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Population dynamics of stubby root nematodes (*Trichodorus* and *Paratrichodorus* spp.) associated with ‘Docking disorder’ of sugar beet (*Beta vulgaris* L.), in field rotations with cover crops in East England

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Abstract

Stubby root nematodes (SRN)—(*Trichodorus* and *Paratrichodorus* spp.) are economically important plant parasitic nematodes (PPNs) in east England and have been reported to cause up to 50% root yield reduction in sugar beet (*Beta vulgaris*). The banning of nematicides such as Vydate (oxamyl) due to environmental concerns limits the management options available to farmers for the management of this nematode. Cover crops (CCs) present a practical option for farmers to manage nematodes whilst enhancing other soil properties such as structure, organic matter content and soil biodiversity, which contributes to the overall soil health. This study evaluated the population dynamics of SRN in field rotations with cover crops. The effect of cover cropping on the yield and quality of follow-up crop, sugar beet, was also evaluated. Field experiments were initiated at two sites in England: Bury St Edmunds, Suffolk (site 1) and Docking, Norfolk (site 2). The cover crops evaluated were—Indian mustard (*Brassica juncea*), oilseed radish (*Raphanus sativus*), daikon radish (*Raphanus sativus* var. longipinnatus), Festuca-lolium hybrid grass (*Festulolium loliaceum*) with endophyte (E+) and without (E−), Italian rye grass (*Lolium multiflorum*), phacelia (*Phacelia tanacetifolia*) and opium poppy (*Papaver somniferum*). At site 1, plots drilled with brassica cover crops, Indian mustard and oilseed radish, had significantly lower SRN reproduction factor (Rf) ($p < .05$) compared to the fallow control and daikon radish. In site 2, plots drilled with the cover crops—Italian rye grass, Indian mustard, grass without endophyte (E−) or left fallow and undisturbed had a significantly higher Rf ($p < .05$) compared to plots with phacelia, opium poppy, and disturbed or sterile fallows. Sugar beet root fanging (%) and root soil tare (%) were lower in plots that had lower SRN reproduction, that is, phacelia, opium poppy, sterile fallow, and disturbed fallow.

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Environmental variables such as rainfall and soil temperature also influenced SRN densities at different sampling points where SRN increased with increasing rain and decreasing soil temperatures. Results from this study indicate that under field conditions the population dynamics of SRN are influenced by multiple factors such as the host status of the CCs grown, weed occurrence which serve as alternative hosts as SRN are polyphagous in nature, soil temperature, rainfall, and soil disturbance. It was also clear that multiplication rate of SRN in CCs such as phacelia and opium poppy was lower despite SRN being able to multiply in all cover crops tested in this study.

KEYWORDS

biofumigation, biomass, incorporation, soil disturbance, suppression, weeds

1 | INTRODUCTION

Sugar beet (*Beta vulgaris* L.) is the second most important sugar crop in the world after sugar cane (Ahmad et al., 2017). Sugar beet is an economically important crop in the East Anglian and East Midlands regions of England, occupying an area of 105,000 hectares. The crop covers 3.7% of the total arable cropping area and supplies 55% of the sugar consumed in the United Kingdom (Tzilivakis et al., 2005).

Plant parasitic nematodes (PPNs) are important pests for many crops globally and result in crop losses that equate to US \$80 billion (Nicol et al., 2011). The sugar beet crop is no exception, being subject to infection by a variety of PPNs such as beet cyst nematode—*Heterodera schachtii* (Wright et al., 2019), root knot nematodes—*Meloidogyne hapla* and *Meloidogyne chitwoodi* (Griffin et al., 1982), stem and bulb nematode—*Ditylenchus dipsaci* (Griffin, 1983; Hillnhütter et al., 2011; Storelli et al., 2021), the pin nematode—*Paratylenchus* spp. (Ghaderi, 2019), needle nematode (*Longidorus* spp.) (Whitehead & Hooper, 1970) and stubby root nematode (SRN)—*Paratrichodorus* and *Trichodorus* spp. (Hafez, 1998; Whitehead & Hooper, 1970). Stubby root nematodes are polyphagous ectoparasites and are widely distributed in light, sandy soils (Cooke, 1973; Whitehead & Hooper, 1970; Winfield & Cooke, 1975). In the United Kingdom, SRN are mainly found in soils with a sand fraction greater than 80% and less than 10% silt (50% of infested sites) (Alphey & Boag, 1976). *Trichodorus primitivus* has been reported as the most prevalent and cosmopolitan species, followed by *Paratrichodorus pachydermus* (Alphey & Boag, 1976). The prevalence of these two species was also recorded in sugar beet fields in Eastern England, where out of seven species of SRN reported, 35% were *P. pachydermus* and 30% were *T. primitivus* (Whitehead & Hooper, 1970). In sugar beet grown in East England, *Trichodorus* and *Paratrichodorus* spp. attack young seedlings, causing a condition known as Docking disorder, named after the village ‘Docking’ where it was first recognised and described (Gibbs, 1959); these nematode genera have been isolated in 75% of samples collected in fields with Docking disorder symptoms (Cooke, 1973).

Foliage of sugar beet suffering from Docking disorder appears stunted and deficient in nitrogen or magnesium (Cooke, 1989; Whitehead & Hooper, 1970). The roots of the attacked plant have

stubby lateral roots, which turn grey-brown and later black as they die and decay. In fields where symptoms persist, sugar beet roots are more fangy, and the yield can be reduced by up to 17.5 t ha⁻¹ as compared to crops from unaffected fields (Cooke, 1973). Yield losses of up to 50% have also been recorded as a result of the fangy root symptoms (Cooke, 1989). Docking disorder severity has been correlated with environmental and agronomic factors such as rainfall, physical conditions of the soil, previous cropping, rate and timing of fertiliser and herbicide applications. Root damage is mostly evident at the end of May, coinciding with higher rainfall, while the symptoms of the foliage are mostly visible in June (Cooke, 1973).

For many years, the management of SRN relied upon the prophylactic use of pesticides, including soil fumigants such as 1,3-dichloropropene in autumn before sowing or as a row application shortly after drilling of sugar beet (Cooke & Draycott, 1971). In the United Kingdom, crops at risk from Docking disorder relied on the application of granular aldicarb at drilling to prevent root damage by SRN, but the expense and inconvenience limited its use (Cooke, 1989). Vydate (Oxamyl) was recently the main nematicide applied by sugar beet growers for the management of SRN until December 2020, when it was banned in the United Kingdom, leaving growers with garlic extract (NEMguard DE) as the only option for SRN management. As the pressure to develop other nematicides continues, other cultural and crop management strategies need to be evaluated as future options for sugar beet growers (Stevens, 2015).

The use of cover crops (CCs) in the United Kingdom has been gaining recognition as there is need to manage soils sustainably, with farmers and the UK government acknowledging the significance of soil in providing ecosystem services and food (Storr et al., 2019). A sustainable management of soils and eradication of soil degradation by 2030 was proposed by the ‘Safeguarding our Soils in England’ strategy (DEFRA, 2009), as soil erosion, compaction, and loss of organic matter are the major soil concerns in England (DEFRA, 2009). As such, the Department for Environment, Food & Rural Affairs (DEFRA) continues to advocate sustainable management of UK soils to achieve a balance between sustainable, dependable, and profitable food production while safeguarding the environment (AHDB, 2018; DEFRA, 2018).

Cover crops present a practical and sustainable option in the management of PPNs and have been extensively used for decades (Couédel et al., 2019; de Araujo et al., 2023; Dutta et al., 2019). Under field conditions, CCs employ diverse mechanisms to successfully suppress nematodes by (i) acting as poor hosts, non-hosts, or resistant hosts, (ii) producing allelochemicals that are toxic or inhibitory, and (iii) providing an ecological niche for antagonistic microbes that can be suppressive to PPNs (Wang et al., 2002). Microbial communities have been reported to suppress numerous pathogens through competition, antibiosis, parasitism, or by inducing systemic plant resistance (Audenaert et al., 2002; Rayns & Rosenfeld, 2006). The incorporation of biomass from CC material provides numerous benefits such as promoting the proliferation of bacteria during the decomposition of the organic material, which becomes a source of food for microbivorous nematodes, which in turn become a food base for nematophagous fungi that are suppressive to PPNs (Carrascosa et al., 2014; Van Den Boogert & Deacon, 1994).

