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Identification of the key morphological sweetpotato weevil resistance predictors in Ugandan sweetpotato genotypes using correlation and path-coefficient analysis

Florence Osaru[1,2] | **Jeninah Karungi**[3] | **Roy Odama**[1] | **Doreen Murenju Chelangat**[1] | **Paul Musana**[1] | **Milton Anyanga Otema**[1] | **Bonny Oloka**[4] | **Paul Gibson**[2] | **Richard Edema**[2] | **Reuben Tendo Ssali**[5] | **George Craig Yencho**[4] | **Benard Yada**[1]

[1]National Crops Resources Research Institute (NaCRRI), Kampala, Uganda
[2]Makerere University Regional Center of Crop Improvement, Makerere University, Kampala, Uganda
[3]School of Agricultural and Environmental Sciences (CAES), Makerere University, Kampala, Uganda
[4]Department of Horticultural Science, North Carolina State University, Raleigh, North Carolina, USA
[5]International Potato Center, Kampala, Uganda

Correspondence
Benard Yada, National Crops Resources Research Institute (NaCRRI), Namulonge, P.O. Box 7084, Kampala, Uganda.
Email: yadabenard21@gmail.com

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Abstract

Sweetpotato weevils (SPWs) can cause up to 100% yield losses in sweetpotato (*Ipomoea batatas*). Nevertheless, there has been limited success in breeding for SPW resistance globally. This is attributed partly to difficulty in screening for resistance because resistance to the SPW is complex and is mediated by several resistance indicators. Measuring all these resistance indicators is costly and time consuming. To enhance efficiency in selection for SPW resistance, there is need to profile and identify key resistance indicators. Potentially, this will better enable breeders to timely and precisely select for SPW resistance. The objective of this study was to identify the most efficient morphological resistance indicators against SPW. Thirty sweetpotato genotypes that varied in resistance to SPW comprising local collections, released varieties, and breeding lines were evaluated at three locations for two seasons in Uganda using an alpha lattice design. Data were collected on storage root yield, SPW root and stem damage, and weevil resistance indicators such as vine vigor (VV), ground cover (GC), vine weight (VW), storage root neck length (NL), latex content, cortex thickness (CT), and dry matter content (DM). Genotype means for all measured traits varied significantly except for CT. Negative relationships were observed between SPW root damage and GC, VW, CT, VV, NL, and DM. However, path coefficient analysis showed storage root NL (direct effect of −0.43, $p < 0.001$) as the most important morphological resistance indicator. Therefore, NL could be the most

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Abbreviations: NaCRRI, National Crops Resources Research Institute; NaSARRI, National Semi-Arid Resources Research Institute; SPW, sweetpotato weevil; SSA, sub-Saharan Africa.

reliable predictor of resistance to SPW among breeding clones, especially at early breeding stages.

1 | INTRODUCTION

Sweetpotato (*Ipomoea batatas* (L.) Lam.) is a dicotyledonous plant belonging to the *Convolvulaceae* family (Austin & Huamán, 1996). The family has about 50 genera and more than 1000 species, but only *I. batatas* has economic importance as a food crop (Woolfe, 1992). The cultivated species, *I. batatas*, is a cross-pollinated crop and hexaploid ($2n = 6x$) crop with 90 chromosomes. It comprises plants that vary in their morphology and is propagated clonally (Low et al., 2009).

Sweetpotato is an important source of many nutritional and bioactive substances: minerals, vitamins, and antioxidants such as anthocyanins and phenolic acids as well as dietary fiber and carotenoids (Musilova et al., 2017). Sweetpotato can be used as a rich source of natural colorant (Mervat & Hanan, 2009), and the shoots and leaves can be eaten as nutritious vegetables (Jia et al., 2022; Leobenstein, 2009). The flesh color (FC) of the roots that is categorized as white, cream, yellow, orange, and purple determines the quantity and quality of the important properties of sweetpotato (Teow et al., 2007).

Sweetpotato weevil (SPW) is by far the most destructive pest of the sweetpotato crop in Sub-Saharan Africa (SSA). It can cause yield losses of up to 100% in susceptible varieties under hot and dry weather conditions (Christiaens et al., 2016; Smit, 1997). The weevil species in Africa are *Cylas puncticollis* and *Cylas brunneus*, while in India, Asia, Oceania, the United States, and the Caribbean countries, it is *Cylas formicarius* that is prevalent (Christiaens et al., 2016). All the SPW species have a similar life cycle. The adult female lays eggs singly in cavities excavated in vines or in storage roots, preferring the latter. The egg cavity is sealed with a protective, gray fecal plug. The developing larvae tunnel in the vine or storage root. Pupation takes place within the larval tunnels. A few days after eclosion, the adult emerges from the vine or storage root. At optimal temperatures of 27°C, *C. puncticollis* has a total development time of about 32 days, whereas *C. brunneus* takes 44 days. Adults of *C. puncticollis* live an average of 100 days, whereas *C. brunneus* die after about 2 months. *Cylas puncticollis* females lay 90–140 eggs in their lifetime, whereas *C. brunneus* females lay 80–115 eggs in their lifetime (Ames et al., 1996).

Most damage to sweetpotato is by the larvae, which live and feed inside the roots and vines but the adults also feed on above-ground parts of the crop. In response to damage, storage roots produce toxic terpenes, which render storage roots inedible. Feeding inside the vines causes malformation, thickening, and cracking of the affected vine (Ames et al., 1996). The damage caused by SPWs to sweetpotato in SSA is significant (Muyinza et al., 2012) and therefore threatening food security, safety, and economic viability of smallholder farmers.

