹ and were much higher than the average yields reported for the country (4.2 Mg ha⁻¹) and the average yields obtained by farmers in the region (9.5 Mg ha⁻¹; Priegnitz et al. 2019a). This might have been due to relatively good crop management practices (van der Zaag 1987), including fertilization of 45 kg N ha⁻¹, spraying against *Phytophthora infestans* and rogueing against bacterial wilt in order to avoid a complete loss of potato plots. It is not known if these relatively good practices may also have reduced the differences between selection treatments. Schulte-Geldermann et al. (2012) showed that under Kenyan conditions, increasing the fertilizer level from 45 to 90 kg N ha⁻¹ increased the yield level, but not the absolute difference in yield from PS and FS selected seed.

Despite the relatively good management practices, yield levels obtained in our experiments were still far from maximum, as shown by the low maximum canopy cover during the seasons during which crops from PS and FS selected seeds were compared (Supplementary Tables 2A–4A). Due to shortage of precipitation (Table 1 and farmers' observation) in the short rainy seasons (2nd and 4th season) the crop suffered a reduction in yield (Experiment 1 (2014—SRS) and Experiment 3 (all

SRS's)). Different seasonal weather conditions seemed to exert their effect on yield especially through changing the size of the tubers. Whereas tuber yield per hectare, tuber yield per plant and average weight per tuber varied strongly and similarly across seasons, the number of tubers per plant did hardly (Fig. 1). This is elaborated below.

A very uncertain factor is the physiological age of the seed tubers and how that affected crop production, yield and crop and tuber health. We expect the age to be relatively young, given the short storage duration of 67–75 days between harvest and planting. This may have resulted in uneven sprouting, relatively few main stems and probably, but not necessarily, late tuberization. Poor emergence in cv. Katchpot 1 might have been related to a longer dormancy of this cultivar. Poor emergence due to dormancy can hinder the effect of positive selection because of the need to be less selective in order to harvest enough seed tubers. Therefore, the average quality of tubers from a poorly emerged crop is most likely lower than with a good stand when positive selection is applied. During storage, tubers were covered by grasses, according to the local practices. This was said to enhance sprouting, which supports the idea of a young physiological age of the tubers being a point of attention.

Plant Losses

The varying number of plants that was harvested not just greatly increased the plot-to-plot variation and thereby the experimental variation, it also resulted in reduction of the yield levels compared to what would have been possible. Losses were often larger in some plots than in others; in the most extreme case, only 54.2% of planted tubers produced harvested plants. Lower number of harvested plants was caused either by a lower number of *emerged plants*, a higher *plant number rogued* because of bacterial wilt or more plant *losses* due to *unaccounted* reasons.

Low plant emergence may have had different reasons. Low emergence was especially found in cv. Katchpot 1 in the short rainy seasons (the 2nd and 4th seasons). The low emergence might be attributed to unfavourable soil conditions (Struik and Wiersema 1999), like lack of rain and adverse soil structure. Drought during short rainy seasons and more uneven sprouting of some seed tubers might have hindered emergence. Additionally, in some cases, the planting depth used by the farmers to plant the experiments might have been deeper than optimum—which also may have affected emergence. At times, also smaller-sized seed tubers had to be used for planting when there were not enough medium-sized seed tubers from the previous harvest (Table 1), and a lower number of plants emerged in the plots when small-sized seed tubers were planted.

During crop growth after emergence, plant losses due to bacterial wilt and/or unaccounted reasons occurred in almost all experiments, seed lots, seasons and selection treatments. Bacterial wilt losses did not occur in Experiment 1, in Karengyere, the site at the highest altitude of the three locations. In Experiments 2 and 3, losses due to bacterial wilt seemed to increase slightly across the seasons (Fig. 1), mostly in farmers' selected seed (Fig. 1, Tables 3 and 4) and mostly in cv. Victoria (Fig. 1). The maximum loss due to bacterial wilt was 28.7% in one season in the seed lot of cv. Victoria from the market (Experiment 3). Unaccounted loss of plants, which again led to fewer plants harvested, appeared more frequent in PS plots than in FS plots; the maximum unaccounted loss of plants was 22.5% in the 1st season in cv. Katchpot 1 in Experiment 2.

All these causes of reduction in the plant number will not only decrease fresh tuber yield per hectare but also necessitate to select a larger percentage of the remaining plants as source for seed tuber production. Priegnitz et al. (2019b) mentioned a low selection pressure as an important factor for the high virus levels found—next to a high basic virus level and a high transmission risk. The necessity to select a relatively large part of the plants adds to reducing this selection pressure.

Tuber Number per Plant

Whereas tuber yield per hectare, tuber yield per plant and average weight per tuber varied strongly across seasons, the number of tubers per plant was relatively stable (Fig. 1). Under the experimental conditions, per plant only c. 5.5 tubers were produced in the seed lots of cv. Victoria and cv. Katchpot 1, with slightly higher numbers in Exp. 3. Inside a plot in which selection was carried out, the number of tubers per plant was only slightly higher in the selected plants than in the non-selected plants (Fig. 2); this difference in number was much smaller than the differences in yield per plant (Fig. 3). A low tuber number might be related to a low stem number due to the relatively physiologically young tubers that had to be planted—with the total period between harvest and planting being only 67–75 days. However, stem numbers only seemed to be related to tuber numbers to some extent in Experiment 3, suggesting a maximum number of tubers set per plant in Experiments 1 and 2 regardless of the stem number per plant (Fig. 5, summarizing data from Tables 2, 3 and 4 and Supplementary Tables 2A–4A).

