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Beyond nutrients: Frass fertilizer legacy effects for sustainable nematode management in potato–African nightshade rotation systems

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ABSTRACT

The utilization of insect frass fertilizer in crop production systems has recently gained significant global interest, but there has been limited evidence of its residual benefits in rotational cropping systems. The legacy effects of black soldier frass fertilizers (BSFFF), conventional organic fertilizer (SAFI), inorganic fertilizer (NPK), synthetic nematicide, and their combinations on potato cyst nematode (PCN) management under potato-African nightshade rotational farming systems were investigated. Eight treatments were evaluated: BSFFF, SAFI, chitin-fortified BSFFF (BSFFF+5chitin), NPK + nematicide, combination of BSFFF and NPK so that each supplies 50% of the nitrogen required by potato (50BSFFF+50NPK), combination of SAFI and NPK so that each supplies 50% of the nitrogen required (50SAFI+50NPK), chitin-fortified BSFFF and NPK so that each applies 50% of the nitrogen required (50BSFFF+5chitin+50NPK), and unfertilized soil (control). The amendments were applied for four consecutive seasons, and the residual benefits were assessed. The yield and crude protein of nightshade produced were 10 – 153% and 21–31% higher, respectively, compared to the control. Moreover, BSFFF treatments enhanced nightshade yield and crude protein content by 15–61% and 27–33%, respectively, relative to the other amendments. Plots amended with BSFFF+ 5chitin produced African nightshade with 47–71% and 23–87% more leaf numbers and branches than the other amendments. The fertilizer amendments significantly reduced the cyst density by 56 – 71%, and cyst eggs and second stage Juveniles (J2) per g of soil by 87 – 94% compared to the control. The BSFFF+5chitin was superior in reducing PCN population (87 – 94%) compared to other amendments. The BSFFF-based fertilizers significantly improved key soil chemical properties (pH, electrical conductivity, mineral nitrogen, and available phosphorus). These findings provide evidence on the residual effects of BSFFF on soil fertility, crop productivity, and PCN management, and act as a benchmark for guiding regenerative strategies for enhancing productivity and sustainability of smallholder potato-nightshade rotation systems.

1. Introduction

Potato cyst nematodes (PCNs) are widely acknowledged as a key pest affecting potato production globally (Camacho et al., 2020; Onditi and Whitworth, 2024). Their presence in agricultural fields often prompts stringent phytosanitary and regulatory interventions due to their remarkable ability to stay in the soil as dormant cysts for up to 40 years (EPPO, 2022; Orlando and Boa, 2023). Within the smallholder potato farming systems, especially in developing countries, the impact of PCNs is frequently underestimated. This is largely due to the misdiagnosis of nematode-induced symptoms as crop nutrient deficiencies, compounded by a general lack of awareness about nematode pests among farmers (Coyne et al., 2018a). As a result, PCNs receive limited attention within national pest management frameworks, often being overshadowed by more conspicuous pests (Coyne et al., 2018a).

Although chemical nematicides offer a rapid method for reducing PCN populations, their continued use is restricted because of growing concerns over their impact on non-target organisms (Sabarwal et al.,

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2018). In response, a range of alternative strategies has emerged, including biological control with specific microbes (Nyang'au et al., 2023), insect frass fertilizer (Anedo et al., 2024), trap cropping (Hickman and Dandurand, 2023), Suicidal hatching with root exudates (Ngala et al., 2021) and innovative techniques such as wrapping potato seeds with the biodegradable banana fibre paper (Ochola et al., 2022). While these approaches have shown varying degrees of success, no single method has demonstrated consistent efficacy against the two key PCN species across diverse agroecological settings (Price et al., 2021). This scenario justifies the need for integrated and ecologically sound management approaches.

The fortification of the black soldier fly frass fertilizer (BSFFF) with pupal exuviae has shown considerable promise in boosting soil functions and potato performance (Anedo et al., 2025). Its ability to suppress potato cyst nematode populations by up to 98% in a pot trial (Anedo et al., 2024) and 76% under field conditions (Anedo et al., 2025) has been demonstrated. In these studies, the frass fertilizer products performed as well as the synthetic nematicides in the suppression of root knot and potato cyst nematodes. While the precise mechanisms underlying this suppression are not yet fully studied, the high chitin content of the exuviae is believed to contribute significantly to enhancing the nematicidal properties of this fertilizer (Oka, 2010; Quilliam et al., 2020). The exuviae contain more than 10% chitin, according to Lagat et al. (2021) and Kemboi et al. (2022). This chitin source is more economically viable and water-soluble compared to the synthetic chitin derived mainly from crustaceans (Mian et al., 1982), which were previously used for nematode management (Rodriguez-Kabana et al., 1987). Moreover, the fertilizer contains elevated nitrogen levels and a low C: N ratio, conditions that promote faster mineralization. These characteristics enhance the release of ammonia and other key chemical compounds that exert nematotoxic effects (Oka, 2010; Anedo et al., 2024).

Trap cropping has also gained attention as a viable method for PCN control, particularly using non-host nightshade species such as *Solanum sisymbriifolium, S. villosum (*Hickman and Dandurand, 2023; Gómez-Armesto et al., 2025), and *S. scabrum* (Chitambo et al., 2019). The root exudates of these plants contain compounds that stimulate the hatching of PCN eggs (Devine and Jones, 2001; Guerrieri et al., 2019). However, they do not allow the nematodes to grow beyond the juvenile stage (Hickman and Dandurand, 2023). This process disrupts the nematode life cycle and reduces population densities over time (Bhatta et al., 2023; Gómez-Armesto et al., 2025). In Kenya, the effectiveness of African nightshade (*Solanum scabrum*), an indigenous and nutritionally important leafy vegetable in reducing PCN population, has been demonstrated (Chitambo et al., 2019). Depending on species, growth conditions, and root length density (Timmermans et al., 2006), trap cropping with nightshades has been reported to reduce PCN populations by up to 99% (Dandurand and Knudsen, 2016; Hickman and Dandurand, 2023).

Farmers also rely on organic fertilizers, including biochar-based fertilizers such as SAFI, for crop production (Beesigamukama et al., 2020a; Anyega et al., 2021; Anedo et al., 2025) and nematode management in Kenya (Atandi et al., 2017; Anedo et al., 2025). The fertilizer (SAFI) is produced through pyrolysis of rice husks at approximately 400 °C with a residence time of 3 h. This yields a stable, carbon-rich material that is mixed with chicken manure and used for crop production. Globally, biochar-based soil amendments have been widely reported to enhance soil nutrient availability and replenish organic matter (Kammann et al., 2015; Hossain et al., 2020), improve soil physical properties by modifying soil structure and increasing water-holding capacity (Hossain et al., 2020), and stimulating soil microbial activities (Minhas et al., 2020; Yang et al., 2025). Through these mechanisms, biochar can improve soil quality and enhance crop productivity in degraded or nutrient-limited soils (Cong et al., 2023; Leogrande et al., 2024).

Although past studies have demonstrated the benefits of chitin-fortified BSFFF in the suppression of potato cyst nematodes (PCN) and improving soil fertility and crop productivity (Anedo et al., 2024, 2025), existing evidence is based on direct effects, and there has been limited research attention on the residual effects. Yet, previous studies indicate that the residual effects of organic amendments on subsequent crops can vary considerably depending on fertilizer type and application rate (Aguilera et al., 2012), as well as other environmental and soil microclimatic conditions (Taaime et al., 2024). The African nightshade is an indigenous vegetable that has shown promise as a trap crop capable of suppressing PCN populations. However, sustainable production requires an adequate nutrient supply using affordable and regenerative fertilizers. It is, therefore, anticipated that the combined use of frass fertilizer and African nightshade would play a key role in increasing the productivity of the trap crop, maintaining soil health through nutrient replenishment, and enhancing nematode suppression due to synergistic effects. However, there are key research gaps in terms of optimizing soil health and nutrient management of the potato-African nightshade rotation systems and unravelling the residual effects of chitin-fortified BSF frass fertilizer on key soil fertility parameters, PCN densities, and reproduction rate under the African nightshade-potato rotation system. We hypothesized that (1) repeated application of frass fertilizer improves soil fertility and suppressiveness of PCN due to residual effects leading to improved crop yield, and (2) that combined use of insect frass fertilizer and African nightshade rotation system reduces soil nematode densities and enhances soil health through continued supply of nutrients, leading to a more productive and sustainable potato-African nightshade rotation system. Therefore, this study seeks to determine the residual effects of insect frass fertilizer, commercial fertilizers, synthetic nematicide, and the potato-African nightshade rotation system on selected soil chemical properties, PCN population density, and African nightshade growth, yield, and nutritional quality. The findings from this study will play a key role in shaping integrated PCN management approaches aimed at improving the agronomic performance of the potato–African nightshade production systems.

2. Methodology

2.1. Overview of the experimental location

The experiments were carried out over four successive growing seasons at the Potato Research Station of the Kenya Agricultural and Livestock Research Organisation (KALRO) in Tigoni, Kiambu County, between December 2022 and June 2024. Tigoni is situated in Kiambu County, part of the lower midland zone (1°09′03.7″S 36°41′08.3″), at an elevation of 2,131m above sea level. The area experiences a bimodal rainfall pattern, with the short rainy season being witnessed between October and December. Also, the onset and cessation of the long rainy season in the area are between March and May. Annual rainfall in the area averages around 1096 mm, and monthly temperatures typically range between 12 °C and 24 °C, with a mean of approximately 18.0 °C. *Humic nitisol*, known for its deep, well-drained, reddish-brown, and friable clay, dominates the soil of the location, while the soil pH is between 4.3 and 5.82 (Rop et al., 2022). Before experiments, soil samples were collected from 0 to 30 cm using an auger and random sampling techniques, air-dried for five days, and subjected to physico-chemical analyses using standard laboratory procedures. The findings show low concentrations of phosphorus and potassium, high acidity, and clay content. The carbon and nitrogen levels were moderate. The initial properties of the soil at the experimental site are presented in Table 1. During the experimental period, meteorological data for the location were retrieved from the NASA POWER meteorological database(https://power.larc.nasa.gov/data-access-viewer/), which provides satellite-derived environmental and agro-meteorological parameters. The meteorological data for the experimental period showed that the average daily temperatures ranged from 17.2 to 22.9 °C during the short rainy season and 17.2–22.2 °C during the long rainy season (Fig. 1A).

Table 1
Chemical properties of experimental soil, frass fertilizers, and conventional organic fertilizer used during the study.

Parameter	Test soil	Black soldier fly frass fertilizer (BSFFF)	Chitin-fortified BSFFF	Conventional organic fertilizer (SAFI)
pH (H_2O)	5.65	5.49	5.71	5.89
Electrical conductivity (mS cm^{-1})	-	11.8	16.1	5.60
Organic carbon (%)	2.74	43.9	43.6	28.5
Total nitrogen (%)	0.23	3.69	3.91	0.53
Phosphorus (%)	0.001	1.54	1.43	0.11
Potassium (%)	0.09	2.37	2.17	0.86
Calcium (%)	0.11	1.00	2.17	0.23
Magnesium (%)	0.02	0.59	0.61	0.12
Manganese (mg kg^{-1})	365	301	552	534
Iron (mg kg^{-1})	92.1	5710	4780	3340
Zinc (mg kg^{-1})	16.1	191	191	39.2
Copper mg kg^{-1})	2.77	31.8	42.1	4.84
Boron mg kg^{-1})	0.71	26.9	24.7	14.4
Sodium (%)	0.01	0.31	0.28	0.02
Carbon/nitrogen ratio	11.9	11.9	11.2	53.8
Cation exchange capacity (Cmol kg^{-1})	16.5	-	-	-
Acid saturation (%)	1.77	-	-	-
Exchangeable acidity (meq $100g^{-1}$)	0.20	-	-	-
Sand (%)	18.7	-	-	-
Silt (%)	19.9	-	-	-
Clay (%)	61.4	-	-	-
Textural class	Clay	-	-	-

Notes: For soil, the available phosphorus was determined, and the concentrations of potassium and secondary and micronutrients represent exchangeable forms. For BSFFF, chitin-fortified BSFFF, and SAFI, total nutrient concentrations were determined.