Resistance to African SPWs *Cylas puncticollis* and *Cylas brunneus* in sweetpotato is complex and quantitative in nature (Anyanga et al., 2017; Stathers, Rees, Kabi et al., 2003, Stathers, Rees, Nyango et al., 2003; Yada et al., 2017). Earlier field trials have suggested that sweetpotato morphological traits such as vine vigor (VV), ground cover (GC), foliage weight, and storage root characteristics such as root depth, cortex thickness (CT), size, shape, arrangement, root latex, and dry matter content (DM) may play important role in conferring field resistance to SPW (Stathers, Rees, Kabi et al., 2003). The biochemical basis of resistance to SPW was examined in Uganda (Stevenson et al., 2009). The authors reported that resistance in "New Kawogo," a released Ugandan landrace variety, is due to antibiosis and quantifiable. It is conferred by hydroxycinnamic acid esters (HCA), including hexadecylcaffeic acid, hexadecylcoumaric acid, heptadecylcaffeic acid, octadecylcaffeic acid, octadecylcoumaric acid, and 5-O-caffeoylquinic acids produced in the storage root surface and latex (Anyanga et al., 2013; Stevenson et al., 2009).

Assessing resistance among breeding lines generally incorporates both field and laboratory investigations, and breeders have over the years measured many potential plant morphological and biochemical attributes associated with resistance. Traits like VV, GC, root depth, latex content, dry matter, and hydroxycinnamic acid esters are being measured to date as resistance indicators. These traits are difficult to phenotype accurately when screening thousands of breeding clones for germplasm enhancement and cultivar improvement. Also, the challenge of breeding for the biochemical basis of SPW resistance is that often some genotypes that express field resistance do not also have a high HCA concentration (Anyanga et al., 2017; Stathers, Rees, Nyango et al., 2003; Yada et al., 2017). Further, understanding the genetic basis of the biochemical mechanism of resistance to SPW has been frustrated by the complex auto-allopolyploid genome ($2n = 6x = 90$) of sweetpotato (Srisuwan et al., 2006). Identifying the key morphological resistance indicator trait(s) for use in phenotyping for SPW resistance among thousands of clones would increase accuracy and precision of selection. Hence, increasing genetic gains reduce the cost of the breeding and possibly result in more timely release of improved sweetpotato varieties for use by farmers.

Wright (1921) proposed correlation and path coefficient analysis to establish the relationship between predictor and response variables. However, linear correlation between a complex quantitative trait and its several component traits cannot provide clear and sufficient information for selection. This is because there are often indirect influences of one trait by another that reduces its actual contribution to the dependent trait (Gurmu et al., 2018; Rao et al., 2017; Nagarajan et al., 2015;2017; Khan & Dar, 2010; Sreckov et al., 2010). This means, caution must be exercised in the interpretation of the results as linear correlation coefficients alone may sometimes give misleading results because correlations between two variables could be due to a third factor that may not be quantified.

Path coefficient analysis extends correlation analyses by providing information on the actual contribution of the independent trait to the dependent trait (Lynch & Walsh, 1998). It is used to measure the direct effect of one variable on another and to separate the correlation coefficient into components of direct and indirect effects (Gurmu et al., 2018; Khan & Dar, 2010). Path analysis has been used to fix the most important components of quantitative traits like yield to aid effective selection for yield improvement in many crops including sweetpotato (Gurmu et al., 2018; Khan & Dar, 2010; Nagarajan et al., 2015; Rao et al., 2017; Sreckov et al., 2010).

This study was conducted to define the key traits indicating resistance to SPW in sweetpotato and characterize the relationship among the traits. Potentially, identification of the key SPW resistance-indicating traits and the relationships among them will better enable breeders to timely and precisely select for SPW resistance for population improvement and variety release in Uganda and elsewhere.

2 | MATERIALS AND METHODS

2.1 | Study sites

Field experiments were carried out at three different agroecological sites in Uganda: National Crops Resources Research Institute (NaCRRI) (Namulonge), Abi-ZARDI (Arua), and National Semi-Arid Resources Research Institute (NaSARRI) (Serere), as shown in the Supporting Information Appendix 1.

2.2 | Plant materials used in the study

A total of 30 sweetpotato genotypes that comprised released varieties, breeding lines, and land races with desirable genetic background for SPW resistance were evaluated in the three locations (Supporting Information Appendix 1) over two seasons for this study. Details of the cultivars are presented in Table 1. In order to obtain clean and enough planting material for the field evaluations, vines of the cultivars were multiplied on-station at NaCRRI in a swamp that stayed wet during the dry season, with the materials being watered regularly depending on the soil moisture condition.

Core Ideas

- Sweetpotato root damage by *Cylas* spp is negatively and significantly correlated with sweetpotato morphological traits.
- The relationship between these morphological resistance indicator traits and root damage by weevils is mostly indirect.
- Only deep storage root neck length accurately reduced the severity of storage root damage by sweetpotato weevils, and it could be used for selection.

2.3 | Rearing of SPW colony

A culture of *C. puncticollis* and *C. brunneus* was maintained on sweetpotato storage roots of a susceptible variety NASPOT1, in cages held at 25 ± 2°C, using the procedures in the bioassay laboratory at NaCRRI (Rukarwa et al., 2013). The weevils for inoculating NaCRRI, NaSARRI, and AbiZARDI trials were collected for rearing from their respective sites.

2.4 | Evaluation for weevil resistance in field experiments

An alpha-lattice design of six blocks/replication by five genotypes/block was used to plant all the experiments with three replications of each genotype per site for two seasons. Each of the genotypes was planted in a plot of three ridges 3 m long spaced 1 m apart. Ten apical cuttings per genotype each 30 cm long were planted per ridge with 30 cm spacing between plants on the ridge giving a total of 10 plants per ridge and 30 plants per plot. Weeding was done at three time periods: at roughly 30 days, 60 days, and 90 days after planting following the methodologies of Muyinza et al. (2012).