The low numbers of tubers per plant have huge consequences for positive selection. The low number of tubers means that even in the ideal case that all tubers of a plant would be of the desired (medium) size for planting (which is not the case) and all planted tubers will result in harvested plants (which is also not the case), it may be difficult under the present farming conditions in southwestern Uganda, to increase the selection pressure to less than 1 plant out of every 5.5 plants. In our experiments in total 15 out of maximum 40 plants were selected (1 out of 2.7). This can be increased under farmer conditions to some extent (because there is no need for extra experimental tubers to plant the guard rows of the experimental plots) and this may also increase the quality of the seed tubers produced. However, in selecting plants for positive selection, it may not be sufficient to select 10–15% of the plants (1 out of 6.7–10 plants). This

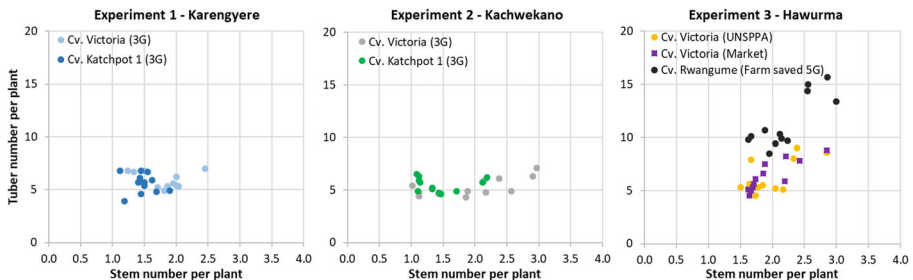


Fig. 5 Overview of the association between the number of stems per plant and the number of tubers per plant in Experiments 1, 2 and 3, based on means of all selection treatments, seasons and seed lots presented in Tables 2, 3 and 4 and Supplementary Tables 2A–4A

will never lead to enough seed tubers for planting the next crop in cultivars that produce only 5.5 tubers per plant and means that under the conditions leading to this multiplication rate, selection pressure may not be as high as would be desired.

Genotypes with a higher number of tubers per plant (like cv. Rwangume in Experiment 3) can improve the situation but may lead to very small tubers in seasons when yields are low. At this moment insight into the factors determining the stem and tuber number under the local conditions is not complete. Methods to increase the stem and tuber number per plant might be investigated, but they might interfere with the idea of positive selection to be carried out inside a ware potato crop. Nevertheless, the present method of positive selection at the present multiplication rate may already be sufficiently attractive for smallholder farmers as a possibility to increase tuber yield in potato.

Concluding Remarks

Vital points to combat seed degeneration due to high virus pressure in the environment are good seed quality and good crop management, because they determine potato tuber yields (Struik and Wiersema 1999; Haverkort and Struik 2015).

Continuous positive selection in multiple seasons was able to maintain yield levels at a higher level than continuous FS. The yield difference in the experiments varied but was on average 12%. The yield increase by using PS usually resulted from higher yields per plant and in Experiment 2 also from more plants harvested compared to using FS. The higher yields per plant under PS were associated with higher weights per tuber whereas the difference between PS and FS in number of tubers was not significant.

The field experimentation had to deal with a variety of circumstances (bacterial wilt, unaccounted plant loss, little rainfall in the short rainy seasons) due to the “real life” conditions in southwestern Uganda that limited the exploitation of the full potential of PS. These circumstances affected plant numbers and yield per plant. The high unaccounted losses in the experiments have hindered the success of positive selection. Crops under PS seemed to suffer more from unaccounted plant losses than crops under FS, but in crops under FS more plants were rogued because of bacterial wilt. It can be justified that continuously applied positive selection is a reliable option to keep yield at higher levels than farmers’ selection.

In all experiments, the healthy-looking plants chosen for positive selection had more tubers and almost always a higher tuber weight per plant than the non-selected plants in the same plot (Figs. 2 and 3) and these tubers also were healthier or less infected (Priegnitz et al. 2019b). This shows that the visual selection based on aboveground performance was also effective in selecting plants with better belowground characteristics. The higher numbers of tubers in PS-selected plants also make the seed selection process and the multiplication slightly more efficient than expected based on average numbers of tubers per plant. This is especially important in cultivars producing only a low number of tubers per plant, like cv. Victoria and cv. Katchpot 1 under the investigated conditions.

The trials with good crop management practices showed that yields up to 25 Mg ha⁻¹ can be achieved—which are much higher than the national mean yield of 4.2 Mg ha⁻¹. The experiments also showed that when seed tubers from positive

selection are planted, an increase in yield can be achieved compared to when tubers from farmers' selection are planted. Positive selection is a tool to fit in the current seed system of southwestern Uganda to lower the degeneration rate in seed potatoes and to gain a higher yield in smallholder potato production.

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Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflicts of interest.

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