The cumulative daily rainfall was 0.31–424.58 mm and 4.69–430.2 mm during the short and long rainy seasons, respectively (Fig. 1B). Cumulative daily root-zone soil moisture ranged from 0.46 to 0.67 cm^3 cm^{-3} during the short rainy season and 0.52 to 0.72 cm^3 cm^{-3} during the long rains (Fig. 1C). This corresponded to approximately 46–72% volumetric soil water content and indicates consistently moist soil conditions close to field capacity and adequate water availability for nightshade growth. The relative humidity during the long rainy season (64–75%) was slightly higher than the values recorded during the short rains (53–75%) (Fig. 1D). These environmental conditions fall within the optimal temperature of 15–35 °C, relative humidity of about 60–90%, moderate rainfall, and adequate soil moisture to support vegetative growth of nightshade (Ojiewo, 2012; Boyomo Sanga Cecile et al., 2025).

2.2. Sources of fertilizers

Black soldier fly frass fertilizer (BSFFF) was sourced from a black soldier fly (BSF) colony maintained at the International Centre of Insect Physiology and Ecology, Nairobi, Kenya. The BSFFF was produced by rearing BSF larvae on brewer's spent grain (barley waste) following the procedure described by Shumo et al. (2019). The larvae were harvested after two weeks, and the resulting frass was composted for five weeks to improve maturity and stability, using the heap composting method described by Beesigamukama et al. (2020a). The chitin-fortified BSFFF (BSFFF+5chitin) was produced by mixing composted BSFFF with a known quantity of BSF pupal exuviae powder to provide 5% chitin, based on the findings of Anedo et al. (2024), who recommended it as the best formulation for nematode suppression. The quantity of pupal exuviae added was based on the pupal chitin concentration of 10% as previously determined by Lagat et al. (2021) and Kemboi et al. (2022). The exuviae were sourced from a BSF colony at *icipe*, washed with tap water, sun-dried for four days, and subsequently ground into a fine powder using a KM-400 mechanical grinder (MRC Laboratory Equipment and Manufacturing, UK). The commercial organic fertilizer SAFI, a biochar-based product, was sourced from Safi Organics Ltd., located in Mwea, Kirinyaga County, Kenya. The fertilizer consists of chicken manure and rice husk-based biochar obtained through pyrolysis at 400 °C for 3 h. Given this widespread use, SAFI was included in this present study as a reference organic amendment to evaluate and compare its agronomic performance and potential for nematode suppression with that of insect frass fertilizer. This comparison will provide insights into the relative effectiveness of these emerging organic soil amendments in improving soil health and managing soil-borne pests.

The mineral fertilizers (muriate of potash [MOP], urea, and triple superphosphate [TSP]) were procured from Kenya Farmers' Association stores in Nairobi. The BSFFF and SAFI were analyzed for nutrient composition and other chemical properties using standard laboratory procedures described by Okalebo et al. (2002). The analytical results are presented in Table 1.

2.3. Treatment structure and experimental design

Eight fertilizer treatments were evaluated in this study. These were: BSFFF, SAFI, BSFFF+5chitin, and NPK, with each applied at a rate equivalent to 150 kg N ha^1, which is recommended for potato production (Otieno and Mageto, 2021). The quantities of organic fertilizers required to meet the nutrient requirements were 4.07 t ha^{-1} for BSFFF, 3.84 t ha^{-1} for BSFFF + 5chitin, and 28.3 t ha^{-1} for SAFI. For the NPK treatment, phosphorus and potassium were applied at 60 kg P ha^{-1}, and 250 kg K ha^{-1}, respectively. Also, a synthetic nematicide was applied to plots treated with NPK for PCN control. The nutrients were supplied using urea (326.1 kg ha^{-1}), triple superphosphate (298.7 kg ha^{-1}), and muriate of potash (1004.3 kg ha^{-1}). The other treatments included combined application of the organic fertilizers (BSFFF, SAFI, and BSFFF+5chitin) and NPK such that each supplied 50% of the total nitrogen required (i.e., 75 kg N ha^{-1}) (50BSFFF + 50NPK). The control treatment consisted of unamended soil. The summary of the treatments and the application rates is provided in Table 2.

The assessment of direct treatment effects was concluded in August 2023 using potato as the test crop and results published in Anedo et al. (2025). The investigation of residual benefits began from September 2023 and ends in June 2024. During the first two cropping seasons (December 2022–August 2023), fertilizer treatments were incorporated at planting by opening the ridges, placing the amendments at an approximate depth of 5 cm, and covering them with soil. Healthy seed tubers of the potato cultivar cv *Shangi* were established in 4 m × 4 m experimental plots, with 75 cm between rows and 30 cm between plants within each row. The trial followed a randomized complete block design (RCBD) with each treatment replicated four times. The fertilizer treatments were applied at the start of each cropping season. Also, the synthetic nematicide (Velum Prime®) (Bayer Crop Sciences UK) was applied at the rate of 0.625 L ha^{-1} based on the company recommendations. The nematicide has fluopyram as the active ingredient.

Following the second potato season, the residual effects of the applied treatments were evaluated by assessing African nightshade performance, as well as the suppression of potato cyst nematodes. The same plots and treatment allocations were retained, and no further fertilizer applications were made. Healthy and pest-free African nightshade seedlings were transplanted into the existing plots at a spacing of 30 cm × 30 cm. The seedlings were irrigated immediately after transplanting to ensure rapid and uniform establishment, and missing plants were replaced two weeks later through gap filling (Ojiewo, 2012). The trial ran for two consecutive cropping seasons, encompassing both the

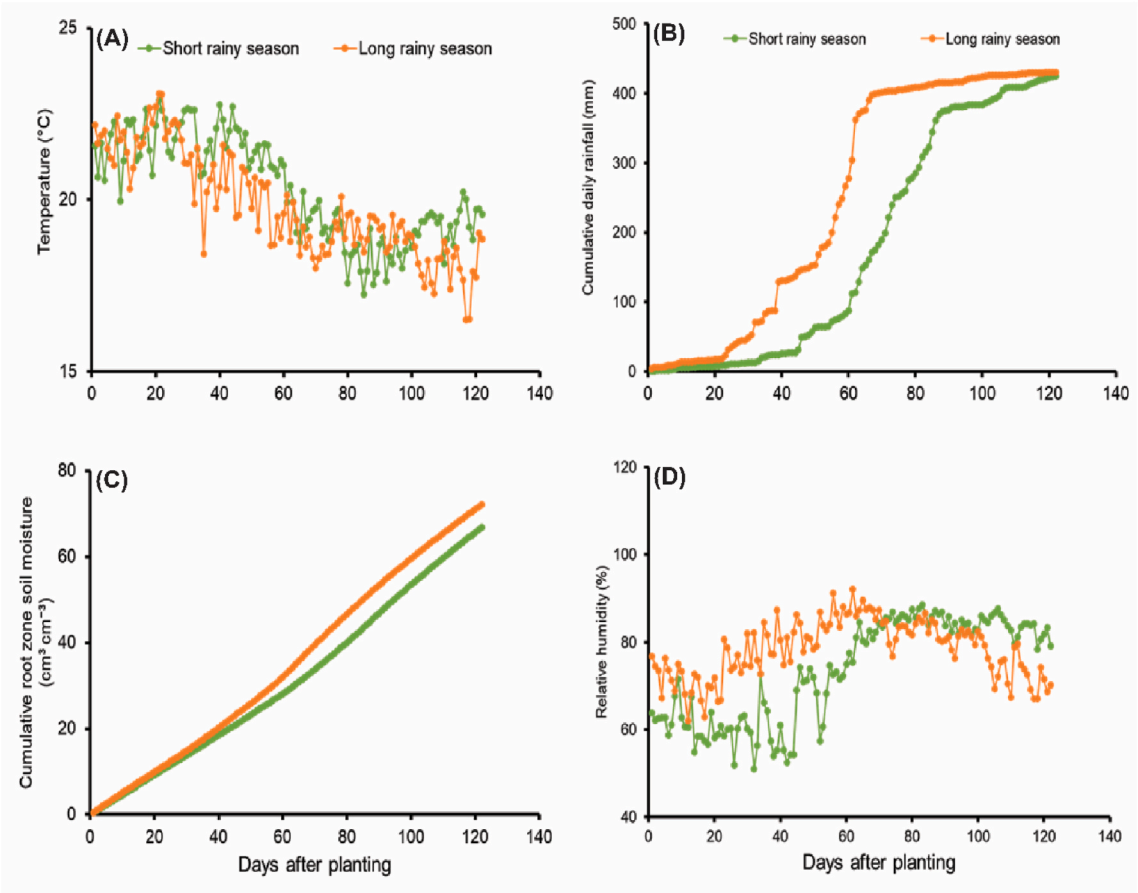


Fig. 1. Daily temperature (A), cumulative daily rainfall (B), cumulative daily root zone soil moisture (C), and relative humidity (D) of the study site during the experimental period.

short and long rainy seasons (September 2023–June 2024). Crop management practices adhered to standard agronomic recommendations for African nightshade (Ojiewo, 2012).

2.4. Data collection on African nightshade growth and yield attributes

Growth attributes of the African nightshade, such as height, leaf count, branch count, stem diameter, and leaf chlorophyll content, were assessed at 8 weeks after planting (WAP). These assessments were done from 10 plants selected at random from the plots. Plant height was measured with the help of a measuring tape. This was done starting from the base to the apical meristem. Leaf counts were recorded by enumerating all the expanded and actively photosynthesizing leaves. Branching intensity was quantified by counting all physiologically active branches on each plant. Stem diameter was assessed from 10 cm above the soil surface with a vernier caliper. Leaf chlorophyll was measured from six fully expanded leaves per plant using a portable SPAD chlorophyll meter. The African nightshades were harvested at two time points, 8 and 12 weeks after planting (WAP). At each harvest, fresh leaves and tender shoots collected from individual plots were weighed with a digital balance, and the measurements were converted to yield on tonnes/hectare basis.

2.5. Soil analysis

At the conclusion of the final experimental season (June 2024), soil samples were randomly picked from each plot at a depth of 0–30 cm and combined to form composite samples in accordance with standard sampling procedures (Knowles and Dawson, 2018). This sampling depth enabled accurate assessment of the effects of fertilizer treatments on the soil nutrient stocks and other parameters in the entire soil depth occupied by both crops used in the rotation (0 – 15 cm for African Nightshade and 0 – 30 cm for potatoes). Representative samples were used for routine soil analysis. Analysis of the soil pH and electrical conductivity was done using a glass-electrode pH meter and an electrical conductivity meter, respectively (Okalebo et al., 2002). Soil organic carbon levels were assessed using the modified Walkley-Black wet oxidation method (Nelson and Sommers, 1996). Mineral nitrogen forms, nitrate (NO_3^-) and ammonium (NH_4^+), were extracted using 0.5 M K_2SO_4 at a 1:10 soil-to-extractant ratio (w/v) and measured colorimetrically at 419 nm and 655 nm, respectively (Okalebo et al., 2002). The available phosphorus in the soil was determined using the Bray II extraction method, followed by colorimetric determination with a spectrophotometer (Jackson, 1973). Exchangeable base cations (K, Ca, Mg, and Na) were extracted with 1 M ammonium acetate (pH 7.0). The exchangeable K was quantified using a flame photometer, while the exchangeable calcium, magnesium, and sodium concentrations were determined by atomic absorption spectrometry at 422.7 nm and 285.2 nm, respectively (Okalebo et al., 2002). Soil cation exchange capacity (CEC) was evaluated by saturating the samples with 1 M ammonium acetate at pH 7 and displacing and quantifying the adsorbed NH_4^+, according to the method described by Bremner (1996).

2.6. Analysis of African nightshade nutritional quality

For the evaluation of nutritional quality, samples were harvested from five pre-selected plants within the central rows of every plot. The collected samples were transported to the laboratory and oven-dried (65 °C) to a constant weight (Seid and Tessema, 2024). The samples were then milled using a mechanical mill (KM-400, MRC Laboratory

Table 2
Summary of treatments used in the study.