Rotating nematode suppressive CCs with cash crops is beneficial in disrupting nematode life cycles and eventually reducing their initial densities at planting of the main crop (Dutta et al., 2019; Nyczepir & Rodriguez-Kabana, 2007). Phytochemicals from widely used CCs such as polythienyls and polyacetylenes from *Asteraceae*, 2-dehydropyrrolizidine from *Asteraceae*, *Boraginaceae* and *Fabaceae*, isothiocyanates from *Brassicaceae*, saponins from *Leguminosae*, and glucosides from *Poaceae* have been shown to suppress nematodes (Thoden et al., 2009). These phytochemicals can be exploited through crop rotations, intercropping, or green manures (Zhou et al., 2012), where the compounds can be released either through volatilisation, exudation, leaching from plant roots, or through decomposition of plant residues (Dutta et al., 2019; Halbrecht, 1996).

In Sorghum Sudan grass, hydrogen cyanide, a hydrolysis product of dhurrin, has been shown to possess nematicidal effects towards *Meloidogyne* spp. (Mojtahedi et al., 1993) and *Criconeoides xenoplax* (Nyczepir & Rodriguez-Kabana, 2007). Hydroxamic acids from rye have been shown to suppress gall-formation in *M. hapla* under field conditions in a rye–tomato rotation (Halbrecht, 1996) and have also been shown to have direct nematicidal activity towards *Meloidogyne incognita* and *Xiphinema americanum* (Zasada et al., 2005). Glucosinolates found in brassicas such as radishes and mustards have also been extensively used in the management of *Globodera pallida* populations in the process of biofumigation (Lord et al., 2011; Ngala et al., 2014), where, upon hydrolysis of glucosinolates, isothiocyanates are released, which have biocidal activity towards the nematodes (Chekanai et al., 2024; Mwangi et al., 2024a; Wood et al., 2017). Saponins in legumes, such as species in the genus *Medicago*, have also been demonstrated to have diverse modes of action towards PPNs, such as nematicidal activity to *Xiphinema index* and *Pratylenchus thornei* (Martín & Magunacelaya, 2005), reduction in cholesterol levels in the eggs of *Meloidogyne* spp. (Ibrahim & Srour, 2013) and inhibited hatching of *Globodera rostochiensis* (D'Addabbo et al., 2020). Lolines and ergot alkaloids found in cool-season grasses colonised by the endophyte *Epichloe* spp. have also been demonstrated to manage PPNs, both *in vitro* and *in planta*, by having repellent activities,

inhibiting hatching, or directly causing death to nematode juvenile stages (Cook & Lewis, 2001; Mwangi et al., 2024b). Some of these phytochemicals have been further exploited for the development of biopesticides for nematode management (Renčo et al., 2014).

The main objective of this study was to investigate the population dynamics of SRN during growth and post incorporation of CCs from diverse plant families and the subsequent impact of the rotation on the quality and quantity attributes of the follow-up crop (sugar beet), that is, root fanging index, soil tare percentage, sugar beet yield, and sugar content.

2 | MATERIALS AND METHODS

2.1 | Experiment design and treatments

Field experiments were conducted at two sites in Eastern England with a previous history of SRN infestation. Site 1 was located at Bury St Edmunds, Suffolk, 52°17'03.0"N 0°43'39.8"E and had a sandy loam soil with 87.7% sand, 7.1% silt, 5.2% clay, pH = 8.07, and 10.12% organic matter. Site 2 was located at Docking, Norfolk, 52°54'01.7"N 0°36'32.4"E and had a sandy loam soil with 88.2% sand, 5.9% silt, 5.9% clay, pH = 7.15, and 9.22% organic matter. The field experiment at site 1 was conducted from June to December in 2021, while the experiment at site 2 was conducted from July 2021 to January 2023. The CCs used in these experiments were selected based on their potential as suppressive CCs and commercial availability. Moreover, the brassica CCs were selected because of their known high glucosinolate content and hence production of bioactive compounds, that is, isothiocyanates, that have been shown to be suppressive to other nematode species such as potato cyst nematodes and root lesion nematodes. The treatment hybrid endophyte grass (*F. loliaceum*) was obtained from the seed supplier as colonised seed with *Epichloe uncinata* (E+), and *F. loliaceum* without endophyte was included as a control. Experiments were laid out in a randomised complete block design. Seed rates were applied according to recommendations by the seed supplier. The experiment at site 1 comprised plots measuring 22 by 4 m, with a 6 m buffer between blocks ($n = 5$). On this site, three brassica species were tested alongside a fallow control. At site 2, seven CC species from four different plant families, that is, *Papaveraceae*, *Brassicaceae*, *Boraginaceae*, and *Poaceae*, were evaluated (Table 1). The CCs were assigned to plots measuring 9 by 6 m and were arranged in four blocks with a 6 m buffer between the blocks. Three fallow controls were included at this site: (i) Sterile fallow—in this fallow, glyphosate was applied as a post-emergence herbicide to ensure that it was weed-free; (ii) Disturbed fallow—this fallow was rotavated and rolled in a similar way to plots containing CCs during the flailing and incorporation period to create a disturbance effect; (iii) Undisturbed fallow—this fallow was left undisturbed and no weed management was undertaken.

2.2 | Site operations

Brassica CCs in site 1 were drilled on 29 June 2021, following spring onions. The CCs were sown following recommendations by the seed

TABLE 1 Cover crop treatments used in Bury St. Edmunds, Suffolk (site 1) and Docking, Norfolk (Site 2).

Species name	Common name	Family	Variety	Seed rate kg ha ⁻¹	Seed supplier	Site
<i>Brassica juncea</i>	Indian (Brown) Mustard	Brassicaceae	Brons	10	Joordens Zaden BV	1 and 2
<i>Raphanus sativus oleiferus</i>	Oilseed radish	Brassicaceae	Terranova	20	Joordens Zaden BV	1 and 2
<i>Raphanus sativus longipinatus</i>	Daikon radish	Brassicaceae	Daikon	20	RAGT seeds UK	1
<i>Festulolium loliaceum</i>	Hybrid endophyte-infected grass (E+)	Poaceae	Green solutions	25	Cropmark Seeds NZ	2
<i>Festulolium loliaceum</i>	Hybrid non-infected grass (E-)	Poaceae	Green solutions	25	Cropmark Seeds NZ	2
<i>Papaver somniferum</i>	Opium poppy	Papaveraceae	Marianne	1.5	Joordens Zaden BV	2
<i>Phacelia tanacetifolia</i>	Phacelia	Boraginaceae	Factotum	8	Joordens Zaden BV	2
<i>Lolium multiflorum</i>	Susceptible control	Poaceae	Syntilla	25	RAGT seeds UK	2
Fallow disturbed	Control	-	-	-	-	2
Fallow undisturbed	Control	-	-	-	-	1 and 2
Sterile fallow	Control	-	-	-	-	2

Note: E+ = seed colonised by *Epichloe uncinata*; E- = without *Epichloe uncinata*.

supplier (Table 1). Plots were uniformly treated with sulphur and nitrogen fertiliser at a rate of 100 kg N and 34 kg S ha⁻¹ at planting, as is the recommended practice when growing brassica CCs for biofumigation. In site 2, CCs were drilled on 28 July 2021 following a crop of spring barley. Glyphosate was applied in the sterile fallow treatment plots 4 weeks after CCs had been drilled to manage weeds. The common weeds in site 2 included: fat hen (*Chenopodium album*), annual meadow-grass (*Poa annua*), knotgrass (*Polygonum aviculare*), redshank (*Persicaria maculosa*), chickweed (*Stellaria media*), common field speedwell (*Veronica persica*), field pansy (*Viola arvensis*), shepherd's purse (*Capsella bursa-pastoris*), black-bindweed (*Fallopia convolvulus*), sow thistle (*Sonchus oleraceus*), red dead nettle (*Lamium purpureum*), groundsel (*Senecio vulgaris*) and volunteer spring barley (*Hordeum vulgare*). Plots drilled with brassica CCs were uniformly treated with sulphur and nitrogen fertiliser at the same rates as site 1. The rest of the CCs were not fertilised to mimic standard agronomic practices. The various field operations and timings for each field experiment are summarised in Table 2. The CCs grew for 71- and 113-days post drilling at site 1 and site 2, respectively.