To supplement the natural weevil population and ensure effective insect pressure, each plot was infested with 10 laboratory-reared unsexed, mixed-age *C. puncticollis* and

C. brunneus adults (10 of each species for a total of 20 SPW). Weevils were applied to vines on the middle ridge of each plot at roughly 90 days after planting (DAP) using procedures described by Stathers, Rees, Kabi et al. (2003).

The first season trials were planted in April, 2017, and the second season trials were planted in November, 2017. Harvesting was done 5 months after planting (MAP) following the procedure of Muyinza et al. (2012) and Anyanga et al. (2017). By 5 MAP, SPW would have caused sufficient damage to the trials for the effective evaluation of the genotypes.

2.5 | Data collection in the field

Data were collected at vegetative and harvest stages of the plants. At harvest time, the number of surviving plants were recorded, internal stem damage assessed, and all vines collected and weighed. Then all the roots from the surviving plants were carefully dug out using hand hoes. Most of the plant traits and root characteristics were scored as described in the international descriptors for sweetpotato (CIP, AVRDC, IBPDR, 1991) and procedures for evaluation and analysis of sweetpotato trials manual (Gruneberg et al., 2019) developed by International Potato Center.

2.5.1 | Vine vigor

VV was determined 1 month after plating and recorded using subjective scores from 1 to 9: 1 = very weak vines (nearly no vines); 2 = weak vines; 3 = weak to medium strong vines, medium thick vines, and long internode distance; 4 = medium strong vines, medium thick stems, and medium internode distances; 5 = medium strong vines, thick vines, and long internode distances; 6 = medium strong vines, thick stems, and medium internode distances; 7 = strong vines, thick stems, short internode distance, and medium long vines; 8 = strong vines, thick stems, short internode distances, and long vines; and 9 = very strong vines, thick stems, short internode distances, and very long vines (Gruneberg et al., 2019).

2.5.2 | Ground cover (%)

This trait was recorded 35–40 days after planting using a scale of 3–9: 3 = low (< 50%), 5 = medium (50–74%), 7 = high (75–90%), 9 = total (>90%) of the ground is covered by the vines and leaves (CIP, AVRDC, IBPDR, 1991).

2.5.3 | Number of plants harvested

We determined the number of plants harvested by counting all the plants per plot at harvest time (Gruneberg et al., 2019).

TABLE 1 Sweetpotato genotypes used in the study of sweetpotato weevil resistance in Uganda.

Entry	Resistance to SPW	Origin/source
ADJ190	Resistant	Land race
APA356	Resistant	Land race
APC136	Resistant	Land race
BEAUREGARD	Susceptible	USA variety
DIMBUKA.B	Resistant	Land race
EJUMULA	Resistant	Uganda variety
MLE171	Resistant	Land race
MPG1136	Resistant	Land race
MSD380	Resistant	Land race
NASPOT1	Susceptible	Uganda variety
NASPOT10	Susceptible	Uganda variety
NASPOT11	Susceptible	Uganda variety
NASPOT12	Susceptible	Uganda variety
NASPOT13	Susceptible	Uganda variety
NASPOT3	Susceptible	Uganda variety
NASPOT8	Susceptible	Uganda variety
NEW KAWOGO	Resistant	Land race
NKB10	Resistant	Breeding line
NKB135	Resistant	Breeding line
NKB156	Resistant	Breeding line
NKB257	Resistant	Breeding line
NKB3	Susceptible	Breeding line
PAL116	Resistant	Land race
PAL134	Resistant	Land race
PAL94	Resistant	Land race
SPK004	Resistant	Land race
SRT02	Resistant	Land race
SRT03	Resistant	Land race
SRT27	Resistant	Land race
TANZANIA	Susceptible	Land race

Abbreviation: SPW, sweetpotato weevil.

2.5.4 | Storage root neck length

Storage root neck length (NL) was measured as the distance from the crown (attachment of the root neck to the main stem) to the adaxial tip of the storage root when the harvested plant was held above the ground for five randomly selected plants per plot and the mean per plot recorded. The mean values were then used to score the root depth on a scale of 0–9: 0 = sessile or absent, 1 = (<2 cm), 3 = (2–5 cm), 5 = (6–8 cm), 7 = (9–12 cm), 9 = (>12 cm) as described by CIP, AVRDC, IBPDR (1991).

2.5.5 | Storage root yield

The storage root yield parameters of total storage root number per plot and total root weight in kilogram per plot were recorded (Gruneberg et al., 2019).

2.5.6 | Storage root shape

Outline of the storage root shape is shown as longitudinal section at the scale of 1–9: 1 = round, 2 = round elliptic, 3 = elliptic, 4 = ovate, 5 = obvate, 6 = oblong, 7 = long oblong, 8 = long elliptic, and 9 = long irregular or curved (CIP, AVRDC, IBPDR, 1991).

2.5.7 | Storage root skin color

A 1–9 scale was used to score for the predominant skin color: 1 = white, 2 = cream, 3 = yellow, 4 = orange, 5 = brownish orange, 6 = pink, 7 = red, 8 = purple red, and 9 = dark purple (Gruneberg et al., 2019).

2.5.8 | Storage root flesh color

This trait was recorded immediately after the storage root was cut cross-sectionally at the scale of 1–9: 1 = white, 2 = cream, 3 = dark cream, 4 = pale yellow, 5 = dark yellow, 6 = pale orange, 7 = intermediate orange, 8 = dark orange, and 9 = strongly pigmented with anthocyanins (purple) (Gruneberg et al., 2019).

2.5.9 | Storage root CT

To determine the storage root CT, we cut a cross-section of one root per plot and measured the root cortex width.at the scale of 1–9: 1 = very thin (<1 mm), 3 = thin (1–2 mm), 5 = intermediate (2–3 mm), 7 = thick (3–4 mm), and 9 = very thick (>4 mm) (CIP, AVRDC, IBPDR, 1991).