Treatment code	Description
Control	Unamended soil
BSFFF	Black soldier fly frass fertilizer applied at a rate equivalent to 150 kg N ha^{-1} per season (i.e., 4.07 t ha^{-1} of BSFFF).
BSFFF+5chitin	Black soldier fly frass fertilizer fortified with 5% chitin from BSF pupal exuviae and applied at a rate equivalent to 150 kg N ha^{-1} per season (i.e, 3.84 t ha^{-1} of BSFFF+5chitin).
SAFI	Conventional biochar-based organic fertilizer applied at a rate equivalent to 150 kg N ha^{-1} per season (i.e., 28.3 t ha^{-1} per season)
NPK + nematicide	Inorganic fertilizer applied at a rate equivalent to 150 kg N ha^{-1}, 60 kg P ha^{-1}, and 250 kg K ha^{-1}, and combined with a synthetic nematicide applied at 0.625 L ha^{-1}.
50BSFFF+50NPK	Combined application of black soldier fly frass fertilizer and inorganic fertilizer so that each supply 50% of the total nitrogen required by potato per season (i.e., 75 kg N ha^{-1} which was equivalent to 2.04 t ha^{-1} of BSFFF and 326.1 kg ha^{-1} of urea). Phosphorus and potassium were applied at rates equivalent to 60 kg P ha^{-1} and 250 kg K ha^{-1}, respectively.
50SAFI+50NPK	Combined application of conventional organic fertilizer and inorganic fertilizer so that each supply 50% of the total nitrogen required by potato per season (i.e., 75 kg N ha^{-1} which was equivalent to 14.15 t ha^{-1} of SAFI and 326.1 kg ha^{-1} of urea). Phosphorus and potassium were applied at rates equivalent to 60 kg P ha^{-1} and 250 kg K ha^{-1}, respectively.
50BSFFF+5chitin +50NPK	Combined application of chitin-fortified black soldier fly frass fertilizer and inorganic fertilizer so that each supply 50% of the total nitrogen required by potato per season (i.e., 75 kg N ha^{-1} which was equivalent to 1.92 t ha^{-1} of BSFFF+5chitin and 326.1 kg ha^{-1} of urea). Phosphorus and potassium were applied at rates equivalent to 60 kg P ha^{-1} and 250 kg K ha^{-1}, respectively.

Notes: These application rates were based on the nutrient requirements for potatoes.

Equipment and Manufacturing, UK) and sieved to obtain particles smaller than 2 mm and stored in sealed polyethylene bags until analysis. The crude protein content of the samples was determined using the methods described by Andualem et al. (2024) (equation (1)). Briefly, 1 g of the milled sample was placed in a Kjeldahl digestion tube and mixed with 12 mL of sulfuric acid, followed by 3 mL of hydrogen peroxide. Three grams of catalyst mixture (copper sulphate and potassium sulphate) was added, and the mixture was allowed to stand for 15 min before digestion at 420 °C for 1 h. The digested samples were subsequently distilled and titrated to determine nitrogen content.

$$\text{Crude protein (\%)} = \text{N (\%)} \times 6.25 \quad (1)$$

Whereby,

N is Kjeldahl nitrogen (%) that was calculated using the formula:

$$\text{N}(\%) = \frac{(\text{Vs} - \text{Vb}) \times \text{M} \times 14.01}{\text{W} \times 10} \quad (2)$$

Vs is the volume of standard acid used to titrate the sample.

Vb is the volume used for the blank.

M is the molarity of HCl.

W is the sample weight (g), and 14.01 is the atomic weight of nitrogen.

The determination of crude ash, crude fiber, and fat was carried out following established standard analytical methods described by Andualem et al. (2024). Analysis of dry matter and metabolizable energy was done using the methods of Islam et al. (2022). The concentrations of mineral elements (Ca, Mg, K, and P) were quantified using inductively coupled plasma–mass spectrometry (ICP-MS) following the procedures outlined by Havlin and Soltanpour (1980).

2.7. Nematode extraction and quantification

At the conclusion of each cropping season, soil was sampled from individual experimental plots and thoroughly mixed to generate composite samples. From each composite, a 200 g subsample was processed for cyst recovery using established extraction procedures (Coyne et al., 2018b). Soil subsamples were dried for seven days (air-drying), followed by cyst recovery using the Fenwick can flotation technique in accordance with EPPO diagnostic guidelines (EPPO, 2013). The cysts were retrieved on milk filter paper, dried for 48 h, and then manually separated using forceps under a stereomicroscope. For assessment of cyst viability, twenty size-uniform cysts were selected per replicate, with three replicates per treatment. The cysts were incubated in 0.01% Nile blue solution (Sigma-Aldrich, USA) for 48 h, following established procedures (Mburu et al., 2020). After staining, the cysts were carefully crushed to release their contents. Viable eggs (unstained), non-viable eggs (stained), and J2s were quantified under a stereomicroscope (LEICA M80) at 40 × magnification. The fertility of the cyst (CF) was defined as the summation of J2s, non-stained and stained eggs per cyst, whereas the viability of the cyst (CV, %) was calculated using equation (3).

$$\text{Cyst viability (\%)} = \frac{\text{J2s} + \text{Viable eggs}}{\text{CF}} \times 100 \quad (3)$$

The efficacy of the fertilizers in suppressing potato cyst nematodes (PCN) was evaluated by determining cyst viability (CV) and the nematode reproduction rate (RR), calculated according to Equations (3) and (4), respectively.

$$\text{Rf} = \frac{Pf}{Pi} \quad (4)$$

Here:

Pf represents the nematode density at harvest, and *Pi* denotes the initial population present before crop establishment (Vanitha et al., 2019).

2.8. Data analysis

The data were first examined for normality using the Shapiro–Wilk test. Thereafter, data on African nightshade growth, yield, nutritional attributes, nematode density, and soil properties were subjected to one-way analysis of variance (ANOVA). Computation of least-squares means was performed with the *lsmeans* package, and differences among treatments were assessed using *Tukey's* test at a significance level of $P \leq 0.05$. To establish the relationship between soil chemical properties and nematode population parameters, principal component analysis (PCA) was performed using the "*prcomp*" function from the "*ggbiplot*" package. For this analysis, nematode and soil data from the long rainy season were used. Due to the bimodal rainfall pattern of the study area, characterized by different climatic conditions, season-based analyses were conducted to evaluate treatment stability under different conditions, and results for growth, yield, and nematode population density were presented based on seasons. All the statistical analyses were performed using the R software (R Core Team, 2025).

3. Results

3.1. Residual effects of insect frass fertilizer on African nightshade yield and nutritional quality

The fertilizer amendments significantly enhanced the African nightshade yield in the two growing seasons (Fig. 2). The nightshade yield increased from 9.56 to 19.88 t ha^{-1} (10–52% increase) in the short rainy season ($P < 0.01$) and from 8.63 to 21.87 t ha^{-1}, representing a 73–153% increase in the long rainy season ($P < 0.001$) relative to the

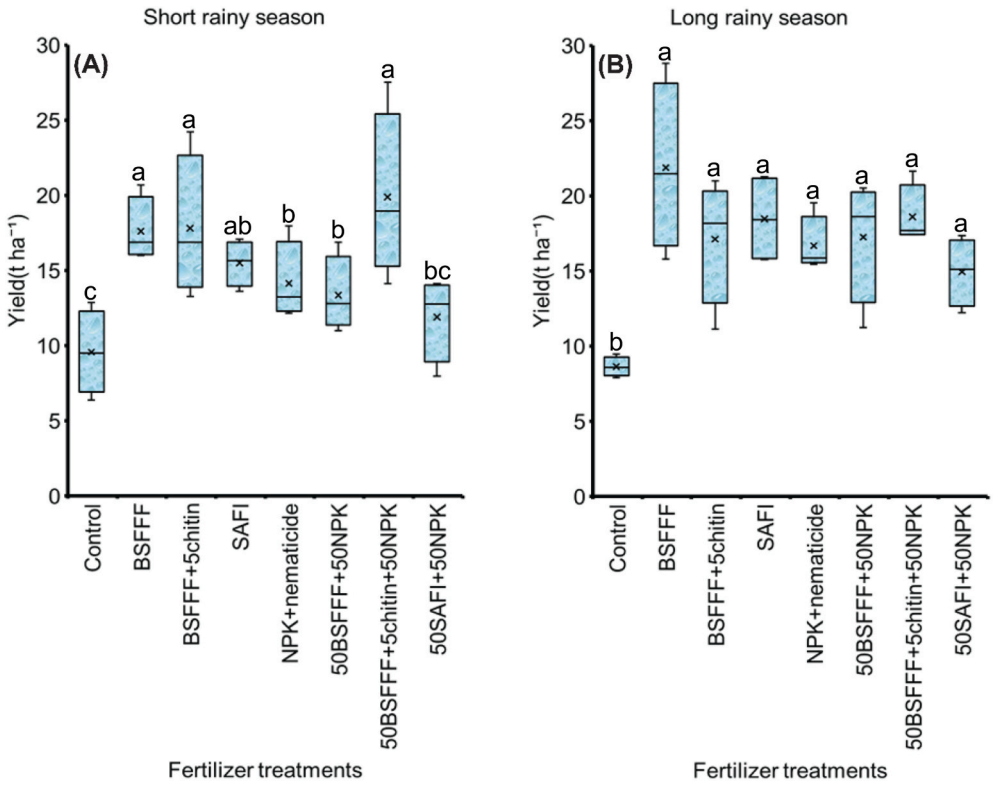


Fig. 2. African nightshade yield as affected by the residual fertilizer treatments.
Control = unamended soil, BSFFF = black soldier fly frass fertilizer applied at a rate equivalent to 150 kg N ha^{-1}, BSFFF+5chitin = black solder fly frass fertilizer applied at a rate of 150 kg N ha^{-1} and fortified with 5% chitin from BSF exuviae, 50BSFFF+50NPK = combined application of black soldier fly frass fertilizer and NPK so that each supplies 50% of the nitrogen required, 50BSFFF+ 5chitin +50NPK = combined application of chitin-fortified BSF frass fertilizer and NPK so that each supplies 50% of the nitrogen required, SAFI=Conventional organic fertilizer applied at a rate equivalent to 150 kg N ha^{-1}, 50SAFI+50NPK = combined application of SAFI and NPK so that each supplies 50% of the nitrogen required, NPK + nematicide = combined application of mineral fertilizer NPK (150 kg N ha^{-1}, 60 kg P ha^{-1} and 250 kg K ha^{-1}) and synthetic nematicide. Per panel, means (± standard error) followed by the same letters are not significantly different at $P < 0.05$.

Table 3
Nutritional quality of the African nightshade as affected by the residual fertilizer treatments.

Treatments	Crude protein (%)	Ash (%)	Crude fat (%)	Crude fiber (%)	Dry matter (%)	Sodium (%)	Calcium (%)	Potassium (%)	Magnesium (%)	Phosphorous (%)	Energy (MJ kg^{-1})
Control	21.00 ± 0.52b	16.9 ± 0.39a	1.1 ± 0.04a	16.5 ± 0.35a	85.4 ± 0.66a	116.2 ± 44.93a	1.3 ± 0.25a	5.5 ± 0.39a	0.4 ± 0.06a	0.3 ± 0.02a	8.8 ± 0.19a
BSFFF	31.1 ± 0.28a	17.8 ± 0.39a	1.4 ± 0.11a	17.1 ± 0.55a	85.6 ± 0.21a	164.2 ± 41.88a	1.4 ± 0.19a	5.3 ± 0.09a	0.4 ± 0.04a	0.4 ± 0.03a	8.8 ± 0.15a
BSFFF + 5 chitin	28.6 ± 0.37a	18.7 ± 0.74a	1.3 ± 0.17a	16.6 ± 0.27a	84.8 ± 0.42a	185.0 ± 26.35a	1.2 ± 0.11a	6.2 ± 0.30a	0.4 ± 0.06a	0.4 ± 0.03a	8.5 ± 0.14a
SAFI	22.8 ± 0.40b	18.0 ± 0.54a	1.1 ± 0.09a	17.6 ± 0.60a	85.5 ± 0.29a	119.0 ± 36.06a	1.1 ± 0.15a	6.0 ± 0.30a	0.3 ± 0.05a	0.4 ± 0.03a	8.6 ± 0.08a
NPK + nematicide	28.6 ± 1.38a	17.7 ± 0.27a	1.0 ± 0.09a	17.0 ± 0.55a	85.1 ± 0.13a	165.3 ± 31.3a	1.3 ± 0.12a	5.8 ± 0.34a	0.4 ± 0.04a	0.4 ± 0.03a	8.6 ± 0.14a
50BSFFF + 50NPK	30.9 ± 1.92a	18.0 ± 0.72a	1.0 ± 0.13a	17.4 ± 0.64a	85.3 ± 0.43a	182.6 ± 50.37a	1.3 ± 0.16a	5.5 ± 0.18a	0.4 ± 0.05a	0.4 ± 0.03a	8.6 ± 0.28a
50BSFFF+ 5chitin +50NPK	28.2 ± 1.15a	17.7 ± 0.82a	1.0 ± 0.07a	17.3 ± 0.65a	84.9 ± 0.23a	162.4 ± 43.61a	1.2 ± 0.03a	5.7 ± 0.12a	0.4 ± 0.03a	0.4 ± 0.03a	8.6 ± 0.23a
50SAFI + 50NPK	29.0 ± 0.31a	17.5 ± 1.00a	1.1 ± 0.08a	16.9 ± 0.28a	84.6 ± 0.24a	168.2 ± 61.46a	1.2 ± 0.11a	5.7 ± 0.24a	0.4 ± 0.03a	0.4 ± 0.03a	8.6 ± 0.18a
LSD	***	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