2.3 | Flailing, ploughing, and incorporation of CC biomass

Cover crops at site 1 were flailed, ploughed, and incorporated on 9 September 2021. Prior to the incorporation of the brassicas, two subplots per plot measuring 1 m² were selected for biomass assessment. At site 2, CCs were flailed and incorporated on the 19 November 2021; prior to incorporation, two subplots per plot measuring 1 m² were selected for biomass assessment. Incorporation at site 2 was done later due to the delayed emergence of the brassica crop and due to the prevailing low soil temperatures at that time that

TABLE 2 Timings of management practices used during the field experiments conducted at Bury St Edmunds, Suffolk (site 1) and Docking, Norfolk (site 2).

Field operations	Site 1	Site 2
Sampling for initial nematode densities (Pi)	29 June 2021	28 July 2021
Cover crop drilling	1 July 2021	30 July 2021
Sampling 4 weeks after cover crop planting (4 WAP)	28 July 2021	25 August 2021
Sampling before cover crop incorporation (Bi)	7 September 2021	16 November 2021
Biomass assessment of Brassica species	7 September 2021	16 November 2021
Cover crop incorporation	9 September 2021	19 November 2021
Sampling after incorporation of cover crop material (Ai)	15 December 2021	4 February 2022
Sugar beet drilling	-	3 March 2022
Sugar beet harvest and Sampling for final nematode densities (Pf)	-	5 January 2023

would have undermined successful biofumigation. At both sites, the subplots were randomly selected at distinct locations within the plot and assessed for plant density; average plant counts were used to represent the number of plants in the whole plot. Ten plants from each subplot were collected, and fresh weight was measured. Dry weight measurements were also taken by first drying the plants at 60°C for 72 h. Nine whole plants were then taken to the lab, where they were separated into roots and shoots and weighed (Ngala et al., 2014).

Average biomass incorporated in 1 m² was determined by multiplying the average weight of individual plants by the number of plants in the area. At incorporation, the green tissue was flailed using a flail topper, followed by incorporation within the top 30 cm of soil using a rotary tiller. The soil surface was immediately rolled using a Cambridge roll to trap volatile compounds produced by the brassica CCs. The same process was applied for the disturbed fallow control, where soil was rotavated and rolled to create a disturbance effect.

2.4 | Soil sampling and nematode assessments

Soil samples were collected at different dates, before CCs drilling, during CCs growth and at the harvest of the main crop (sugar beet), as summarised in Table 2. A W-shape sampling pattern per plot was used with random sampling points along the pattern. Soil samples were collected to a depth of 30 cm using a 2 cm diameter corer. At each sampling point, detritus on the soil surface, such as dead plant material, was removed before sampling (Boag et al., 1989). At least 28 cores were taken from each plot to make approximately a 1–1.5 kg composite sample. At sites 1 and 2, soil samples were collected (i) prior to CCs drilling to establish the initial nematode densities (Pi), (ii) 4 weeks after CCs planting (4WAP), (iii) before CCs incorporation (Bi), and (iv) post-incorporation of CCs residues (Ai). At site 2, soil samples were also collected at sugar beet harvest to establish the final SRN densities (Pf). Soil was carefully placed in labelled zip-lock bags and stored in the cold room at 4°C awaiting extraction. Monthly rainfall and soil temperature data covering the different sampling dates were obtained from the nearest meteorological station to each site, that is, Brooms Barn station and Denver station for Bury St Edmunds, Suffolk (site 1) and Docking, Norfolk (site 2), respectively.

2.5 | Nematode extraction, identification, and quantification

Stubby root nematodes were extracted using the centrifugal flotation method, using magnesium sulphate heptahydrate (MgSO₄·7H₂O) as the extraction solvent (Van Bezooijen, 2006). The bulk sample collected per plot was gently mixed and passed through a 2 mm sieve to remove large stones before taking a 200 mL subsample for extraction. The soil was divided into four 50 mL centrifuge tubes, and 80 mL of MgSO₄·7H₂O at 1.15 specific gravity was added into each tube. The tubes were gently agitated to mix the extraction fluid and the soil and then centrifuged at 2680 RCF (1150 g) for 5 min. The supernatant was then decanted onto 215 and 53 μm sieves and gently rinsed in tap water before being washed into sample bottles. The suspension was concentrated into a smaller volume, which was wholly quantified under a compound microscope at 20× magnification. Morphological characteristics, such as, spicule shape in males, body cuticle, and vaginal characteristics of the females, were used to distinguish the genus and species of *Trichodorus* and *Paratrachodorus* spp. following the key

as described by Decraemer (1995), and species composition was determined (Table 3).

2.6 | Sugar beet yield and quality assessments

The sugar beet crop was drilled on 3 March 2022 (site 2), 3 months after CCs incorporation. Sugar beet was grown for 10 months and harvested on 5 January 2023. At harvest, two rows of sugarbeet per plot were lifted by hand and a total of 25–30 roots were scored for fanging using a score scale from (a)–(e); the shape of each root had no evidence of fanging (a), roots were moderately fangy, but the main taproot was evident (b), roots were moderately fangy and showed bearding (c), roots exhibited severe fanging (d), or roots were very severely fanged and possessed no main tap root (e). Fanging index for each plot was calculated using the formula (Cooke, 1973):

$$\text{Fanging index(\%)} = \left(\frac{2b + 2c + d + e}{a + b + c + d + e} \right) \times 100.$$

The whole plot was then harvested, bagged, and sent for sugar and impurity analysis at the BBRO tarehouse at the Wisington beet sugar factory (Norfolk, UK). Each sample was weighed while dirty and then washed and reweighed to obtain a soil tare, that is, the amount of soil that adheres to the storage root at harvest. Soil tare was calculated to express the proportion of dirt as follows (Wright et al., 2022):

$$\text{Soil tare(\%)} = \left(\frac{\text{Dirty sample weight} - \text{clean sample weight}}{\text{Dirty sample weight}} \right) \times 100.$$

Sugar content of the beet was calculated using polarimetry, while impurity levels of the beet were determined using flame photometry (sodium and potassium impurities) and colorimetry (amino nitrogen) according to standard methods. Sugar (Sucrose) yield of the entire sample was calculated by multiplying the sugar % of the sample by the clean weight (De Whalley, 2013).

2.7 | Data analysis

All data were analysed using R-studio software (R Core Team, 2022). Data from the two sites were analysed separately. Data from each sampling date were also analysed separately. Data were analysed either using linear mixed effects models (LMMs) or Poisson generalised linear mixed effects models (GLMMs) using a log-link function, with block as a random effect and CCs treatments as a fixed effect. The initial nematode densities (Pi) were included as a covariate in the model when analysing the difference between treatments at each sampling point to account for the baseline differences between the plots prior to CCs planting. The package Emmeans was used to generate contrasts and least square differences (LSD) used for pairwise comparisons at a 5% significance level ($p < .05$). Linear mixed effects

TABLE 3 Average composition of stubby root nematode species (SRN) \pm SE, extracted from 200 mL soil samples ($n = 10$) at Bury St Edmunds, Suffolk (Site 1) and Docking, Norfolk (Site 2).