2.5.10 | Storage root latex content (sap)

This trait was recorded immediately after cutting the storage root transversely at the scale of 3–7: 3 = little sap, 5 = some sap, and 7 = abundant sap (CIP, AVRDC, IBPDR, 1991).

2.5.11 | Storage root DM

Determination of DM (%) was done using an oven drying method where approximately 100 g of fresh storage root samples from each plot was sliced using a knife, weighed, and recorded as dry matter fresh (DMF) and then dried in paper bags at 65°C for 72 h in an oven to a constant weight. The dry samples were then weighed immediately and recorded as dry matter dry (DMD). Storage root DM was calculated as DM = (DMD/DMF) × 100% as described by Gruneberg et al., 2019.

2.5.12 | Internal stem damage index assessment

Five plants per plot were randomly selected for internal weevil damage assessment at harvest. A basal segment (15 cm from the crown) was cut from each vine of the five selected plants. Each piece was split lengthwise using a knife to reveal internal weevil damage and visually assessed and scored for internal weevil damage using a scale of 1–5: 1 = 0%–20% of the basal segments damaged, 2 = 21%–40%, 3 = 41%–60%, 4 = 61%–80%, and 5 = 81%–100% (Muyinza et al., 2012). After scoring for stem damage, all the vines in the plot were collected, weighed, and recorded as fresh vine weight (VW).

2.5.13 | Storage root damage assessment

The storage roots were sorted into weevil-damaged (roots with characteristic dark scarred spots on the surface of the root typical of weevil penetration and feeding) and weevil-clean roots (no dark surface spotting). The incidence of the damage was calculated by expressing the number of weevil-damaged roots as percentage of total number of the roots in a plot (Stathers, Rees, Kabi et al., 2003).

The severity of damage per plot was also recorded at the scale of 1–9: 1 = no damage, 2 = very minor (unclear weevil damage symptoms on the damaged roots per plot), 3 = minor (clear weevil damage symptoms at less than 5%), 4 = minor to moderate (clear weevil symptoms at 6%–15%), 5 = moderate (clear weevil symptoms at 16%–33%), 6 = moderate to heavy (clear weevil damage symptoms at 34%–66%), 7 = heavy (clear weevil damage symptoms at 67%–99%), 8 = heavy to severe (clear weevil damage symptoms on all roots per plot), and 9 = severe (clear weevil damage symptoms on all roots nearly rotting) (Gruneberg et al., 2019).

2.6 | Analysis of variance

Analysis of variance (ANOVA) was performed using an unbalanced ANOVA procedure in Genstat 18th edition statistical packages. The linear model described below was used for analysis of variance across locations and seasons.

$$Y_{\mathrm{ijklm}} = \bar{\bar{Y}} + G_{\mathrm{i}} + L_{\mathrm{j}} + S_{\mathrm{k}} + L_{\mathrm{j}}S_{\mathrm{k}} + G.L_{(\mathrm{ij})} + G.S_{(\mathrm{ik})}$$
$$+ G.L.S_{(\mathrm{IJK})} + L.S/R_{\mathrm{l}} + L.S/\mathrm{Rep}/B_{\mathrm{lm}} + \mathrm{Residual}_{\mathrm{ijklm}}$$

where Y_{ijklm} is the observation, $\bar{\bar{Y}}$ is the grand mean, G_i is the effect of genotype i, L_j is the effect of location j, S_k is the effect of season k, L_jS_k is the interaction of L_j with S_k, $G.L_{(ij)}$ is the interaction of genotype i by location j, $G.S_{(ik)}$ is the interaction of genotypes (i) by season (k), $G.L.S_{(IJK)}$ is the interaction of genotypes (i) by location (j) in season (k), $L.S/R_l$ is the replication effect nested in locations and seasons, and $L.S/\mathrm{Rep}/B_{lm}$ is the block effect nested in locations, seasons, and reps.

2.7 | Correlation and path coefficient analysis

Phenotypic correlations were performed using "corr.test" function from the "psych" package in R-statistical software (Ri386 3.4.1) (R Core Team, 2022). The magnitude and direction of relationships between multiple variables was displayed in heatmap using the "corrplot.mixed" function from "corrplot" package. For all traits that showed significant correlation with field damage of sweetpotato by the SPWs, the "sem" function of "lavaan" package and the "sempaths" function of "semplot" package were used to run the path analysis in R. Path analysis was used to separate the significant correlation coefficients into direct and indirect effects of the independent traits (resistance indicators) on the dependent trait (root damage by SPW).

3 | RESULTS

3.1 | Mean performance of the genotypes, locations, seasons, and their interactions

The combined analysis of variance across the three sites (AbiZARDI, NaSARRI, and NaCRRI) for the two seasons 2017A and 2017B is provided in Table 2. The three locations differed significantly for all the measured traits except for storage root NL. The two seasons used in this study varied significantly for all the studied traits except for storage root shape, storage root weevil damage incidence, and severity. Replications across locations and seasons were not significantly different for most of the traits studied except for stem damage and yield (Table 2).

The effect of genotypes was significantly different for all the measured traits ($p < 0.05$) except for storage root CT. The genotype interaction with location was only significant for VV, storage root damage severity, and FC. Similarly, significant genotype by season interactions were observed for storage FC, storage root DM, and root yield (Table 2).

Three-way interaction ($G.L.S$) effects were highly significant for VV, GC, VW, storage root FC, and DM ($p < 0.001$); storage root skin color and storage root shape ($p < 0.01$); and storage root damage incidence and severity, storage root latex content, and yield ($p < 0.05$). However, the three-way interaction was nonsignificant for root NL, stem damage, and root CT (Table 2).

3.2 | Relationships between weevil field damage and SPW resistance-indicator traits

Means for weevil damage (internal stem damage, root damage incidence, and severity), storage root yield, and SPW resistance-indicator traits averaged over three locations and two seasons are shown in Table 3. Phenotypic correlation coefficients showing the magnitude and direction of relationships between SPW field storage root damage, storage root yield, and SPW resistance-indicator traits combined across locations and seasons are shown in Figure 1.