*** = $P < 0.001$, ns = non-significant. Control = unamended soil, BSFFF = black soldier fly frass fertilizer applied at a rate equivalent to 150 kg N ha^{-1}, BSFFF+5chitin = black solder fly frass fertilizer applied at a rate of 150 kg N ha^{-1} and fortified with 5% chitin from BSF exuviae, 50BSFFF+50NPK = combined application of black soldier fly frass fertilizer and NPK so that each supplies 50% of the nitrogen required, 50BSFFF+ 5chitin +50NPK = combined application of chitin-fortified BSF frass fertilizer and NPK so that each supplies 50% of the nitrogen required, SAFI=Conventional organic fertilizer applied at a rate equivalent to 150 kg N ha^{-1}, 50SAFI+50NPK = combined application of SAFI and NPK so that each supplies 50% of the nitrogen required, NPK + nematicide = combined application of mineral fertilizer NPK (150 kg N ha^{-1}, 60 kg P ha^{-1} and 250 kg K ha^{-1}) and synthetic nematicide. Per column, means (± standard error) followed by the same letters are not significantly different at $P < 0.05$.

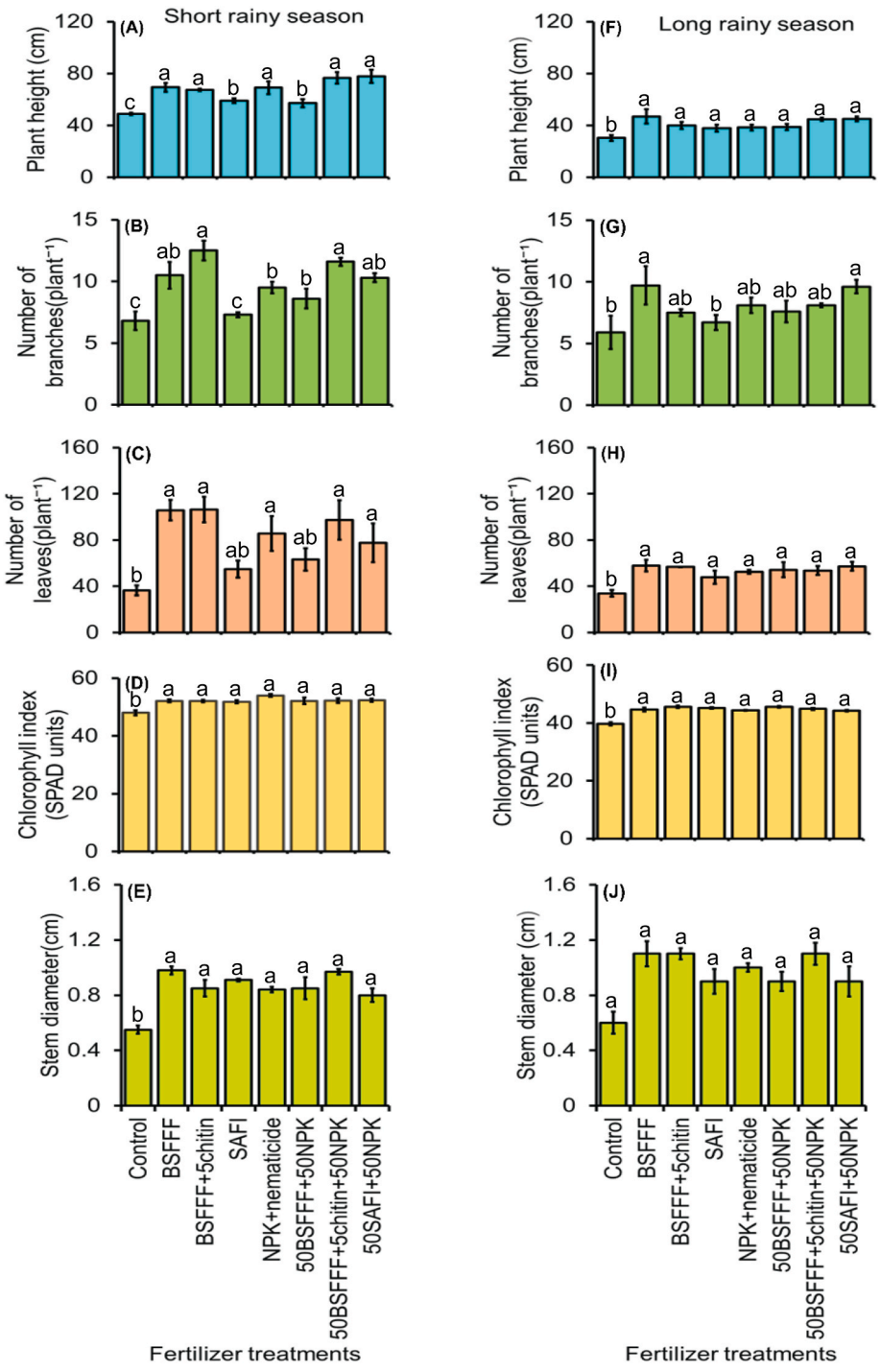


Fig. 3. Residual effects of insect frass fertilizer on African nightshade growth attributes: Height (A and F), branches (B and G), leaves (C and H), chlorophyll index (D and I), and stem diameter (E and J). Figs A–E present growth parameters in the short rainy season, while Figs F – J present growth parameters in the long rainy season.

Control = unamended soil, BSFFF = black soldier fly frass fertilizer applied at a rate equivalent to 150 kg N ha^{-1}, BSFFF+5chitin = black solder fly frass fertilizer applied at a rate of 150 kg N ha^{-1} and fortified with 5% chitin from BSF exuviae, 50BSFFF+50NPK = combined application of black soldier fly frass fertilizer and NPK so that each supplies 50% of the nitrogen required, 50BSFFF+ 5chitin +50NPK = combined application of chitin-fortified BSF frass fertilizer and NPK so that each supplies 50% of the nitrogen required, SAFI=Conventional organic fertilizer applied at a rate equivalent to 150 kg N ha^{-1}, 50SAFI+50NPK = combined application of SAFI and NPK so that each supplies 50% of the nitrogen required, NPK + nematicide = combined application of mineral fertilizer NPK (150 kg N ha^{-1}, 60 kg P ha^{-1} and 250 kg K ha^{-1}) and synthetic nematicide. Per panel, different letters indicate significant differences at $P \leq 0.05$.

unamended soil. During the short rainy season, the 50BSFFF +5% chitin +50NPK treatment had the highest yield increase (19.88 t ha^{-1}). This yield increase was statistically comparable to the BSFFF, BSFFF+5chitin, and SAFI other fertilizer treatments, but higher than 50SAFI +50NPK, 50BSFFF+50NPK, NPK + nematicide, and the unamended soil by 24%, 49%, 41%, and 108%, respectively. During the long rainy season, plants treated with BSFFF had the highest yield increase (21.87 t ha^{-1}). Though statistically comparable to the other treatments, it was higher than the unamended soil by 153%.

The treatments also significantly affected the crude protein content of African nightshade ($P < 0.001$). The crude protein levels increased from 21% to 31.1% (Table 3). The most pronounced protein levels were observed in BSFFF-treated soils (31.1%), which were comparable to other fertilizer treatments but 36% and 48% higher than SAFI and the unamended soil, respectively. No significant effects were observed on other nutritional or quality parameters studied.

3.2. Residual effects of insect frass fertilizer on African nightshade growth attributes

3.2.1. African nightshade height and leaf counts

Application of the amendments led to a significant enhancement of African nightshade height in both the short rainy ($P < 0.001$) and the long rainy ($P < 0.001$) seasons, respectively (Fig. 3). During the short rainy season, the amendments increased the African nightshade heights from 48.8 cm to 77.6 cm. This represents an increase of 17% to 59 % compared to the control. Nightshade grown on SAFI-amended soil produced the tallest plants (77.59 cm). This was statistically similar to the other treatments, but higher than the heights of plants under 50SAFI +50NPK, 50BSFFF +50NPK, and the unamended soil by 24%, 26%, and 37%, respectively. In the long rainy season, the amendments increased the nightshade height from 30.2 cm to 46.9 cm, representing a 25 to 55% increase compared to the unamended soil. Among all the treatments, plants treated with BSFFF were the tallest. Though statistically comparable to the other treatments, it was higher than the unamended soil by 55%. The leaf counts were noticeably enhanced by the amendments in both the short rainy season ($P < 0.001$) and long rainy season ($P < 0.01$) (Fig. 3).

During the short rainy season, the amendments significantly increased the leaf counts from 37 to 107 leaves per plant, representing an increase of 50–192% when compared to the control. Among the treatments, the BSFFF +5% chitin resulted in the highest leaf counts (107 leaves per plant). These leaf counts were comparable to other fertilizer treatments but 107% higher than the unamended soil. In the long rainy season, the amendments increased the number of leaves from 34 to 58 per plant. This represents an increase of 41–71% compared to the unamended soil. BSFFF-treated plants produced the highest leaf counts, which were only higher than the control by 71%.

3.2.2. African nightshade branches, diameter, and leaf chlorophyll content

During the short rainy season, the fertilizer amendments significantly increased nightshade branching from 7 to 13 branches per plant ($P < 0.001$). This represents an increase of 28–87% compared to the unamended soil. Plants treated with BSFFF +5% chitin had the highest number of branches (13 branches) (Fig. 3). This value was statistically comparable to BSFFF and 50BSFFF+5chitin+50NPK but was 23–87% higher than the other fertilizer amendments. In the long rainy season, the fertilizer amendments significantly ($P = 0.05$) affected the nightshade branching. The amendments increased the number of branches from 6 to 10, representing a 13–65% increase compared to the unamended soil. Plants treated with BSFFF had 46% and 65% higher numbers of branches than SAFI and the unamended soil.

The African nightshade stem diameter was highly influenced by the treatments in both the short rainy ($P < 0.001$) and the long rainy ($P < 0.01$) seasons, respectively (Fig. 3). In the short rainy season, the amendments increased the stem diameter from 0.6 to 1.0 cm, representing a 44–78% increase compared to the control. Among the treatments, BSFFF-treated plants had the highest increase in stem diameter. This value was statistically similar to the other fertilizer treatments but higher than the control by 78%. In the long rainy season, the fertilizer amendments increased the plant stem diameter from 0.6 to 1.1 cm, representing a 47–86% increase compared to the control. The combined treatment of 50BSFFF +5% chitin +50NPK resulted in the largest stem diameter. This was higher than the unamended soil by 86%.

The Fertilizer application led to a significant increase in leaf chlorophyll index during both the short rainy ($P < 0.001$) and long rainy ($P < 0.001$) seasons (Fig. 3). In the short rainy season, the fertilizer amendments increased the leaf chlorophyll index from 48 to 54 SPAD units. This represents an increase of 8–13% compared to the control. The NPK + nematicide-treated plants produced leaves with the highest chlorophyll index. Although not significantly different from the other treatments, it was 13% higher than the control. During the long rainy season, the residual fertilizer amendments increased the leaf chlorophyll index from 39.7 to 45.6 SPAD units. This represents a 12% to 15% increase compared to the control. The BSFFF+5%chitin treatment produced plants with the highest leaf chlorophyll index. Although it was comparable to the other treatments, but 15% higher than that of the unamended soil.