Stubby root nematode species (SRN)	Site 1		Site 2	
	Males	Females	Males	Females
<i>Trichodorus primitivus</i>	14 \pm 5.09	10 \pm 5.24	15.53 \pm 2.20	48.40 \pm 5.11
<i>Trichodorus cylindricus</i>	-	-	4 \pm 0.68	7.6 \pm 1.03
<i>Paratrichodorus pachydermus</i>	8 \pm 4.06	16 \pm 5.33	1.35 \pm 0.28	2.5 \pm 0.40
Juveniles	43 \pm 8		7.10 \pm 0.87	

TABLE 4 Shoot and root fresh and dry weights ($t\ ha^{-1}$) of Indian mustard, daikon radish, and oilseed radish at Bury St Edmunds, Suffolk (Site 1) and Docking, Norfolk (Site 2).

Cover crop	Site 1				Site 2			
	Fresh weight		Dry weight-NS		Fresh weight		Dry weight	
	Shoots-NS	Roots-NS	Shoots-NS	Roots-NS	Shoots-NS	Roots ^a	Shoots ^a	Roots ^a
<i>Raphanus sativus</i> var. longipinatus	48.53 \pm 5.43	4.25 \pm 0.47	5.75 \pm 0.66	0.77 \pm 0.80				
<i>Brassica juncea</i>	45.65 \pm 6.95	6.73 \pm 1.29	4.81 \pm 0.73	1.03 \pm 0.16	17.67 \pm 9.17	1.2 \pm 0.71	3.97 \pm 2.47	0.33 \pm 0.19
<i>Raphanus sativus</i> ssp. oleiferus	42.42 \pm 4.48	5.72 \pm 0.95	4.16 \pm 0.37	1.19 \pm 0.14	12.18 \pm 4.45	8.86 \pm 4.65	0.89 \pm 0.23	1.92 \pm 1.31

Note: Values are the average of 5 blocks for site 1 and 4 blocks for site 2; NS—values following each other in that column are not significantly different ($p > 0.05$, Wald-test).

^aValues following each other in that column are significantly different ($p < .05$, Wald-test).

models were used to analyse CCs biomass, sugar beet root yield, and other sugar beet quality variables, as inspection of residuals revealed the normality of assumptions for this model had been met. Block was used as a random effect and treatment as the fixed effect in the model. Spearman and Pearson rank correlation coefficients were generated to determine the relationship between the different yield variables and to determine the relationship between SRN densities, soil temperature, and rainfall using ggscatter in library ggpubrr on R studio.

3 | RESULTS

3.1 | Cover crop effects on SRN densities

3.1.1 | Site 1

At Bury St Edmunds, Suffolk (site 1), the study evaluated the effect of growing and incorporating brassica CC in the process of biofumigation (Table 1). SRN densities were monitored at different time points during the growth and post-termination of the CCs (Table 2). The SRN species present at this site were identified as *T. primitivus* and *P. pachydermus*, and the composition ratio was 1:1 for the two species, with more juveniles present than males and females (Table 3). The brassica CC at this site established well, achieving high biomass of 42, 46, and 49 $t\ ha^{-1}$ for oilseed radish, Indian mustard, and daikon, respectively, and no significant differences were recorded in both root

and shoot biomass among the three brassica CCs (Table 4). The general trend was a decline of SRN densities from initial densities (Pi) after CC incorporation (Pf), with variations observed at different sampling points (Figure 1). At 4 weeks after CC drilling (4WAP), plots drilled with brassica CC had significantly lower SRN compared to the fallow control (LSD = 54, $df = 16$, $p < .05$)—(Figure 1b). The SRN densities of plots drilled with brassicas were also significantly lower compared to the fallow control at Ai (LSD = 12, $df = 15$, $p < .05$). Indian mustard and oilseed radish at this point had significantly lower densities compared to daikon radish (Figure 1c). A resurgence in SRN densities was then observed 6 weeks after cover crop incorporation (PF). Plots following Indian mustard had significantly lower SRN densities compared to daikon and oilseed radish at this sampling point (LSD = 8, $df = 15$, $p < .05$)—(Figure 1d). Comparison of the overall reproduction factor of SRN calculated as Pf/Pi showed that SRN significantly reproduced in plots following daikon radish and the fallow control, while plots following oilseed radish and Indian mustard had significantly lower Rf (Figure 1e).

3.1.2 | Site 2

At Docking Norfolk (Site 2), CC from diverse plant families were included (Table 1). At this site, SRN densities were monitored before and during CC growth and at harvest of the sugar beet crop (Table 2). The SRN species identified at this site were *T. primitivus* (80%), *Tylenchorhynchus cylindricus* (15%), and *P. pachydermus* (5%), where

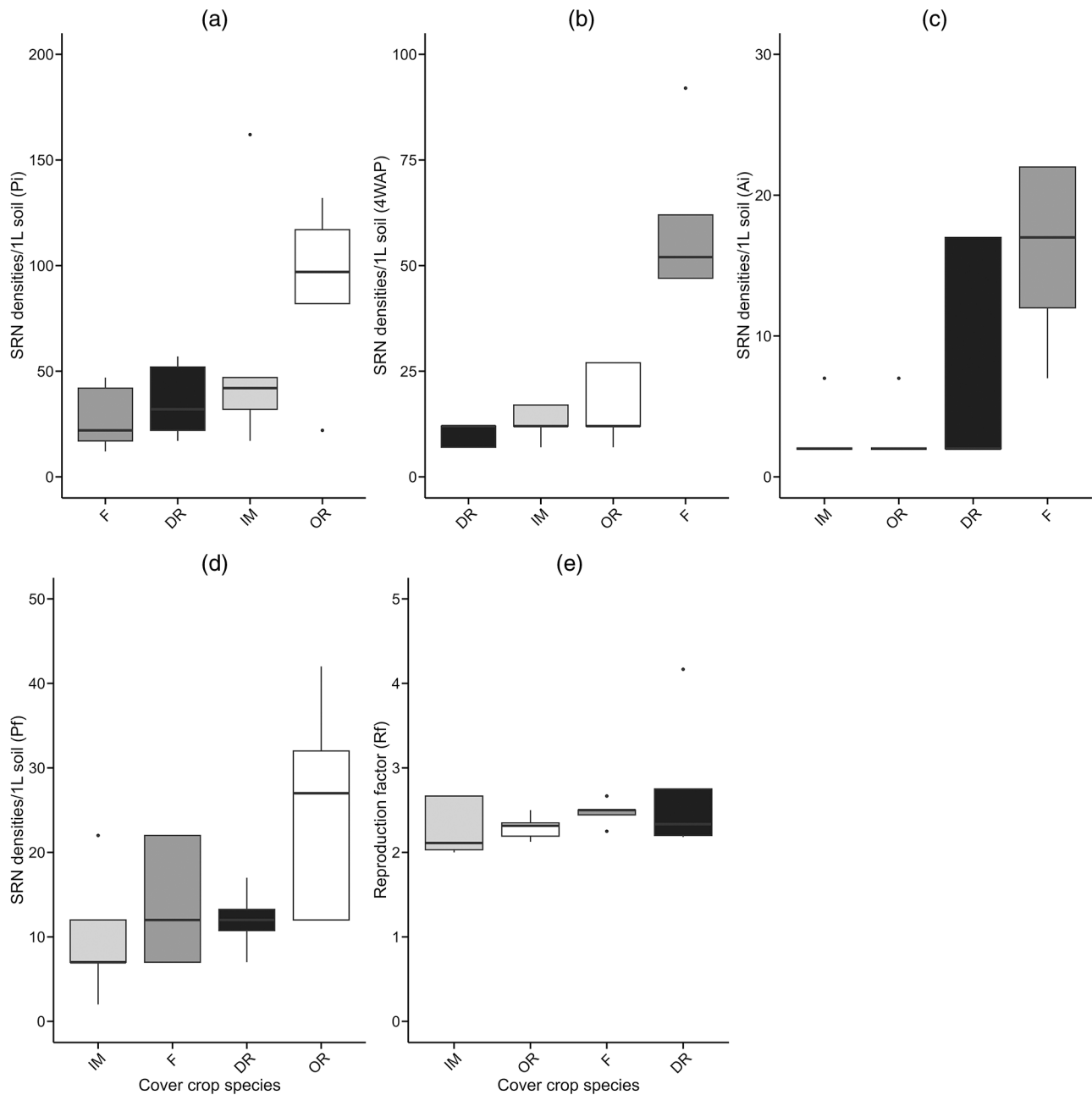


FIGURE 1 Boxplots showing stubby root nematode (SRN) densities sampled in Bury St. Edmunds, Suffolk (site 1), at different time points: (a) Initial densities before drilling cover crops (Pi), (b) 4 weeks after drilling cover crops (4WAP), (c) at cover crop incorporation (Ai), (d) 6 weeks after cover crop incorporation (Pf), (e) reproduction factor ratio (Rf) calculated as (Pf/Pi), in plots drilled with different cover crop species: Indian mustard (IM), oilseed radish (OR), daikon radish (DR), and control fallow (f).