Storage root damage incidence by SPW correlated negatively and significantly with GC ($r = -0.7$), VW ($r = -0.7$), storage root CT ($r = -0.4$), and DM ($r= -0.4$). Conversely, storage root damage severity correlated negatively and significantly with root NL ($r= -0.6$); storage root DM ($r = -0.4$); VV, GC, and VW. Storage root damage severity was positively correlated and significantly with storage root yield ($r = 0.6$). The present study also showed significant interrelationships among resistance indicator traits (Figure 1).

3.3 | Path coefficients

Several significant interrelationships among the resistance indicator variables and their direct and indirect influences on SPW storage root damage (response variable) were observed in this study (Tables 4 and 5; Figures 2 and 3). All traits that had significant correlation with the SPW root damage incidence showed nonsignificant path coefficients at $p < 0.05$ level (Table 4). Although the path diagram shows GC as a fair indicator of root damage incidence (Figure 2), the direct effect was not significant (Table 4). The nonsignificant direct effects despite significant single-factor correlations is a reflection of the substantial correlations between SPW resistance indicator traits.

For the root damage severity, only storage root NL and yield are shown to be significant indicators at $p < 0.001$. Other traits like VV, GC, VW, and DM had significant correlation with root damage severity but did not have significant direct effects on storage root damage severity (Table 5 and Figure 3).

TABLE 2 Mean squares for weevil infestation, storage root yield, and sweetpotato weevil (SPW) resistance-indicator traits averaged over three locations and two seasons.

Source of variance	df	Vine vigor	Ground cover	Vine weight	Storage root neck length	Stem damage	Storage root damage incidence	Storage root damage severity	Storage root skin color	Storage root flesh color	Storage root latex content	Storage root shape	Storage root cortex thickness	Storage root dry matter	Storage root yield
Location (*L*)	2	11.0***	12.8***	8495.4***	2.1 ns	31.7***	44201***	273.5***	2.0*	1.9**	6.1**	14.7*	77.7***	399.5***	5650.9***
Season (*S*)	1	182.0***	46.1***	6375.7***	66.8***	44.6***	113 ns	2.7 ns	21.5***	4.0***	7.1*	0.3 ns	19.0***	355.3***	6560.8***
L.S	2	108.0***	71.1***	41,481.7***	0.1 ns	8.6***	1739***	3.1*	14.0***	3.2***	0.1 ns	6.7 ns	53.1***	155.7***	3545.6***
L.S/rep	12	4.5 ns	5.9 ns	341.4 ns	1.3 ns	3.3*	391 ns	1.4 ns	1.4 ns	0.3 ns	2.5 ns	5.7 ns	2.6 ns	6.5 ns	121.7*
L.S/rep/block	72	3.5***	3.6***	184.1***	3.3*	1.6***	228**	2.0***	6.0***	3.6***	2.2***	5.5*	2.3 ns	41.7***	61.5***
Entry (*G*)	29	17.7***	16.3***	816.0***	8.6**	2.6**	605**	10.2**	67.3***	64.2***	6.3***	47.6***	5.7 ns	331.9***	204.8*
L.G	58	4.1**	3.2 ns	142.7 ns	2.4 ns	1.2 ns	282 ns	2.2*	1.3 ns	0.6**	1.4 ns	5.7 ns	3.0 ns	19.5 ns	74.3 ns
S.G	29	2.7 ns	2.6 ns	89.4 ns	3.1 ns	1.1 ns	227 ns	1.8 ns	0.7 ns	2.1***	1.7 ns	9.5 ns	3.2 ns	49.7*	87.0*
L.S.G	57	2.1***	2.7***	250.1***	2.0 ns	0.9 ns	213*	1.5*	0.9**	0.7***	1.7*	6.5**	2.1 ns	23.7***	47.1*
Residual	181-260	0.69	0.96	76.7	2.34	0.82	146	0.99	0.56	0.35	1.07	3.75	1.79	12.03	26.13

Note: Trials were conducted at three locations (NaCRRI, AbiZARDI, NaSARRI) and two seasons in Alpha lattice design (5 by 6) with three replications per location in Uganda in 2017.

*, **, *** Significant at $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively. ns, not significant.

TABLE 3 Means for weevil damage, storage root yield, and sweetpotato weevil (SPW) resistance-predictor traits averaged over three locations and two seasons.