3.3. Residual effect of insect frass on potato cyst nematode suppression

3.3.1. Cyst counts, cyst eggs, and J2s counts per cyst

The cyst counts per 200g of soil were significantly reduced in the two cropping seasons (Table 4). During the short rainy season, the fertilizer amendments significantly ($P < 0.001$) reduced the cyst counts from 477 to 148 cysts per g of soil. This represents a 15–69% reduction compared to the unamended soil. However, in the long rainy season, the cysts were reduced from 356 to 104 cyst per g of soil, representing a 17–71% reduction compared to the control. In both seasons, soils amended with BSFFF +5 chitin achieved the highest cyst suppression. This amendment decreased cyst counts by 64% and 49% compared to SAFI and NPK + nematicide, respectively, in the short rainy season. It also reduced cyst counts by 56% and 65%, relative to NPK + nematicide and SAFI, respectively, in the long rainy season. The progressive decline in cyst counts per 200g of soil before the fertilizer applications, after the two seasons of the potato experiments, and the two seasons of the African nightshade rotation system are presented in Fig. 4.

A marked decline in the eggs and J2s density per cyst was observed in the two seasons (Table 2). Relative to the control, the amendments significantly ($P < 0.001$) lowered egg and J2 densities per cyst from 104 to 26, representing a 29–75% reduction during the short rainy season. In the long rainy season, the amendments significantly ($P < 0.001$) lowered the eggs and J2s density from 73.4 to 16.0, representing a 29–78% reduction compared to the unamended soil. Across both seasons, the BSFFF+5chitin exhibited the strongest suppressive effect on cyst eggs and J2s. The treatment reduced the number of eggs and J2s per cyst by 29% and 35% compared to SAFI and NPK + nematicide, in the short rainy season. However, in the long rainy season, its effect was 69% and 69% higher compared to SAFI and NPK + nematicide, respectively.

3.3.2. Cyst eggs and J2 counts per gram of soil and nematode reproduction rate

The residual fertilizer amendments resulted in a significant decline in cyst eggs and J2s per g of soil during both the short rainy ($P < 0.001$) and the long rainy ($P < 0.001$) seasons, respectively (Table 4). In the short rainy season, the amendments reduced the number of cyst eggs and J2s per g of soil from 232 to 19.5, representing a 35–92% reduction compared to the unamended soil. The amendments also reduced the number of cyst eggs and J2s per g of soil from 130 to 8, representing a 41–94% reduction in the long rainy season. Across seasons, the BSFFF +5 chitin amendment resulted in the highest reduction of cyst eggs and J2s per g of soil. It reduced the number of cyst eggs and J2 densities by

Table 4
Potato cyst nematode population density as affected by the residual fertilizer treatments.

Treatments	Short rainy season					Long rainy season				
	Cyst counts per 200g of soil	Eggs and Juveniles count per cyst	Eggs and Juveniles counts per g of soil	Reproduction rate	Nematode reduction (%)	Cyst counts per 200g of soil	Eggs and Juveniles count per cyst	Eggs and Juveniles counts per g of soil	Reproduction rate	Nematode reduction (%)
Control	447.3 ± 17.84a	104.3 ± 4.71a	232.3 ± 5.69a	0.23 ± 0.02b	0	356.0 ± 18.02a	73.4 ± 6.47a	130.1 ± 11.82a	0.6 ± 0.04a	0
BSFFF	182.0 ± 20.24c	32.8 ± 3.39c	30.48 ± 5.63c	0.18 ± 0.05b	86.9	146.5 ± 11.12c	24.8 ± 1.98c	18.1 ± 1.72d	0.7 ± 0.14a	86.1
BSFFF +5 chitin	147.8 ± 17.84c	26.3 ± 3.75c	19.5 ± 3.94c	0.34 ± 0.07b	91.6	104.3 ± 2.29d	16.00 ± 1.13c	8.3 ± 0.64d	0.5 ± 0.13a	93.6
SAFI	409.0 ± 28.91a	74.4 ± 4.27b	152.0 ± 14.15b	0.24 ± 0.04b	34.6	297.0 ± 10.6b	52.2 ± 2.60 ab	77.1 ± 2.52b	0.52 ± 0.04a	40.7
NPK + nematicide	288.8 ± 92.43b	67.9 ± 1.61b	71.9 ± 9.46 ab	3.16 ± 0.44a	69.0	245.8 ± 42.93b	50.9 ± 5.50 ab	63.2 ± 13.43b	0.9 ± 0.21a	51.4
50BSFFF + 50NPK	294.3 ± 62.49b	56.7 ± 11.16b	76.00 ± 4.73 ab	0.62 ± 0.16b	67.3	152.0 ± 24.51c	50.1 ± 5.38 ab	37.6 ± 7.14c	0.5 ± 0.12a	71.1
50BSFFF+ 5chitin +50NPK	242.3 ± 26.21b	73.0 ± 5.10b	86.7 ± 4.76 ab	0.32 ± 0.08b	62.7	177.0 ± 23.93c	44.3 ± 3.64b	38.8 ± 5.24c	0.5 ± 0.07a	70.2
50SAFI + 50NPK	288.8 ± 92.43b	61.1 ± 4.27b	89.2 ± 38.29 ab	0.26 ± 0.09b	61.6	163.3 ± 17.15c	44.2 ± 6.08b	37.5 ± 8.64c	0.5 ± 0.12a	71.2
LSD	***	***	***	***		**	***	***	ns	

*** = $P < 0.001$, ** = $P < 0.01$, ns = nonsignificant. Control = unamended soil, BSFFF = black soldier fly frass fertilizer applied at a rate equivalent to 150 kg N ha^{-1}, BSFFF+5chitin = black solder fly frass fertilizer applied at a rate of 150 kg N ha^{-1} and fortified with 5% chitin from BSF exuviae, 50BSFFF+50NPK = combined application of black soldier fly frass fertilizer and NPK so that each supplies 50% of the nitrogen required, 50BSFFF+ 5chitin +50NPK = combined application of chitin-fortified BSF frass fertilizer and NPK so that each supplies 50% of the nitrogen required, SAFI=Conventional organic fertilizer applied at a rate equivalent to 150 kg N ha^{-1}, 50SAFI+50NPK = combined application of SAFI and NPK so that each supplies 50% of the nitrogen required, NPK + nematicide = combined application of mineral fertilizer NPK (150 kg N ha^{-1}, 60 kg P ha^{-1} and 250 kg K ha^{-1}) and synthetic nematicide. Per column, means (± standard error) followed by the same letters are not significantly different at $P < 0.05$.

87% and 73% compared to SAFI and NPK + nematicide, respectively, in the short rainy season. During the long rainy season, its performance was 87% and 94% greater than NPK + nematicide and SAFI, respectively. The dynamics of cyst egg and J2 populations before fertilizer application, after two consecutive potato cropping seasons, and after the two seasons of the African nightshade rotation are presented in Fig. 5.

The residual fertilizer amendments significantly ($P < 0.001$) reduced the PCN reproduction rate during the short rainy season (Table 4). The lowest nematode reproduction rate (0.18) was observed under BSFFF-amended soil. While there are no significant differences between the other amendments in lowering the PCN reproduction rate, a higher nematode multiplication rate of 3.16 was observed under NPK + nematicide treatment. The nematode reproduction rate was not significantly influenced by the treatments in the long rainy season ($P = 0.154$).

3.4. Effect of the residual fertilizer treatments on soil chemical attributes

The amendments had a significant impact on soil pH ($P < 0.05$) (Table 5). Compared to the unamended soil (pH 5.43), the amended soils exhibited higher pH values, increasing to a maximum of 6.18, an approximate rise of 0.8 units. The highest pH was observed in soils receiving BSFFF alone. Although statistically comparable to other fertilizer treatments, this value was 12% greater than that of the unamended soil. Soil ammonium (NH_4^+) concentrations were also significantly affected by the fertilizer amendments ($P < 0.001$) (Table 3). The NH_4^+ concentration in the amended soil increased from 14.2 to 22.2 mg kg^{-1}. The most pronounced rise in NH_4^+ was recorded in soils amended with BSFFF +5 chitin (2.22 mg kg^{-1}), which, despite being statistically similar to the other fertilized treatments, was higher than the unamended soil by 36%. In addition, soil nitrate (NO_3^-) levels varied significantly among the amendments ($P < 0.01$). The NO_3^- concentration in the amended soil increased from 10.8 to 19.8 mg kg^{-1}. However, the highest NO_3^- concentration (19.8 mg kg^{-1}) was noticed in plots treated with 50BSFFF+5%chitin+50NPK, a value comparable to other treatments but 45% higher than unamended soil.

The fertilizer amendments significantly influenced the available phosphorus concentrations in the soil ($P < 0.001$) (Table 5). The amendments increased the soil available P from 14.1 to 23.1 mg kg^{-1}. However, the most significant enhancement in available P (23.11 mg kg^{-1}) was recorded in SAFI-amended soils. This response was similar to that observed under BSFFF, 50BSFFF + chitin +50NPK, NPK + nematicide, and 50BSFFF +50NPK, but greater than the other amendments by 21–39%. The residual fertilizer amendments significantly ($P < 0.001$) increased the soil organic carbon levels from 3.1 to 4.3% (Table 5). Among the treatments, SAFI-treated soils had the most pronounced rise in soil organic carbon levels (4.3%). This was noticeably higher by 9–28% when compared to the other treatments. Also, the soil electrical conductivity (EC) was highly influenced by the residual fertilizer treatments ($P < 0.001$). Significant improvements in the soil electrical conductivity (EC) were also observed. The amendments increased the soil EC from 57.8 to 95.9 μS cm^{-1}. The most pronounced increase in EC (95.9 μS cm^{-1}) was observed in 50BSFFF + 5 chitin +50NPK-treated soil. Although statistically similar to most of the treatments, this value was 39%, 40%, and 40% higher than those recorded under 50SAFI +50NPK, BSFFF +5% chitin, and the unamended soil, respectively.

3.5. Multivariate analysis of the relationship between soil chemical properties and nematode population parameters

The principal component analysis (PCA) of soil chemical properties and potato cyst nematode population parameters revealed a clear relationship between the two variables. The first two principal components explained 59.1% of the total variance. PC1 accounted for 36.1% of the total variance, while PC2 accounted for 23.0% (Fig. 6). Along PC1, nematode population parameters (cyst counts, eggs, and J2 per cyst,