there were more females than males and juveniles (Table 3). The brassica CC at this site did not establish well. The fresh shoot biomass of Indian mustard was 2.7 times lower, while the fresh shoot biomass for oilseed radish was 3.5 times lower at site 2 compared to site 1. The fresh root, dry shoot, and roots were significantly higher in oilseed radish as compared to the Indian mustard (Table 4). Prior to CC drilling, the initial densities (Pi) were not uniform, with some plots having significantly higher SRN densities than others (LSD = 34, $df = 30$, $p < .05$)—(Figure 2a). For this site, Pi was used as a covariate in the

analysis to account for the baseline differences. Four weeks after CC planting (4WAP), all treatments were not significantly different from the fallow undisturbed control, except for oilseed radish, which was significantly lower, and grass without endophyte (E−), which was significantly higher than the fallow undisturbed control (LSD = 146, $df = 30$, $p < .05$)—(Figure 2b). During CC growth, before incorporation of biomass (Bi), there was a spike in SRN densities when compared to the previous sampling points. However, the rate at which the increase occurred significantly differed among the different treatments ($df = 9$,

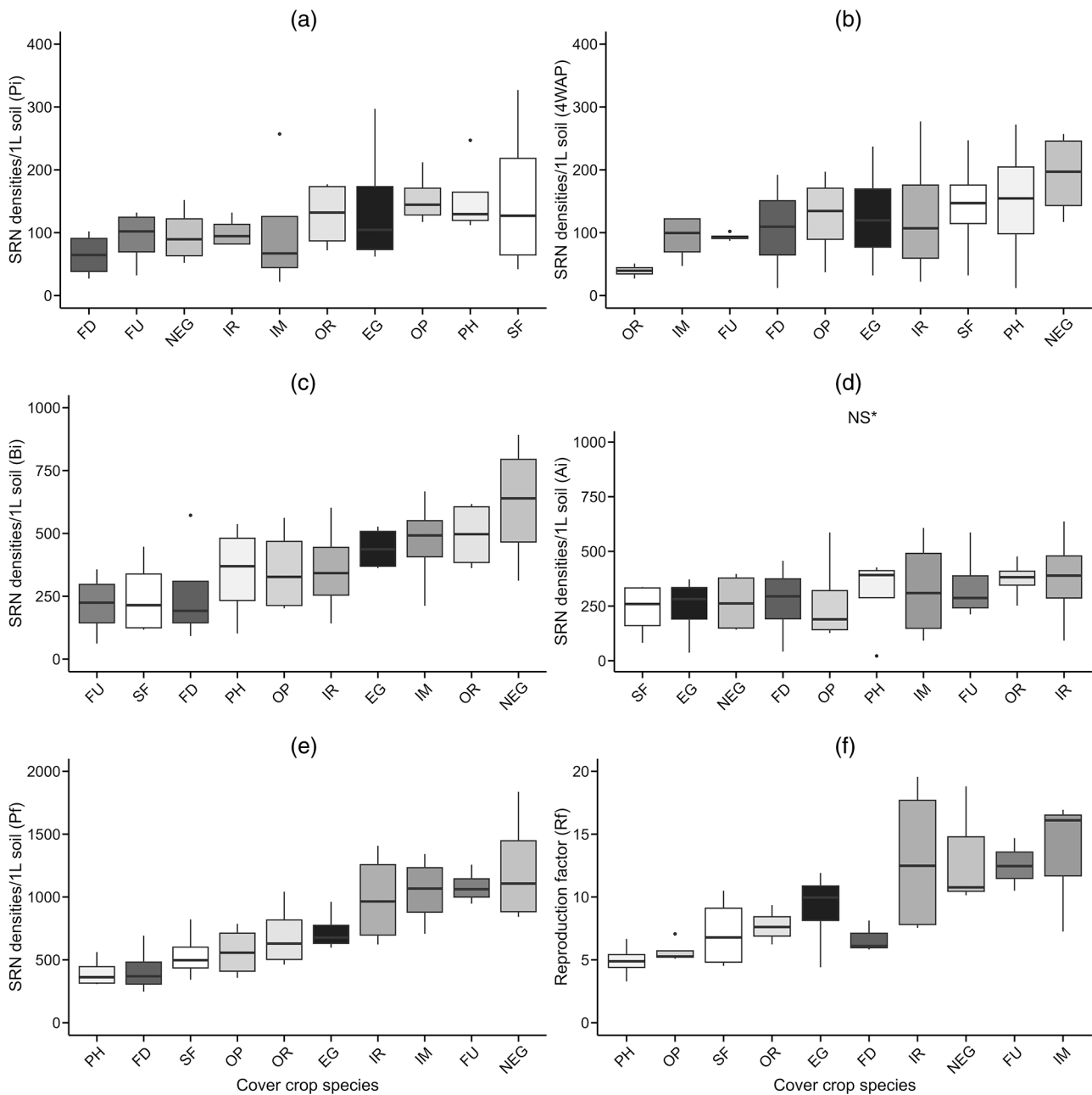


FIGURE 2 Boxplots showing the effect of different cover crop species (CC) on stubby root nematode (SRN) densities sampled in Docking, Norfolk (Site 2), at different time points: (a) Initial SRN densities in plots assigned to the different cover crop species before drilling (Pi), (b) 4 weeks after drilling cover crops (4WAP), (c) before cover crop incorporation (Bi), (d) 6 weeks after cover crop incorporation (Ai), (e) final SRN densities after sugarbeet harvest (Pf), (f) reproduction factor ratio (Rf) calculated as (Pf/Pi), in plots drilled with different cover crop species; Phacelia (PH), Indian mustard (IM), oilseed radish (OR), Endophyte-infected grass (EG), non-infected grass (NEG), Opium poppy (OP), Italian ryegrass (IR) and fallow controls—disturbed fallow (FD), undisturbed fallow (FU) and sterile fallow (SF). Boxplots consist of the median and interquartile range. NS*—not significantly different ($p \geq .05$, LSD).