Entry	Vine vigor	Ground cover	Vine weight	Neck length	Stem damage	SPW damage incidence	SPW damage severity	Skin color	Flesh color	Latex content	Storage root shape	Root cortex thickness	Storage root dry matter	Storage root yield
	Score	Score	Kg/plot	Score	Score	%	Score	Score	Score	Score	Score	Score	%	kg/lot
ADJ 190	6.8	6	12	6.5	2.1	8.6	1.5	7.6	4.5	5.5	4.6	5	39.8	4.5
APA 356	6.9	5.9	15.5	3.9	1.8	9	2.5	5.6	2.3	3.6	4.1	4	39.4	9.8
APC 136	7.9	7.5	26.6	4.9	2.3	11.3	2.4	2	3.4	4.6	2.9	4.4	37.1	8.1
BRD	3.9	3.5	2	3.3	2.8	33.3	3.9	5.7	8	3.3	3.6	3.1	19.5	12.9
DIMBUKA B.	7.2	6.6	22.5	4.7	2.8	7	2	2.9	3.9	3.9	5.1	3.6	42.7	3.7
EJUMULA	5.3	5	8.1	4.6	2.7	17.8	3.1	3.2	7.8	4	6.4	4.7	34.3	12
MLE 171	6.5	6.2	14	4.9	2.2	11.5	2.8	2	9	5.2	3.5	5.8	43.7	10
MPG 1136	7.7	7	18.5	3.3	2	14.4	3.7	7.9	3.3	5.8	5.1	4.8	41.6	18.4
MSD380	7.2	6.5	16.9	4.6	1.7	12	2.4	4.1	3.2	5.7	4.4	4.2	34.6	10.6
NASPOT 1	7.9	7.1	26.2	2.7	2.6	11.1	2.5	2	4.1	5.2	8.9	4.5	28	4.9
NASPOT 10	6.2	5.6	12	5.9	2.6	14.4	2.9	6.4	7.4	5.1	6	4.8	31.2	16.2
NASPOT 11	7.7	7.2	21.7	4.8	2.3	8.3	1.9	6.6	2.9	4.5	3.4	4.9	30.9	14.4
NASPOT 12	7.7	7.4	30.3	4.5	1.5	12.5	2.2	8	7	5.7	1.1	4.6	32.4	11.8
NASPOT 13	7.1	6.9	25.7	4.4	2	6.3	2.1	4.3	7.7	4.2	4.8	5	33.7	17.2
NASPOT 3	7.3	6.7	20.3	5.2	2.4	9.7	2.6	2	2.9	5.6	4.9	4.9	36	10.6
NASPOT 8	6.8	6.7	21.8	5.6	1.8	11	2.5	7.4	6.6	4.1	2.7	3.9	34.3	18
NK	8.2	7.6	24.9	4.5	1.6	4.6	1.6	7.2	2.8	3.9	3.9	5	40.2	8.1
NKB 10	4.2	3.9	4.9	3.6	2.9	23	3.7	5.8	4.6	3.5	2.1	4.5	34.5	9.8
NKB 135	6.3	5.7	15.9	3.4	2.7	18.7	4.3	6.3	7.9	4.4	3.1	5.1	29.5	18.3
NKB 156	6.6	5.1	7.7	3.6	2.7	16.5	3.6	5.8	3.8	3.9	3.8	4.9	31.9	12.2
NKB 257	4.7	4.2	7.6	3.7	1.9	16.9	3.3	6.1	5.9	5	4.7	4.4	23.4	11.3
NKB 3	5.5	5	9.2	2.8	2.6	24.2	4.7	6.8	7.4	4.4	3	4.7	30.5	20.8
PAL 116	7.4	6.3	19.1	4.1	2.6	16.1	2.3	7.1	2.7	5	4.6	4.7	38.2	8.8
PAL 134	7.1	6.5	20.5	5	2.3	20.3	2.6	2	3.4	5.3	3.7	6	35.2	6.5
PAL 94	6	5.6	12	4.8	1.7	17.1	2.9	2	2.4	4.1	8.4	5	34.7	14.4
SPK 004	6.5	5.9	16.6	4.3	1.9	7.3	1.7	6.3	6.4	4.6	3.7	4.4	34.1	7
SRT02	4.1	4.3	2.1	5.2	2.1	36.4	2.8	2	3.2	3.7	4.3	3.2	38.2	10
SRT03	6.9	6.7	20.5	3.9	2.4	18.3	3.7	7.6	3.2	4.4	5.4	3.8	39.4	14

(Continues)

TABLE 3 (Continued)

Entry	Vine vigor	Ground cover	Vine weight	Neck length	Stem damage	SPW damage incidence	SPW damage severity	Skin color	Flesh color	Latex content	Storage root shape	Root cortex thickness	Storage root dry matter	Storage root yield
SRT27	7.2	7	24.8	4.8	2.1	15.1	3.1	4.7	3.7	4.5	7.4	4.5	37.9	12.3
TZ	6.2	5.6	12.5	3.9	3.4	15.8	3	2	4.4	4.8	6.2	4	30.9	13.3
Minimum	3.9	3.5	2	2.7	1.5	4.6	1.5	2	2.3	3.3	1.1	3.1	19.5	3.7
Maximum	8.2	7.6	30.3	6.5	3.4	36.4	4.7	8	9	5.8	8.9	6	43.7	20.8
Overall mean	6.6	6.0	16.4	4.4	2.3	15.0	2.8	5.0	4.9	4.6	4.5	4.5	34.6	11.7
LSD	1.4	1.2	10.6	2.1	0.7	11.2	1	0.8	1	0.9	2.1		4.8	6.4

Note: Trials were conducted at three locations (NaCRRI, AbiZARDI, NaSARRI) and two seasons with three replications per location in Uganda in 2017.

4 | DISCUSSION

The highly significant differences among the locations (*L*) and entry (*G*) for almost all the studied traits showed considerable diversity in the Ugandan agroecological zones and the sweetpotato germplasm for these traits. This high genetic variation offers a greater chance of obtaining clones with desirable traits and can be effective for heterosis breeding (Oladosu et al., 2015). For instance, among the 30 cultivars used in this study, eight cultivars had a mean field weevil damage incidence of less than 10% and 10 cultivars had mean field weevil damage severity of 1–2. These results could probably be because of the range of sources of origins and genetic history of the genotypes used in this study. Several authors have reported significant cultivar differences among sweetpotato accessions for many important sweetpotato traits (Karan & Sanli, 2021; Gurmu et al., 2018; Hlerema et al., 2017; Muyinza et al., 2012; Mwanga et al., 2003; Stathers, Rees, Kabi et al., 2003; Stathers, Rees, Nyango et al., 2003). Earlier on, farmers from the major sweetpotato growing districts (Masindi, Kasese, Kabale, Wakiso, Soroti, and Gulu) in Uganda identified six sweetpotato land races that they grow to be resistant to the *Cylas* spp. (Okonya et al., 2014). Therefore, these results on resistance could provide potential sources of resistance for breeding purposes. However, there is need for further investigation on these materials to assess their value because Mwanga et al. (2009) indicated that there is no sweetpotato cultivar with high resistance to the *Cylas spp*. among the available germplasm in the world.