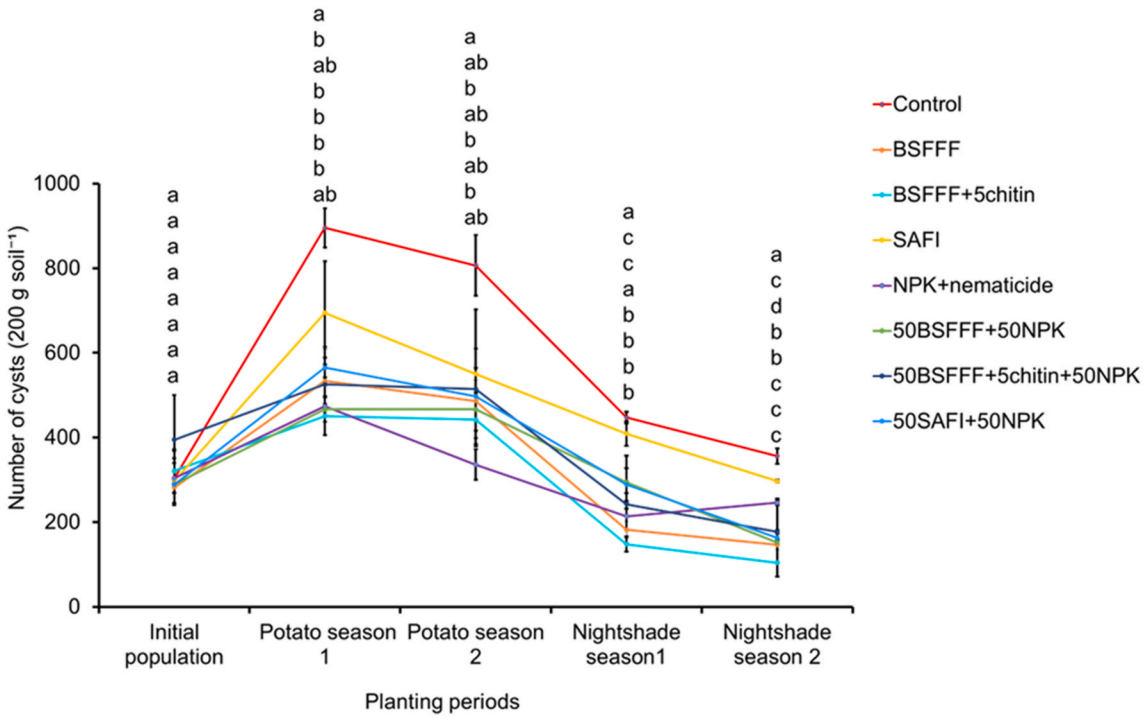


Fig. 4. Progressive decline in cyst counts per gram of soil in the potato-African nightshade rotation system.
Control = unamended soil, BSFFF = black soldier fly frass fertilizer applied at a rate equivalent to 150 kg N ha^{-1}, BSFFF+5chitin = black solder fly frass fertilizer applied at a rate of 150 kg N ha^{-1} and fortified with 5% chitin from BSF exuviae, 50BSFFF+50NPK = combined application of black soldier fly frass fertilizer and NPK so that each supplies 50% of the nitrogen required, 50BSFFF+ 5chitin +50NPK = combined application of chitin-fortified BSF frass fertilizer and NPK so that each supplies 50% of the nitrogen required, SAFI=Conventional organic fertilizer applied at a rate equivalent to 150 kg N ha^{-1}, 50SAFI+50NPK = combined application of SAFI and NPK so that each supplies 50% of the nitrogen required, NPK + nematicide = combined application of mineral fertilizer NPK (150 kg N ha^{-1}, 60 kg P ha^{-1} and 250 kg K ha^{-1}) and synthetic nematicide. The letters at different points of the line graph indicate statistical differences in correspondence with the order of treatments per data point. Per data point, different letters indicate significant differences at $P \leq 0.05$.

eggs and J2 per gram soil, and reproduction rate) were closely aligned, indicating strong positive correlations among these variables. This pattern suggests that increases in cyst density were associated with higher egg and juvenile populations.

In contrast, cation exchange capacity (CEC), EC, calcium, potassium, magnesium, ammonium nitrogen, pH, and organic carbon were clustered together in the negative direction. This indicates negative correlations between these selected soil chemical properties and nematode population parameters. This distribution suggests that improvements in these soil chemical parameters were generally associated with enhanced nematode suppression. Additionally, amendments associated with improved soil chemical properties tended to cluster away from the nematode population parameters. However, the unamended soil (control) was more closely associated with higher nematode populations. Generally, the PCA indicates an inverse relationship between soil chemical properties and nematode population dynamics. These findings suggest that the efficacy of insect frass fertilizer (BSFFF) in improving soil fertility and nematode suppression can extend beyond one cropping season.

4. Discussion

4.1. African nightshade performance as affected by the residual fertilizer treatments

Understanding the residual effects of soil amendments is critical for developing sustainable nutrient management strategies, particularly in smallholder production systems where fertilizer inputs are often limited (Demelash et al., 2014; Leogrande et al., 2024). Residual fertility from previously applied organic or integrated nutrient sources can impact soil nutrient availability, plant growth, and crop productivity beyond the initial cropping season (Aguilera et al., 2012; Reeve et al., 2012; Taaime et al., 2024). This carry-over effect is especially relevant for organic amendments, which release nutrients gradually and improve soil biological and physicochemical properties over time (Reeve et al., 2012). Such benefits are key for rotational cropping systems whose productivity relies greatly on soil nutrient stocks and subsequent management practices. This scenario is common in smallholder farms of sub-Saharan Africa and other developing countries that rely on small pieces of land with little or no external nutrient inputs.

In the present study, the residual effects of insect frass fertilizer and their integration with mineral fertilizers significantly enhanced the vegetative growth, yield, and nutritive value (crude protein concentration) of African nightshade, a key crop in the rotation system due to its role in augmenting pest suppression. To derive maximum benefit from such systems, proper soil health and pest management are imperative. Our results further suggest that organic fertilizers such as black soldier fly frass fertilizer or its combination with mineral fertilizers can provide longer-term agronomic benefits compared with sole mineral fertilization, largely due to their ability to improve soil fertility while simultaneously enhancing soil biological processes. Therefore, the sustained improvements in African nightshade performance as seen in our study could be attributed to enhanced soil fertility from continued application of organic amendments as previously reported (Dhaliwal et al., 2023; Onyuka et al., 2025). Importantly, these responses persisted beyond the first cropping cycle, demonstrating a carry-over fertility effect attributable to the applied fertilizer regimes (Demelash et al., 2014). Such residual carryover benefits are commonly attributed to sustained improvements in soil properties (Otieno et al., 2022), root development, nutrient availability, and moisture storage, leading to better nutrient

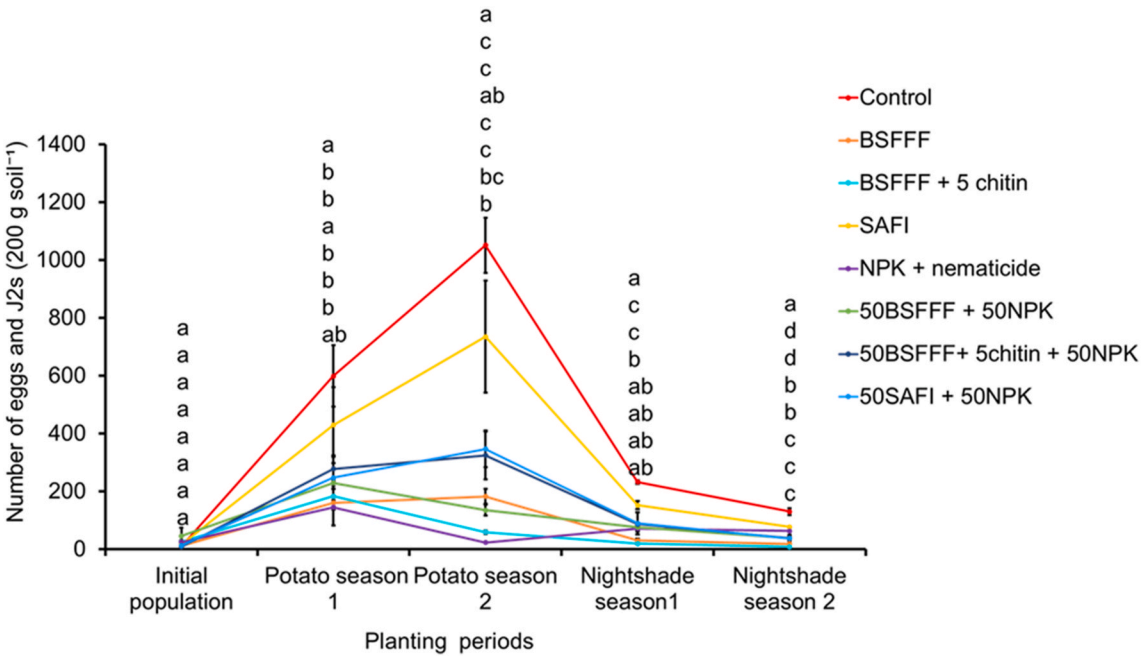


Fig. 5. Progressive decline in cyst eggs and infective J2 counts per gram of soil in the potato-African nightshade rotation system.
Control = unamended soil, BSFFF = black soldier fly frass fertilizer applied at a rate equivalent to 150 kg N ha^{-1}, BSFFF+5chitin = black solder fly frass fertilizer applied at a rate of 150 kg N ha^{-1} and fortified with 5% chitin from BSF exuviae, 50BSFFF+50NPK = combined application of black soldier fly frass fertilizer and NPK so that each supplies 50% of the nitrogen required, 50BSFFF+ 5chitin +50NPK = combined application of chitin-fortified BSF frass fertilizer and NPK so that each supplies 50% of the nitrogen required, SAFI=Conventional organic fertilizer applied at a rate equivalent to 150 kg N ha^{-1}, 50SAFI+50NPK = combined application of SAFI and NPK so that each supplies 50% of the nitrogen required, NPK + nematicide = combined application of mineral fertilizer NPK (150 kg N ha^{-1}, 60 kg P ha^{-1} and 250 kg K ha^{-1}) and synthetic nematicide. The letters at different points of the line graph indicate statistical differences in correspondence with the order of treatments per data point. Per data point, different letters indicate significant differences at $P \leq 0.05$.

uptake and improved crop performance (Tilahun-Tadesse et al., 2013; Taaime et al., 2024).

The findings of this study align with earlier reports demonstrating the beneficial effects of BSF frass fertilizer amendments on production through enhanced nutrient uptake and use efficiency in crops such as kales, spinach, and French beans (Anyega et al., 2021), broccoli (Kagehi et al., 2025), Swiss chard (Abiya et al., 2022, 2025), maize (Beesigamukama et al., 2020b; Tanga et al., 2021), Chicory and Plantain (Hodge and Conway, 2022), beans and cereal seedlings (Carroll et al., 2023; Chepkorir et al., 2024). Moreover, frass fertilizer is associated with improved plant defence through the suppression of aboveground and belowground pests, attraction of natural enemies (Kimuli et al., 2025; Kiriga et al., 2026), and induction of systemic plant resistance through upregulation of defence genes (Mutyambai et al., 2025). Furthermore, residual benefits of organic inputs have been widely linked to improvements in soil fertility and better synchrony of nutrient release for uptake by crops (Beesigamukama et al., 2020a, 2020b; Bhalshakar, 2020; Dhaliwal et al., 2023). This process leads to increased biomass accumulation and higher yield in subsequent seasons (Nasar et al., 2022; Taaime et al., 2024).

Beyond observed yield responses, the elevated crude protein content of African nightshade under BSFFF and BSFFF + NPK treatments highlights the additional benefit of improved nutritive value of crops, which is key for ensuring food and nutrition security. This is because vegetables are key contributors to household food security globally. The improved nutritive value is likely driven by improved soil nitrogen availability and enhanced nitrogen use efficiency, both of which are critical determinants of protein synthesis in food crops (Dimante et al., 2024; Kurt et al., 2025). Our results, therefore, corroborate earlier findings indicating that BSFFF application can enhance crude protein content in crops (Beesigamukama et al., 2020b; Anyega et al., 2021; Kagehi et al., 2025), mainly through sustained improvements in nitrogen supply and uptake (Beesigamukama et al., 2020a). This is because nitrogen is a key element that helps in amino acid and protein synthesis, and its availability has been shown to directly influence protein accumulation in different crops (Öztürk et al., 2010; Martirosyan et al., 2024).

On the other hand, the relatively higher nightshade yield achieved using biochar-based organic fertilizer (SAFI) may be linked to improvements in soil physicochemical properties (Hu et al., 2023), a response that has also been documented in soils amended with biochar-based fertilizers (Luis Moreno et al., 2022; Singh Karam et al., 2022). Our results align strongly with earlier research evidence demonstrating that carbon-rich soil amendments enhance crop productivity by promoting improved soil functional processes (Raboin et al., 2016; Cong et al., 2023). Future studies should consider the integration of frass fertilizer with SAFI to ensure balanced improvements in both physical and chemical properties that are key for yield maximization.

The integration of organic and synthetic nutrient sources has been demonstrated to balance nutrient supply and improve synchronization between nutrient release and crop demand, resulting in balanced plant nutrition (Abedi et al., 2010). These readily available mineral nutrients support early crop demand while organically bound nutrients are released more gradually, contributing to sustained soil health for better crop productivity (Demelash et al., 2014). Such a nutrient release pattern likely explains the superior crop performance observed under BSFFF-based treatments, either applied solely (van de Zande et al., 2024) or integrated with NPK (Anyega et al., 2021), and highlights the potential of BSFFF-based amendments as a sustainable nutrient management strategy for improving the productivity and nutritional quality of low-nutrient input cropping systems such as the potato-African nightshade rotation system that was assessed during the study.

Table 5
Residual effect of the fertilizer treatments on soil chemical attributes.