$p = .003$, Wald-test). All the fallow treatments at this sampling point were not significantly different from each other; however, each had significantly lower numbers of SRN compared to plots drilled with CCs. Nil-endophyte (E−) had significantly higher SRN densities compared to all other treatments, whereas CCs like opium poppy, phacelia, and Italian ryegrass and grass without endophyte (E−) had significantly lower SRN densities when compared to Indian mustard,

oilseed radish, and grass with endophyte (LSD = 189, $df = 16$, $p < .05$)—(Figure 2c). There was a reduction in SRN densities after flailing and incorporation of CC materials (Ai); however, no significant differences were observed among treatments. SRN densities decreased in all plots except in the fallow undisturbed plots and in plots that previously had Italian ryegrass and grass without endophyte (E−), where densities increased instead (Figure 2d). A resurgence of SRN densities

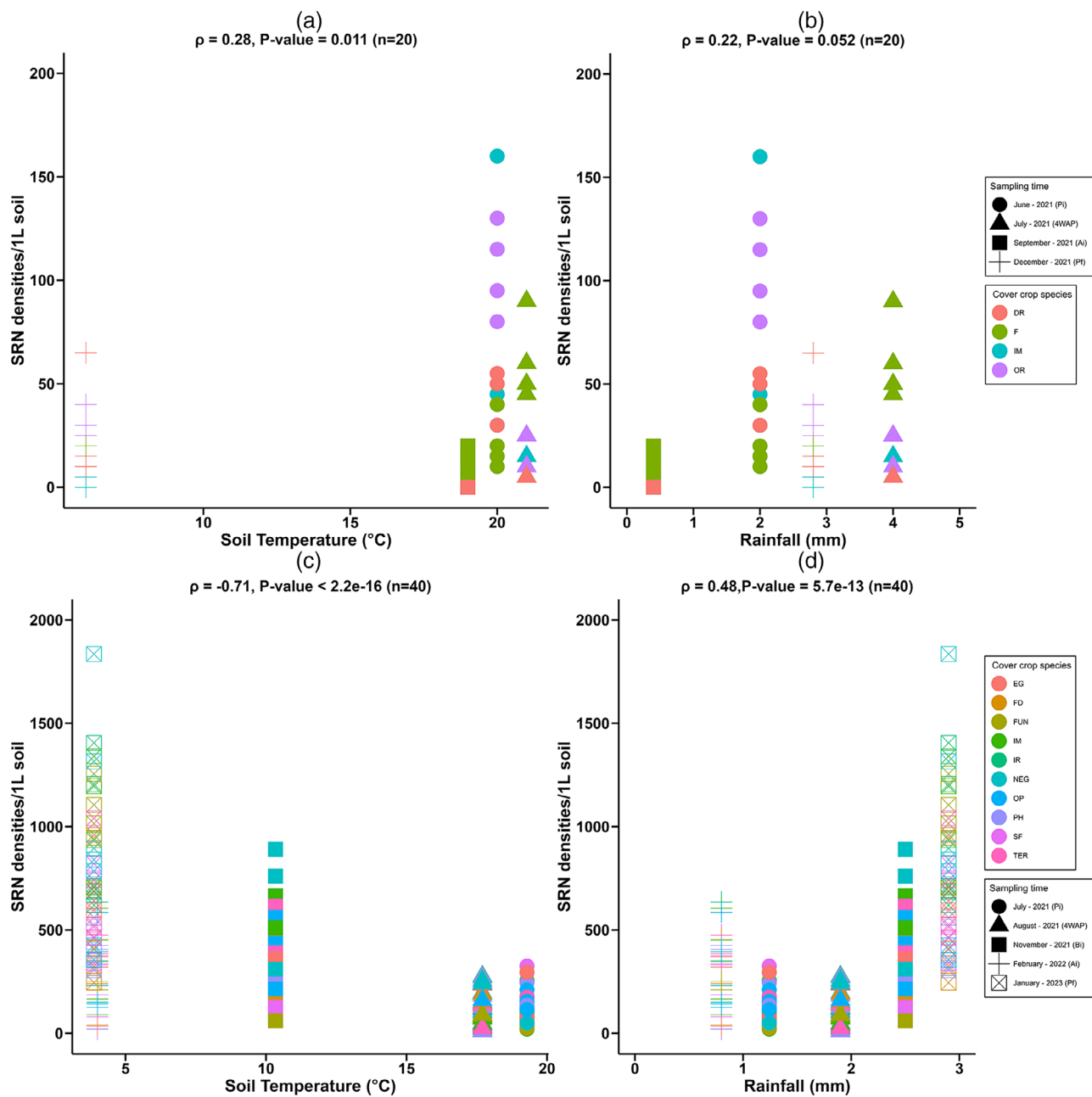


FIGURE 3 Relationship between average monthly soil temperature and rainfall on densities of stubby root nematodes (SRN) at different sampling dates in Bury St Edmunds, Suffolk—Site 1 (a and b) in plots drilled with different cover crop species: Indian mustard (IM), oilseed radish (OR), daikon radish (DR) and control fallow (F) and Docking, Norfolk—Site 2 (c and d) in plots drilled with: Phacelia (PH), Indian mustard (IM), oilseed radish (OR), Endophyte-infected grass (EG), non-infected grass (NEG), Opium poppy (OP), Italian ryegrass (IR) and fallow controls—disturbed fallow (FD), undisturbed fallow (FU) and sterile fallow (SF).

(Pf) was recorded at sugar beet harvest, where an increase was observed in all the plots. However, significant variations were observed in the plots following the different treatments ($df = 9$, $p = 3.9e-10$, Wald-test). Plots with nil-endophyte grass (E-) had significantly high SRN densities compared to all the treatments. Plots with fallow disturbed and phacelia treatments had significantly fewer SRN compared to the fallow undisturbed, followed by opium poppy, sterile fallow plots, oilseed radish, and grass with endophyte (E+) (LSD = 131, $df = 19$, $p < .05$)—(Figure 2e). The SRN densities

recorded at sugar beet harvest were positively correlated ($r = 0.45$, $p = .0014$) with densities recorded before sugar beet drilling (Ai). The effect of soil disturbance during the CC incorporation was observed, where the fallow disturbed plots had significantly lower SRN compared to the fallow undisturbed control. The sterile fallow, which was weed-free, also had significantly lower SRN densities than the undisturbed fallow control. An overall Rf was calculated from CC drilling to sugar beet harvest. This Rf indicated that different CCs multiplied SRN at different rates. Differences were observed between and

within different CC species ($df = 9$, $p = 2.6 \times 10^{-5}$, Wald-test). Phacelia and opium poppy had lower multiplication rates when compared to CCs such as Indian mustard and Italian ryegrass with and without endophyte (E+ and E-), which greatly multiplied SRN. Variations were also observed within plant families, for example, Indian mustard multiplied SRN three times more than the oilseed radish. Similarly, the grass with endophyte (E+) had seven times fewer SRN than the grass without endophyte (E-) (Figure 2f).

3.2 | Effect of environmental variables on SRN densities

The sampling dates for SRN densities were characterised by differences in soil temperature and rainfall (Figure 3). At site 1, the sampling dates were in the same season in 2021. The soil temperatures were reasonably consistent in June, July, and September, with sampling points ranging from 18 to 21°C, except for the last sampling date in December, where the soil temperatures reduced to an average of 6°C. The rainfall was relatively high in July (4 mm), greatly decreased in September (<1 mm), and then increased to 2.8 mm towards the end of the year in December 2021. At this site, weak relationships were recorded between SRN numbers and soil temperatures ($\rho = 0.28$, $p = .011$) and rainfall ($\rho = 0.22$, $p = 0.052$)—Figure 3a, d. At site 2, the average soil temperatures at sampling in 2021 were higher, ranging from 10 to 20°C, compared to 2022 and 2023, where soil temperatures were ranging from 3 to 5°C at the time of sampling. A negative relationship between the soil temperatures and SRN densities was recorded ($\rho = -0.71$, $p < 2.2 \times 10^{-16}$) (Figure 3c). Rainfall at sampling was lowest in February 2022 and July 2021 and highest towards the end of the year in November 2021. The highest rainfall amount at sampling was recorded in January 2023, and a positive relationship was observed between high rainfall amount and increasing nematode densities ($\rho = 0.48$, $p = 5.6 \times 10^{-13}$)—Figure 3d.