However, the significant genotype by location and season interaction observed for SPW root damage indicates that environmental differences greatly affect the resistance of the genotypes to SPW. Significant genotype-by-environment interaction effects on SPW root damage have been reported by previous studies (Anyanga et al., 2017; Yada et al., 2017). This implies that multilocational and multiseasonal trials are necessary when evaluating for SPW resistance. In addition to SPW resistance, this study also showed that most resistance indicator traits measured are sensitive to G*E interactions as demonstrated by the three-way interaction between genotypes, locations, and seasons except for storage root NL.

The fact that storage root damage (incidence and severity) by SPW correlated negatively with traits such as VV, GC, VW, root NL, storage root CT, and DM imply that an increase in the values of these traits may lead to a significant decrease in damage by the weevils. This also means that resistance to SPW is not expressed independently, but rather, it is a result of complex interaction of contributing traits (Khan et al., 2022; Mekonnen et al., 2020). These results are similar to the earlier publications that reported some plant factors and storage root characteristics such as foliage weight, foliage cover, and deep rootedness are associated with resistance to

TABLE 4 Direct effects of the resistance-indicator traits on sweetpotato storage root damage incidence (%), obtained from path analysis.

Resistance indicator	Estimate	Standard error	*z* value	*p* value (> |*z*|)
Ground cover (score)	−3.49	3.24	−1.08	0.28
Vine weight (kg/plot)	−0.14	0.43	−0.33	0.74
DM (%)	−0.07	0.21	−0.32	0.75
Cortex thickness (score)	−1.77	1.51	−1.18	0.24

Note: Any predictor had no significant direct effect on root damage incidence, despite the highly significant simple correlations with root damage incidence.

TABLE 5 Direct effects of the resistance-indicator traits on root damage severity score, obtained from path analysis.

Resistance indicator	Estimate	Standard error	*z* value	*p* value (> |*z*|)
Vine vigor (score)	−0.06	0.26	−0.23	0.82
Ground cover (score)	−0.21	0.47	−0.46	0.65
Vine weight (kg/plot)	−0.01	0.04	−0.18	0.86
Root neck length (score)	−0.42	0.10	−4.10	0.00
DM (%)	0.02	0.02	1.26	0.21
Yield (kg/plot)	0.09	0.02	4.42	0.00

Note: Root neck length had the only significant direct effect on root damage severity according to path analysis, despite significant simple correlations of the above traits with root damage severity.

SPW (Mwanga et al., 2001; Stathers, Rees, Kabi et al., 2003). Since the variation among the genotypes used in this study for these important weevil resistance predictor traits were significant, it can be supposed that the available germplasm contains genotypes that can be used as parents to increase these traits and hence reduce damage by SPW in breeding lines. However, the positive correlation between storage root yield and root damage by SPW was expected. This is because the clones used in this study comprised released varieties, local farmer varieties, and advanced breeding lines, which are high yielding. High yield leads to more soil cracking on the ridges, hence exposure of the storage roots to the weevils. Soil cracking is reported to correlate positively with weevil damage (Stathers, Rees, Kabi et al., 2003).

Through path coefficient analysis, SPW root damage (incidence and severity) was considered as a manufactured object (dependent trait) of all the contributing traits (independent traits), as shown in Figures 2 and 3. Path coefficient analysis is a form of multiple regression analysis through which independent variables produce both direct and indirect effects on a dependent variable (Gurmu et al., 2018; Khan & Dar, 2010; Khan et al., 2022). In this study, because there are some interrelationships among the resistance indicator traits (Figure 1), the variables showed both direct and indirect effects on the root damage by the SPW. We observed significant direct effects of storage root NL and yield on sweetpotato root damage severity by the weevils. This suggests that these traits are true direct indicators of root damage severity. It also implies that these traits have actual contribution to the sweetpotato damage by the weevil (Singh & Chaudhary, 1985). But the positive direct effect of storage root yield on SPW root damage severity is not useful in the context of breeding for resistance. So, this leaves us with deep storage root NL as the only morphological trait in sweetpotato with sufficient predictive power for low root damage severity by the SPW. This may be because deep rooted genotypes tend to render the storage roots inaccessible to the weevils, since the weevils can only burrow a very short distance in soils (Smit, 1997; Stathers, Rees, Kabi et al., 2003). Since the interaction between genotypes and locations and seasons for root NL was not significant, it means genotypes can be reliably selected for long root NL from single environment such as at observational trial (the earliest stage of sweetpotato breeding). Perhaps root NL is under simple genetic control (Yan & Tinker, 2006).

Mwanga et al. (2001) and Stathers, Rees, Kabi et al. (2003) reported that deep rooted genotypes are less likely to be damaged by SPW.

Traits such as VV, GC, VW, DM, and storage root CT that showed significant correlation with root damage incidence and or severity did not show significant direct effects on root damage. This shows the importance of path coefficient analysis in identifying more influential predictor traits than simple correlation analysis. Pavlov et al. (2015, in maize), Gurmu et al. (2018, in sweetpotato), Oladosu et al. (2018, in rice), and Khan et al. (2022, in Bambara groundnuts) reported that path coefficient analysis could be more valuable method than simple correlation analysis in identifying the most influential traits.