Treatments	pH(H_2O)	Electrical conductivity (µS cm^{-1})	Ammonium (mg kg^{-1})	Nitrate (mg kg^{-1})	Available phosphorus (mg kg^{-1})	Potassium (Cmol kg^{-1})	Calcium (Cmol kg^{-1})	Magnesium (Cmol kg^{-1})	Sodium (Cmol kg^{-1})	CEC (Cmol kg^{-1})	Organic carbon (%)	Sulphur (mg kg^{-1})
Control	5.4 ± 0.17b	57.8 ± 1.34b	14.2 ± 0.27b	10.8 ± 0.62b	14.1 ± 0.29b	1.72 ± 0.26a	6.0 ± 0.88a	1.2 ± 0.08a	0.08 ± 0.01a	16.2 ± 1.55a	3.1 ± 0.04b	11.5 ± 1.91a
BSFFF	6.2 ± 0.19a	84.5 ± 6.95 ab	21.2 ± 1.16a	17.1 ± 1.85 ab	23.1 ± 0.51a	2.6 ± 0.22a	9.0 ± 0.78a	2.4 ± 0.23a	0.08 ± 0.02a	18.3 ± 0.91a	3.9 ± 0.03 ab	12.1 ± 0.31a
BSFFF+5 chitin	5.9 ± 0.11 ab	57.4 ± 5.77b	22.2 ± 0.38a	14.5 ± 1.97 ab	18.2 ± 1.41 ab	2.1 ± 0.25a	6.5 ± 0.54a	1.8 ± 0.18a	0.07 ± 0.01a	14.5 ± 0.74a	3.7 ± 0.16 ab	11.2 ± 0.95a
SAFI	6.1 ± 0.17a	69.4 ± 3.88 ab	20.8 ± 0.68a	12.9 ± 0.93 ab	23.1 ± 1.52a	2.4 ± 0.16a	7.6 ± 1.50a	1.9 ± 0.19a	0.05 ± 0.01a	15.8 ± 0.71a	4.3 ± 0.23a	11.4 ± 0.31a
NPK + nematicide	5.5 ± 0.17 ab	72.0 ± 6.37 ab	22.0 ± 1.22a	13.7 ± 1.51 ab	21.4 ± 2.09a	2.5 ± 0.17a	7.3 ± 0.77a	1.8 ± 0.23a	0.06 ± 0.01a	16.0 ± 0.83a	3.5 ± 0.16 ab	11.4 ± 0.31a
50BSFFF+50NPK	5.8 ± 0.20 ab	68.2 ± 2.27 ab	20.1 ± 0.67a	13.2 ± 2.18 ab	18.3 ± 0.96 ab	2.3 ± 0.33a	6.7 ± 0.93a	1.8 ± 0.30a	0.06 ± 0.01a	14.9 ± 1.02a	3.7 ± 0.38 ab	13.4 ± 1.91a
50BSFFF+5chitin+50NPK	5.8 ± 0.09 ab	95.9 ± 15.33a	20.8 ± 0.24a	19.8 ± 3.00a	22.2 ± 0.21a	2.3 ± 0.12a	8.0 ± 0.86a	2.1 ± 0.19a	0.04 ± 0.01a	17.0 ± 1.05a	3.7 ± 0.17 ab	12.0 ± 0.80a
50SAFI+50NPK	5.8 ± 0.14 ab	58.5 ± 6.51b	21.0 ± 1.29a	12.1 ± 0.13 ab	17.88 ± 1.15 ab	2.1 ± 0.23a	7.6 ± 0.78a	1.9 ± 0.31a	0.05 ± 0.01a	16.0 ± 1.90a	3.6 ± 0.21 ab	11.5 ± 0.36a
LSD	*	***	***	**	***	ns	ns	ns	ns	ns	*	ns

*** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$. CEC = cation exchange capacity, Control = un amended soil, BSFFF = black soldier fly frass fertilizer applied at a rate equivalent to 150 kg N ha^{-1}, BSFFF+5chitin = black solder fly frass fertilizer applied at a rate of 150 kg N ha^{-1} and fortified with 5% chitin from BSF exuviae, 50BSFFF+50NPK = combined application of black soldier fly frass fertilizer and NPK so that each supplies 50% of the nitrogen required, 50BSFFF+ 5chitin +50NPK = combined application of chitin-fortified BSF frass fertilizer and NPK so that each supplies 50% of the nitrogen required, SAFI=Conventional organic fertilizer applied at a rate equivalent to 150 kg N ha^{-1}, 50SAFI+50NPK = combined application of SAFI and NPK so that each supplies 50% of the nitrogen required, NPK + nematicide = combined application of mineral fertilizer NPK (150 kg N ha^{-1}, 60 kg P ha^{-1} and 250 kg K ha^{-1}) and synthetic nematicide. Per column, means (± standard error) followed by the same letters are not significantly different at $P < 0.05$.

4.2. Potato cyst nematode population dynamics as affected by residual fertilizer treatments

Organic amendments and/or their integration with mineral fertilizers are widely recognized for their capacity to influence soil nematode communities and population dynamics (Cadet and Thioulouse, 1998; Li et al., 2010; Stefanovska et al., 2022; Tian et al., 2025). These inputs can modify soil physicochemical and biological properties, thereby altering habitat conditions and resource availability for plant-parasitic nematodes (Oka, 2010). However, despite the growing body of research on the immediate impacts of organic amendments on nematode populations, little attention has been given to their residual effects on nematode suppression across subsequent cropping cycles. Understanding such carry-over effects is important because organic amendments often release nutrients gradually and induce longer-term changes in soil biological activity (Hallmann et al., 1999; Oka, 2010; Tian et al., 2025).

In this study, the observed higher decline in potato cyst nematode populations in plots amended with chitin-fortified frass fertilizer (BSFFF + 5chitin) suggests that the suppressive effects of this organic input are not confined to a single season, a game changer for sustainable nematode management. The findings of this study indicate that insect frass fertilizer exhibits a residual nematode-regulating influence that persists into subsequent cropping cycles. This enhanced nematode suppression associated with the BSFFF+5chitin is likely mediated through biologically driven mechanisms, particularly the stimulation of chitinolytic microbial communities (Jung et al., 2002). These microbes either directly attack nematode eggs or synthesize antimicrobial compounds that inhibit nematode development (Jin et al., 2005). Also, this suppressive response may be driven by enhanced soil chitinase activity and the presence of other chitin-degrading enzymes (Mwaheb et al., 2017), which are widely recognized for their role in mediating biological nematode suppression (Rodriguez-Kabana et al., 1987). Furthermore, increased soil food web complexity associated with organic inputs promotes predatory and antagonistic microorganisms that contribute to biologically mediated suppression (Liang et al., 2020; Rahman et al., 2024).

Changes in soil chemical properties induced by organic amendments may further contribute to PCN suppression. For instance, changes in the soil organic carbon, electrical conductivity, pH, and other soil chemical properties following the application of organic inputs can create less favorable conditions for nematode survival, development, and reproduction (Tian et al., 2020; Abdelkader et al., 2022). The negative correlation between soil chemical properties and nematode population parameters, as observed in the principal component analysis (Fig. 6), validates these claims and further positions insect frass fertilizer as a biorational input for both immediate and sustained nematode suppression.

Studies have shown that the suppressive effects of organic amendments on plant parasitic nematodes are influenced by several interacting factors, including the type and quality of the amendment, their chemical composition, application rate, target nematode species, timing of incorporation, and prevailing agronomic and environmental conditions (Oka, 2010; Radwan et al., 2012; Renčo et al., 2016). Therefore, future research efforts should explore the effect of different application rates and placement methods of chitin-fortified BSF frass fertilizer on nematode suppression parameters, with a focus on different species of pant parasitic nematodes and the time required to reduce the populations to values below economic injury.

The significantly higher nematode reproduction rate observed under the NPK + nematicide treatment during the short rainy season can be attributed to the absence of sustained chemical suppression following nematicide (Velum®) application. Although fluopyram (the active ingredient in Velum®) has been shown to reduce nematode populations shortly after application, its efficacy declines over time due to chemical degradation and microbial transformation in soil (Khanal et al., 2022; Alam et al., 2023). Consequently, the suppressive effect is transient, and

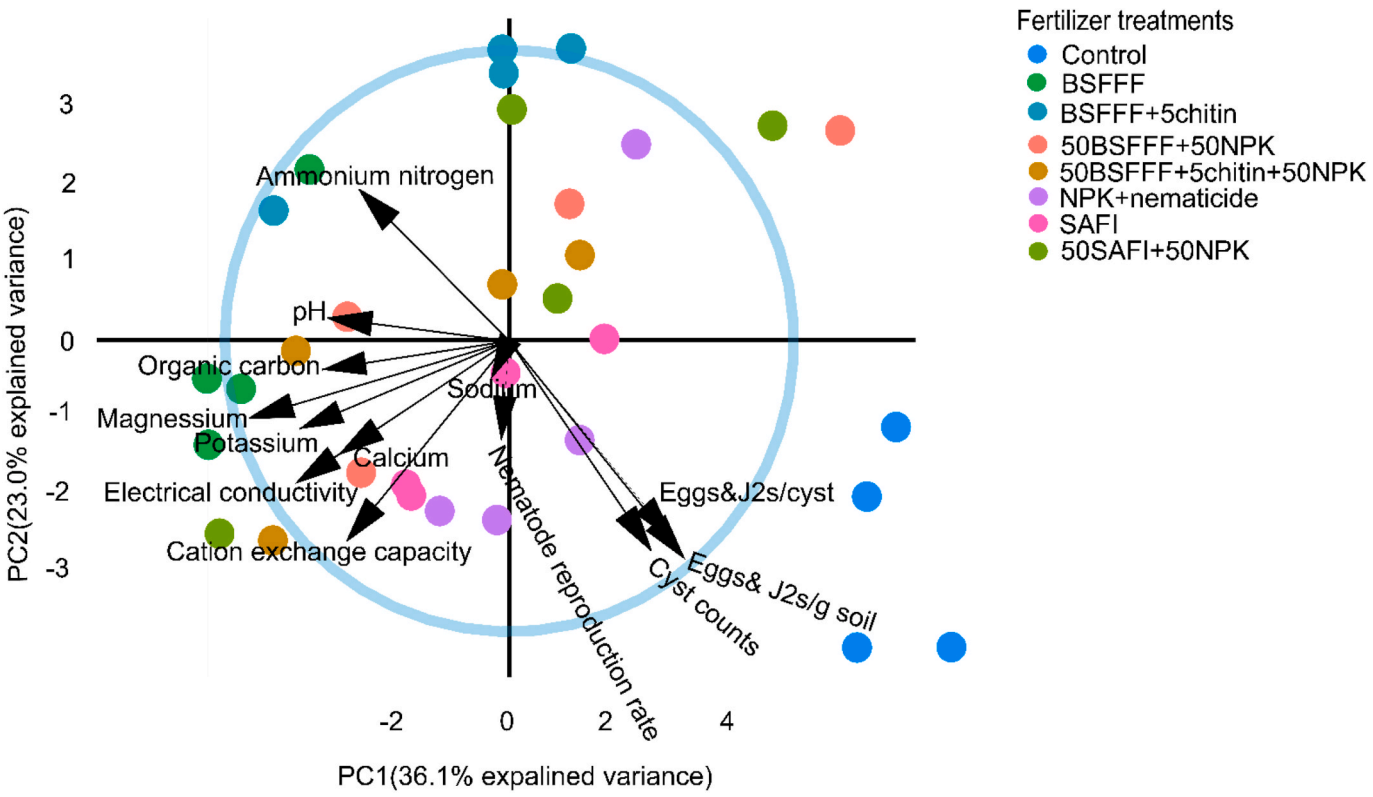


Fig. 6. Biplots showing the relationship between selected soil chemical properties and nematode population parameters for the first two principal components (PC1 and PC2).
Control = unamended soil, BSFFF = black soldier fly frass fertilizer applied at a rate equivalent to 150 kg N ha^{-1}, BSFFF+5chitin = black solder fly frass fertilizer applied at a rate of 150 kg N ha^{-1} and fortified with 5% chitin from BSF exuviae, 50BSFFF+50NPK = combined application of black soldier fly frass fertilizer and NPK so that each supplies 50% of the nitrogen required, 50BSFFF+ 5chitin +50NPK = combined application of chitin-fortified BSF frass fertilizer and NPK so that each supplies 50% of the nitrogen required, SAFI=Conventional organic fertilizer applied at a rate equivalent to 150 kg N ha^{-1}, 50SAFI+50NPK = combined application of SAFI and NPK so that each supplies 50% of the nitrogen required, NPK + nematicide = combined application of mineral fertilizer NPK (150 kg N ha^{-1}, 60 kg P ha^{-1} and 250 kg K ha^{-1}) and synthetic nematicide.

as the active compound dissipates, nematode populations may recover, particularly in soils lacking enhanced biological antagonism. From a farming systems perspective, this indicates that reliance on chemical nematicide may not offer a sustainable nematode management strategy, due to pest resurgence after dose depletion from the soil. Moreover, continued application of synthetic nematicides could affect the survival of non-target microorganisms with a key role in PCN suppression and induce nematode resistance, leading to an increase in the densities of plant parasitic nematodes in soil. On the contrary, this study has demonstrated that the biologically active insect frass fertilizer fosters residual soil suppressiveness that strengthens long-term agroecosystem resilience and reduces dependency on repeated chemical interventions.