3.3 | Effect of cover cropping on sugar beet variables

Cover cropping had no effect on the sugar beet root yield as no significant differences were recorded among the different treatments (Table 5), although there was a negative correlation ($\rho = -0.61$, $p < .001$) between sugar beet root yield and SRN densities recorded 4 weeks after CC drilling. Plots with records of high SRN densities at 4WAP had lower root yield at sugar beet harvest. High root yield was also positively correlated ($\rho = 0.47$, $p = .002$) to sugar percentage. Sugar content was not significantly affected by CC treatments ($p > .05$, LSD) but was negatively correlated ($r = -0.39$, $p = .01$) to high SRN densities recorded at harvest. Cover cropping also had no effect on sucrose yield, and the differences observed were mainly due to block effect rather than a treatment effect. Sucrose yield was positively correlated ($r = 0.46$, $p = .003$) to sugar %. The sugar impurities potassium, sodium, and amino-nitrogen impurities were also not

affected by cover cropping. Despite the root yield being unaffected by cover cropping, the root fanging percentage was significantly affected by the treatments. The root fanging was lower in plots following opium poppy, phacelia, sterile fallow, and disturbed fallowed as compared to plots following Indian mustard. The SRN densities recorded at sugar beet planting (Ai) were positively correlated ($\rho = 0.45$, $p = .003$) with the degree of fanging at sugar beet harvest. The soil tare % was also significantly higher in plots following Indian mustard and fallow undisturbed control as compared to plots following phacelia and in fallow disturbed plots. The soil tare % was positively correlated to the root fanging ($r = 0.34$, $p = .02$); plots with the highest fanging score, that is, following Indian mustard, had the highest soil tare %.

4 | DISCUSSION

The SRN species *T. primitivus* and *P. pachydermus* were recorded at the two field sites. These species were also reported to be prevalent in a previous UK survey (Alpey & Boag, 1976) and abundant in fields in East England with sugar beet crops exhibiting Docking disorder symptoms (Whitehead & Hooper, 1970). *Trichodorus cyndricus* was recorded in site 2 but was absent in site 1. The distribution and prevalence of SRN is influenced by agronomic practices, environmental conditions, and soil physical properties (Cooke, 1973; Winfield & Cooke, 1975). In this study, the type of CCs, environmental variables, that is, soil temperature, rainfall, soil disturbance, and presence of weeds greatly influenced the population dynamics of SRN. The sampling dates were characterised by differences in rainfall and soil temperature, and this had an effect on the SRN densities recorded (Figure 3). This observation is in agreement with previous studies, which reported that densities of SRN were positively correlated to high rainfall in May (Cooke, 1973). The strong negative correlation between soil temperature and SRN densities in our study can be explained by the behaviour of trichodorids, where they tend to move deeper in the soil profile during dry conditions, as they are highly susceptible to desiccation (Winfield & Cooke, 1975). Despite SRN being able to feed and reproduce in many crop species, due to their polyphagous nature (Ayala et al., 1970), it was clear in this study that the rate of reproduction was significantly different among the CCs species tested. Phacelia and opium poppy were less suitable hosts compared to CCs such as grass without endophyte (E-), Indian mustard, and Italian ryegrass. One of the beneficial effects of phacelia as a CC is its ability to suppress weed infestation (Błażewicz-Woźniak et al., 2016); the allelochemicals produced in roots, stems, leaves, and flowers of phacelia inhibit germination of seedlings (Kliszcz et al., 2023). In previous host-status studies with *M. hapla*, phacelia was classified as a maintenance host, which implies that nematode densities neither increased nor decreased during the cropping cycle (Viaene & Abawi, 1998). It has also previously been classified as a poor host for *M. chitwoodi* (Van Himbeek et al., 2024) and a fair host to *Ditylenchus dipsaci* (Augustin & Sikora, 1989), while for *H. schactii*, it was categorised as a non-host (Gardner & Caswell-Chen, 1993). Phacelia was

TABLE 5 Average sugar beet quality and quantity variables \pm standard error, measured at harvest following different cover crop treatments.

Treatment	Soil tare (%) ^a	Sugar (%)—NS	Potassium—NS ^b	Amino nitrogen—NS ^b	Sodium—NS ^b	Sucrose yield (t ha ⁻¹)—NS	Root yield (t ha ⁻¹)—NS	Fanging (%) ^a
<i>Festulolium loliaceum</i> (E+)	4.79 \pm (0.78)	17.32 \pm (0.36)	1654.43 \pm (41.52)	58.94 \pm (4.01)	108.79 \pm (8.18)	18.28 \pm (1.95)	114.23 \pm (12.19)	58.82 \pm (9.86)
<i>Festulolium loliaceum</i> (E-)	4.92 \pm (0.47)	16.8 \pm (0.25)	1663.05 \pm (70.74)	44.54 \pm (5.34)	149.25 \pm (19.44)	14.89 \pm (1.34)	93.08 \pm 8.36	58.75 \pm (8.93)
<i>Brassica juncea</i>	5.61 \pm (0.59)	17.06 \pm (0.24)	1632.04 \pm (94.45)	53.91 \pm (10.89)	132.23 \pm (25.73)	17.64 \pm (0.68)	110.28 \pm (4.24)	73.06 \pm (4.31)
<i>Lolium multiflorum</i>	5.28 \pm (0.27)	17.53 \pm (0.50)	1698.61 \pm (33.14)	70.62 \pm (10.41)	95.16 \pm (16.22)	17.18 \pm (1.15)	107.40 \pm (7.18)	70.08 \pm (4.85)
<i>Raphanus sativus</i> oleiferus	5.02 \pm (0.69)	17.48 \pm (0.69)	1674.70 \pm (89.18)	65.30 \pm (2.47)	97.28 \pm (5.00)	19.84 \pm (1.79)	124.03 \pm (11.17)	63.16 \pm (2.65)
<i>Papaver somniferum</i>	4.63 \pm (0.39)	18.3 \pm (0.65)	1591.93 \pm (57.88)	53.09 \pm (7.17)	117.29 \pm (12.29)	17.59 \pm (2.96)	109.97 \pm (18.49)	57 \pm (4.02)
<i>Phacelia tanacetifolia</i>	4.01 \pm (0.25)	17.61 \pm (0.44)	1676.73 \pm (93.92)	51.90 \pm (3.17)	116.35 \pm (5.51)	19.34 \pm (1.75)	120.91 \pm (10.91)	57.25 \pm (4.03)
Sterile fallow	4.43 \pm (0.92)	17.63 \pm 0.53	1553.57 \pm (39.88)	51.38 \pm (8.86)	141.63 \pm (22.72)	15.94 \pm (2.07)	99.66 \pm (12.94)	56.28 \pm (5.52)
Fallow undisturbed	5.11 \pm (0.33)	17.58 \pm 0.46	1646.39 \pm (43.71)	41.12 \pm (2.05)	152.38 \pm (10.45)	17.90 \pm (1.51)	111.31 \pm (4.79)	67.25 \pm (2.75)
Fallow disturbed	3.49 \pm (0.40)	17.58 \pm 0.50	1587.71 \pm (63.09)	44.24 \pm (3.74)	144.09 \pm (16.69)	18.09 \pm (1.55)	103.21 \pm (11.98)	56.81 \pm (4.71)

Note: NS—Values following each other in that column are not significantly different ($p \geq .05$, LSD).

^aIndicates significant differences among some treatments within a column according to the LSD test at the $p \leq .05$ significance level.

^bValues are average impurity components of four blocks in milligrams/100 g of sugar.

also shown to suppress densities of *M. hapla* when its seeds were coated with *Pochonia chlamydosporia* (Uthoff et al., 2024).

Similar to our study, opium poppy has also been shown to be a less preferred host for several PPNs. For instance, under field conditions, 12 species of nematodes in the family Tylenchidae were recorded in low frequencies ranging from 1% to 41% in poppy in the Afyon region of Turkey (Akgül & Ökten, 2001). Poppy was also recorded to be a non-host to *P. thornei* and *Merlinius brevidens* in glasshouse experiment studies (Tobar et al., 1995). During a field survey to investigate nematodes parasitising poppies, only 10%–12% of poppy infected with *M. incognita* showed stunting symptoms (Pandey et al., 1999).