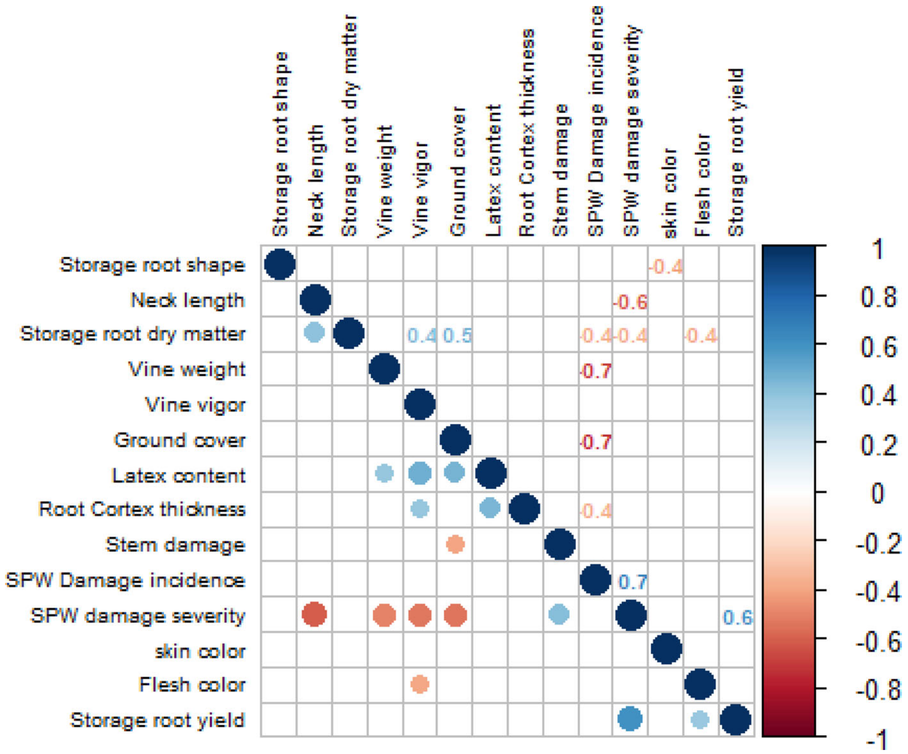

FIGURE 1 Correlation heatmap showing magnitude and direction of relationships among root damage by sweetpotato weevil (SPW), storage root yield, and the resistance-indicator traits.

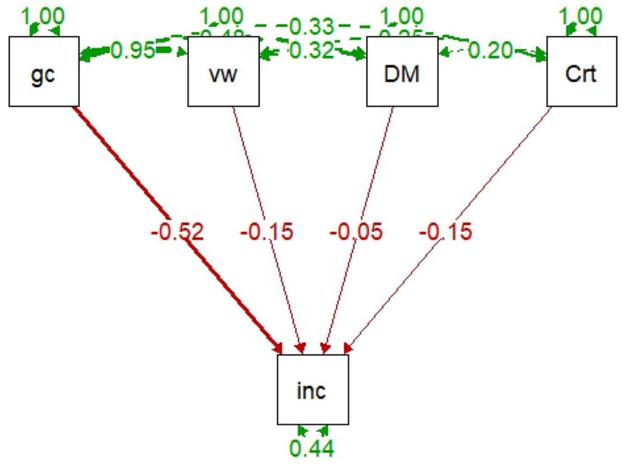

FIGURE 2 Path diagram showing direct and indirect effects of sweetpotato weevil resistance indicator traits on storage root damage incidence (inc). gc, ground cover; vw, vine weight; DM, dry matter content; Crt, cortex thickness.

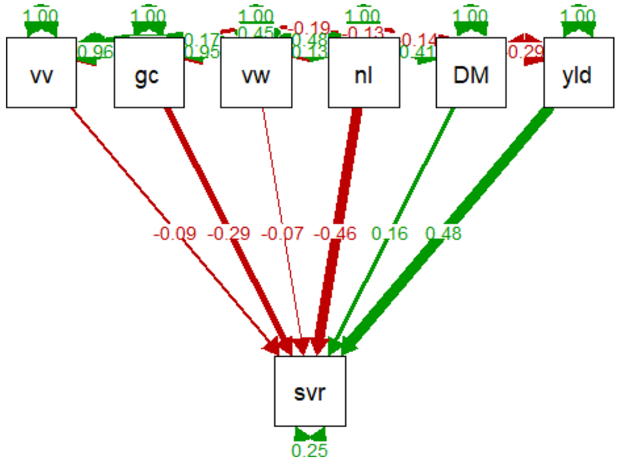

FIGURE 3 Path diagram showing direct and indirect effects of sweetpotato weevil resistance indicator traits on root damage severity (svr). vv, vine vigor; gc, ground cover; vw, vine weight; nl, storage root neck length; DM, dry matter content; yld, yield.

5 | CONCLUSIONS

The relationship between the morphological SPW resistance indicators and field damage by weevils is mostly indirect except for storage root NL. Deep storage root NL may possibly lessen SPW root damage severity. Storage-root NL showed a strong direct effect in path coefficient analysis and may be the most reliable predictor of resistance to SPW among breeding clones at the early breeding stages, which could be done at a single site before advancing clones for multilocation evaluation and analysis for biochemical hydroxycinnamic acids.

AUTHOR CONTRIBUTIONS

Florence Osaru: Conceptualization; data curation; formal analysis; investigation; visualization; writing–original draft. **Jeninah Karungi**: Conceptualization; methodology; supervision; writing–review and editing. **Roy Odama**: Investigation.

Paul Musana: Conceptualization; investigation; methodology. **Milton Anyanga Otema**: Conceptualization; validation; writing–review and editing. **Bonny Oloka**: Writing–review and editing. **Paul Gibson**: Conceptualization; supervision. **Richard Edema**: Project administration. **Reuben Tendo Ssali**: Writing–review and editing. **George Craig Yencho**: Funding acquisition; writing–review and editing. Benard Yada: Conceptualization; funding acquisition; methodology; resources; supervision; writing–review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data collected and used in this work are available upon request from the corresponding author.

ORCID

Reuben Tendo Ssali https://orcid.org/0000-0002-8143-6564

George Craig Yencho https://orcid.org/0000-0001-6583-0628

Benard Yada https://orcid.org/0000-0002-3853-4724

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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