Trap crops contribute to PCN management through the induction of "suicidal hatching," which is stimulated by specific allelochemicals exuded from nightshade roots. This mechanism also contributed to the significant reduction in nematode population density reported in this study (Devine and Jones, 2001; Bhatta et al., 2023). These root-derived compounds are known to trigger the hatching of PCN juveniles from cysts (Devine and Jones, 2001; Ochola et al., 2020). However, because African nightshade is a non-host crop, the hatched juveniles are prevented from completing their life cycle, leading to starvation and subsequent disruption of nematode population renewal. This mechanism ultimately results in a gradual but sustained decline in PCN densities over time (Guerrieri et al., 2019).

The observed responses are in agreement with earlier findings demonstrating the effectiveness of several *Solanum* species, including *S. sisymbriifolium*, *S. villosum*, and *S. scabrum*, in suppressing PCN populations through trap-cropping effects (Hickman and Dandurand, 2023; Gómez-Armesto et al., 2025). Notably, *S. scabrum*, a commonly consumed indigenous leafy vegetable in Kenya, has been validated as a promising trap crop for PCN management (Chitambo et al., 2019). The degree of nematode suppression achieved using nightshade species is determined by numerous factors, among them being the species, duration of growth, cultivation environment (field versus pot), and root system architecture, with suppression levels reported to reach up to 99% when conditions are ideal (Timmermans et al., 2006; Gómez-Armesto et al., 2025).

Despite these advances, the complete eradication of PCN from infested fields remains a global challenge, largely due to the absence of a single management strategy that is universally effective against both major PCN species (Price et al., 2021). Our study provides evidence supporting the integration of insect frass fertilizer within a potato–African nightshade rotation as an integrated and regenerative approach for sustainable PCN management strategy for smallholder farming systems. While both chitin-fortified BSF frass fertilizer (Anedo et al., 2024, 2025) and African nightshade (Chitambo et al., 2019) individually demonstrated potential to reduce PCN population densities, our findings show that their combination enhances efficacy for PCN management. This is probably due to the complementary effects of the two methods as discussed above. Nonetheless, future investigations are warranted to unravel the mechanisms underpinning PCN suppression due to the synergistic effects of chitin-fortified frass fertilizer and African nightshade-potato rotation systems.

4.3. Changes in soil chemical properties as affected by the residual fertilizer treatments

Evaluating the residual effects of fertilizer treatments is critical for advancing sustainable soil management practices and safeguarding environmental quality (Leogrande et al., 2024). In our study, the pronounced residual improvements in key soil properties demonstrate that insect frass fertilizer (BSFFF) can deliver sustained soil fertility benefits beyond the initial cropping season. This positions BSFFF as both a viable alternative to, and a complementary input alongside, synthetic fertilizers within smallholder production systems. Our findings are corroborated by earlier reports, which proved that the impact of organic amendments or their integrated application with mineral fertilizer can last beyond a single cropping season (Reeve et al., 2012; Demelash et al., 2014).

The observed improvements in pH as reported in this study reinforce the capacity of the BSFFF to ameliorate soil acidity, a critical challenge to agricultural productivity in tropical soils (Beesigamukama et al., 2021). Also, the improvements in soil pH correlate negatively with reductions in the nematode population parameters (Fig. 6). This highlights the role of soil pH in regulating soil nematode populations. Also, the rise in soil electrical conductivity (EC) in treatments receiving the organic inputs, or their integration with mineral fertilizers, is likely due to increased concentrations of soluble salts in these amendments. For instance, EC has been recognized as an indicator of nutrient release and organic matter mineralization (Smith and Doran, 1997; De Neve et al., 2000). The current findings align with previous reports documenting increased EC following BSF frass fertilizer application (Alattar et al., 2016; Axelrod et al., 2021). Past studies on sustainable intensification have advocated for integrated soil fertility management through the combined application of organic and mineral fertilizer inputs (Ozlu et al., 2018; Kang et al., 2022), and frass fertilizer would play a key role in advancing this paradigm due to its multiple benefits on soil health restoration. Taken together, this implies that sustainable crop production requires holistic solutions that address soil degradation and below-ground pests like potato cyst nematodes while boosting plant vigour and defence against other biotic stress factors.

Fertilizer application plays a key role in regulating soil carbon cycling through interacting biological, chemical, and physical processes (Chen et al., 2022; Yang et al., 2025; Bai et al., 2026). Mineral fertilizers mainly influence soil organic carbon (SOC) indirectly by stimulating crop growth, thereby increasing plant biomass, root development, and the return of crop residues and root-derived carbon to the soil (Chen et al., 2022; Leogrande et al., 2024). In contrast, organic fertilizers directly supply exogenous carbon and nutrients, stimulating microbial activity and promoting processes such as organic matter decomposition, humification, and aggregate formation that enhance carbon stabilization (Kramer et al., 2002; He et al., 2018; Eduah et al., 2025). The higher SOC observed in BSFFF and BSFFF+5chitin-amended soils likely reflects the combined effect of increased nutrient inputs and carbon-rich substrates that stimulate microbial processes and soil carbon accumulation. Enhanced soil organic matter creates an unfavorable environment for nematode survival, development, and reproduction through the increase in the activities of antagonistic microbes and the release of nematicidal compounds (Tian et al., 2020; Abdelkader et al., 2022). This process explains the negative correlation between soil organic carbon and nematode population parameters (Fig. 6). As reported in this study, similar SOC improvements have been reported following repeated applications of organic fertilizers or their integration with mineral fertilizers (Demelash et al., 2014; Bamboriya et al., 2023; Leogrande et al., 2024).

Likewise, the increased SOC in SAFI-amended soils aligns with previous reports highlighting the capacity of biochar to enhance SOC (Cong et al., 2023; Yang et al., 2025; Bai et al., 2026). However, the effectiveness of biochar largely depends on feedstock type and pyrolysis conditions, particularly temperature (Saffari et al., 2020; Joseph et al., 2021). Biochar produced at lower pyrolysis temperatures generally contains greater proportions of labile organic carbon, whereas higher temperatures tend to generate more recalcitrant carbon fractions (Saffari et al., 2020). The relatively low pyrolysis temperature (400 °C) used to produce SAFI likely preserved more labile carbon fractions, which can stimulate microbial activity and promote carbon incorporation into the soil, thereby improving SOC and overall soil chemical properties.

Generally, enhanced nutrient availability, coupled with increased inputs of carbon-rich substrates, likely created favorable conditions for microbial growth and functions (Mandal et al., 2020; Ruan et al., 2026). This process increases soil carbon turnover and stabilization processes (Bamboriya et al., 2023). The patterns observed in this study have been documented in previous studies, demonstrating that organic inputs, applied solely or integrated with synthetic inputs, enhance soil microbial functions while simultaneously supplying substrates that support carbon mineralization (Adams et al., 2020; Bamboriya et al., 2023), enhancing soil carbon stabilization (He et al., 2018; Eduah et al., 2025).

The observed rise in ammonium nitrogen concentrations following BSF frass fertilizer application could be related to its inherent low carbon-to-nitrogen ratio. This attribute promotes rapid mineralization and stimulates microbial activity (Boudabbous et al., 2023) and also enhances nematode suppression (Rodríguez-Kábana, 1986; Oka, 2010). The negative correlation between ammonium nitrogen and nematode population parameters, as shown by the PCA (Fig. 6), validates this assumption. Moreover, the higher nitrate concentrations relative to ammonium indicate an active nitrification process (Xiong et al., 2023), potentially intensified by the addition of BSF frass fertilizer and chitin-enriched frass fertilizer. These observations highlight the role of such amendments in stimulating nitrogen transformation pathways (Gebremikael et al., 2022) and enhancing nitrogen uptake (Beesigamukama et al., 2021). Similarly, the marked rise in the available P in soils amended with BSF frass fertilizer is consistent with previous findings demonstrating the capacity of insect frass fertilizers to reduce phosphorus fixation (Agustiyani et al., 2021; Guo et al., 2021). Furthermore, the observed improvement in phosphorus availability may partly be explained by enhanced microbial activity that promotes the solubilization of organically bound phosphorus, thereby increasing plant-accessible pools (Adnan et al., 2022). In addition, humic substances associated with organic amendments may further enhance nutrient availability through complexation and chelation mechanisms that improve nutrient mobility and uptake (Ahmad et al., 2025).

Despite the non-significant differences in the available potassium (K) content of the amended soils, the exchangeable potassium values obtained in this study (1.72–2.6 cmol kg^{-1}) indicate a high K status. Similar ranges (1.5–3.0 cmol kg^{-1}) have been reported within the study area, where potassium availability is generally high due to K-rich parent materials (Mwendwa et al., 2022). In contrast, lower values of 0.2–1.6 cmol kg^{-1} have been reported in some cultivated soils in western Kenya, primarily due to continuous cropping and lack of adequate and sustainable K management practices (Kanyanjua et al., 2006). These findings show that insect frass fertilizer not only improves the soil's suppressiveness against pests but also boosts nutrient availability and replenishes the lost nutrients.

5. Conclusions

Our findings demonstrate that BSF frass fertilizer can deliver meaningful residual benefits for both rotational crop productivity and potato cyst nematode management, while contributing to the long-term improvement of soil fertility. The enhanced growth performance and elevated protein levels in the African nightshade, especially in plots amended with either BSF frass fertilizer or integrated with mineral fertilizer, indicate that the agronomic benefits of this multipurpose input extend beyond a single cropping season. These outcomes highlight a pronounced soil legacy effect, whereby BSF frass fertilizer improves not

only yield but also the nutritional quality of subsequent crops in the rotation system. Moreover, the enhanced suppression of PCN achieved through the integration of chitin-fortified BSF frass fertilizer within a potato–African nightshade rotation underscores its potential as a regenerative nematode management strategy. Adoption of this approach could substantially improve the productivity and resilience of smallholder potato and African nightshade production systems, while reducing reliance on synthetic fertilizers and offering an environmentally sound alternative for PCN management.

To encourage the wider adoption of this cropping system, further research is warranted to quantify the economic viability of this integrated system and to elucidate the mechanisms underpinning PCN suppression in soils treated with a combination of chitin-fortified BSF frass fertilizer and African nightshade as a trap crop. Given that both potato and African nightshade belong to the *Solanaceae* family, it will be important to understand the broader implications of this rotational system on other economically important pests and diseases. Moreover, the exploration of the interactive effects of frass fertilizer and African nightshade on the soil microbiome, free-living nematodes, and beneficial anthropoids is critical for generating evidence on biological soil fertility. This will guide the integration of this regenerative approach into existing agroecological PCN management strategies and provide a basis for increased adoption in various farming systems.

CRediT authorship contribution statement

Emmanuel O. Anedo: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Dennis Beesigamukama:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Benson Mochoge:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Formal analysis, Data curation. **Nicholas K. Korir:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Formal analysis, Data curation. **Solveig Haukeland:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Formal analysis, Data curation. **Xavier Cheseto:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation. **Moses Nyongesa:** Writing – review & editing, Writing – original draft, Resources, Investigation. **Patrick PwaiPwai:** Writing – review & editing, Writing – original draft, Resources, Investigation. **Sevgan Subramanian:** Writing – review & editing, Writing – original draft, Resources, Funding acquisition. **Abdou Tenkouano:** Writing – review & editing, Writing – original draft, Resources, Funding acquisition. **Chrysantus M. Tanga:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Data availability statement

All data generated in the study are included in the article/supplementary material.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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