In this study, the differences in SRN reproduction were not only recorded between crop species from diverse plant families but also within families, where the reproduction factor in grass containing endophyte (E+) was significantly lower compared to grass without endophyte (E-). The difference observed is likely to be due to the endophyte status of the grass. The symbiotic relationship between *Festulolium* spp. and the endophyte *E. uncinata* results in the production of bioactive secondary metabolites known as lolines (Meyer et al., 2013, 2020; Mwangi et al., 2024b). The lolines are exuded from plant roots and are also abundant in the stems and leaves of the grass; hence these compounds continue to be released when grass residues are decomposing (Blankenship et al., 2001; Bush et al., 1993; Roberts & Lindow, 2014). A similar study reported low densities of *Paratrichodorus minor* in tall fescue colonised by *Epichloë coenophialum* when compared to non-colonised fescue (Pedersen et al., 1988). The densities of *Pratylenchus scribneri* recovered in 100 cm³ soil from pots with tall fescue containing the endophyte *Epichloë coenophialum* (E+) were 49–85 compared to 467–750 nematodes from pots with tall fescue without endophyte (E-), indicating that the presence of the endophyte had a suppressive effect on the nematode (Bacetty et al., 2009).

Brassica species also performed differently within and between sites. In site 1, plots drilled with brassicas significantly suppressed SRN densities as early as 4 weeks after planting. The decrease in SRN densities in the drilled plots could be explained by the glucosinolate and myrosinase reaction in brassicas, which leads to the release of isothiocyanates, which have been shown to have nematicidal effects towards SRN in in vitro assays using commercially sourced isothiocyanates (Mwangi et al., 2024a). In this case, the glucosinolates may have been exuded through the young roots, which have been documented to possess high concentrations of glucosinolates during early growth. The roots of brassicas such as oilseed rape (Choesin & Boerner, 1991) and mustard (Schreiner & Koide, 1993) are also known to release glucosinolates into the root rhizosphere. Soil microbes, in turn, hydrolyse the glucosinolates into isothiocyanates by releasing the enzyme myrosinase (Dutta et al., 2019). Exudation of isothiocyanates from actively growing roots has also been reported (Elliott & Stowe, 1971) and is thought to be due to superficial cell damage during active root development when the plant is young (Ngala et al., 2015). Conversely, when the plant matures, the glucosinolates become more concentrated in the reproductive organs, that is, flowers, and are incorporated into the soil in the biofumigation process (Bellostas et al., 2004).

The biofumigation effect was observed at site 1 upon cutting and incorporation of Indian mustard and oilseed radish residue, but the effect was not observed for daikon radish, where densities were higher than the fallow plots. The oilseed radish used in this study (Terranova) was bred for resistance to nematodes, and this probably explains why it performed better than the daikon radish. At site 2, cultivation of oilseed radish resulted in greater SRN suppression than Indian mustard, where it had lower SRN densities compared to the fallow undisturbed control, while Indian mustard was not different from the control. The differences in the performance of the brassicas at the two sites might be due to different factors. At site 1, the initial nematode densities at drilling were not as high as at site 2. Initial nematode densities at planting play an important role in the rate of multiplication of nematodes (Mwangi et al., 2019). The other factor is the establishment of the brassicas, whereby high biomass (40–48 t ha⁻¹) was achieved at site 1, close to the target of 50 t ha⁻¹ (Lazzeri et al., 2004) whereas at site 2 the biomass was 3–4 times lower than the recommended rate. Previous studies have reported that low levels of brassicaceous residues incorporated (0.02 t ha⁻¹) were not effective in suppression of *M. incognita* as compared to 0.06 t ha⁻¹ which effectively reduced infection and damage of *M. incognita* in *Vigna subterranea* (Fourie et al., 2016). A similar observation was made where increasing the rate of *Brassica oleracea* residues increased the percentage reduction of *M. incognita* (Youssef & Lashein, 2013). High amounts of root biomass produced by *Raphanus sativus* were also associated with high concentrations of glucosinolates, leading to the release of toxic isothiocyanates that enhanced efficacy in reducing the viability of encysted eggs of *G. pallida* in partial biofumigation (Ngala et al., 2014).

The disturbance effect created in the process of flailing and rotavating during CC incorporation was shown to influence SRN densities in this study. Fallow disturbed plots had lower SRN densities compared to the fallow undisturbed plots, indicating the sensitivity of SRN to disturbance. Various studies have reported the susceptibility of SRN to mechanical damage. Manual handling and transportation of soil were attributed to reduced *Pyrenophora teres* densities, whereby soil carefully transported from field to laboratory yielded 2240 nematodes L⁻¹ soil compared to soil transported via post in a cardboard box, yielding 628 nematodes L⁻¹ soil (Bor & Kuiper, 1966). In Holland, the effect of biofumigation on nematode communities was attributed to combined tillage and green manuring (Vervoort et al., 2014). The impact of weeds recorded at site 2 on SRN densities was also evident in this study; plots where weeds were managed using glyphosate (sterile fallow) had lower SRN densities. SRNs have been reported to harbour and transmit viruses, that is, tobacco rattle virus (TRV) in many arable weed species such as field pansy, knotgrass, groundsel, shepherd's purse, and chickweed (Cowgill, 2015) indicating that weed management serves as a very important practice in keeping SRN densities low in fallow land.

Cover cropping had an effect on the quality variables of the roots of sugar beet at harvest. Root fangings and soil tare were significantly lower in plots that had lower SRN reproduction. SRN densities at sugar beet drilling were positively correlated with root fangings; hence, plots with high nematode pressure recorded higher root fangings, which was positively correlated to the soil tare as increased fangings

leads to more accumulation of dirt in the roots. Direct feeding on roots of young sugar beet seedlings by SRN causes stubby lateral roots (fangings) which later turn roots grey-brown and then black as they die and decay (Christie & Perry, 1951; Winfield & Cooke, 1975). Young sugar beet have been shown to be more susceptible to SRN infestation in a study where high densities of *T. cylindricus* or *P. pachydermus* were common mostly around young seedlings (1500 L⁻¹) than around large plants (600 L⁻¹) at Gayton, Thorpe, England (Whitehead & Hooper, 1970); hence, this explains the positive correlation of root fangings and initial SRN densities at sugar beet drilling observed in our study. In this study, cover cropping did not affect the root yield of sugar beet. Previous studies have shown that sugar beet suffering from docking disorder may recover later in the season (Cooke, 1973). This might explain why differences in yield were not recorded, even though root fangings symptoms were still visible during scoring at harvest.

At sugar beet drilling, high SRN densities were positively correlated to higher rainfall and lower soil temperature. The combination of these factors may have contributed to the degree of root fangings. Similar observations were recorded where severe damage to young sugar beet seedlings was correlated with high total rainfall in the month of May (Cooke, 1973; Jones et al., 1969; Winfield & Cooke, 1975). The influence of soil moisture on SRN densities can be explained by the fact that trichodorids are most active when soils are at or near field capacity (Cooke, 1973). Trichodorids have also been shown to be more susceptible to desiccation than other nematode species, that is, *Rotylemus* and *Pratylenchus* spp. (Rössner, 1971). The type of soil inhabited by SRN is mostly sandy, and this means that there is high drainage where the topsoil dries out as water percolates deeper through the soil profile (Cooke, 1973). This scenario causes the SRN to move up and down the soil profile following the soil moisture, and, as such, densities of SRN are likely to vary depending on the time of sampling (Cooke, 1973). Higher rainfall also leads to leaching of soil nutrients such as nitrogen and manganese, which has been associated with a high incidence of Docking disorder symptoms (Whitehead & Hooper, 1970).

In conclusion, the study shows that the population dynamics of SRN under field conditions are influenced by multiple factors such as the host-status of the CCs grown, the prevailing environmental conditions, the susceptibility of the follow-up crop, the presence of weeds, and field operations that involve soil disturbance. It was clear in this study that brassicas can be optimised to manage SRN effectively, as seen in site 1, where the suppression effect was greater as the brassicas established well and had high biomass compared to site 2. Cover crops such as phacelia and opium poppy were also shown to have lower SRN multiplication compared to the fallow, and more research is needed to see how they can be optimised under field conditions to enhance their efficacy for the management of SRN.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

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