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Organic intercropping legacy reduces *Fusarium* pathogens and root rot in subsequent durum wheat

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Abstract

Intercropping is a sustainable practice becoming increasingly popular in the Canadian Prairies. However, its long-term impact on diseases in subsequent sole crops is not well understood. We examined root rot and associated fungal communities in durum wheat [*Triticum turgidum* L. ssp. *durum* (Desf.) Husn.], following different ratios of lentil (*Lens culinaris* Medik.)–yellow mustard (*Sinapis alba* L.), and field pea (*Pisum sativum* L.)–oat (*Avena sativa* L.) intercrops, and respective monocultures, in a semi-arid region of the Canadian Prairies (2018–2019). The previous crop(s) impacted disease severity in durum wheat and had a significant impact on the composition of fungal communities. Durum grown after the mustard monoculture and its high-ratio intercrop had 15% less severe root rot than after the lentil monoculture and its high-ratio intercrop, while durum following the oat monoculture and its intercrops had 16% more severe root rot than after mustard and its intercrops. *Fusarium* species were the most frequent fungal isolates, accounting for 70% of total isolations. The main *Fusarium* cereal pathogens were >1.7x–25.5x higher following the oat than the mustard monoculture and 2x–3x higher after the pea–oat than the lentil–mustard intercrops. In turn, isolation of the main fungi with biocontrol potential (antagonists) was 4.3x–5x higher after the mustard than oat monoculture, and 2x higher after lentil–mustard than pea–oat. The prevalence of antagonists in mustard-containing treatments, and their negative correlation with disease levels, suggest a dual mechanism of disease suppression: a direct pathogen inhibition through the mustard's allelopathy and enhanced populations of indigenous microbial antagonists.

Plain Language Summary

Intercropping is becoming more common in the Canadian Prairies, but information of its impact on root rot and associated fungal species in the subsequent sole crop

Abbreviations: FHB, Fusarium head blight; ITC, isothiocyanate; MJJ, May, June, July; PCA, principal component analysis; SI, subcrown internode.

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is lacking. These were examined in durum wheat grown after lentil–mustard and pea–oat intercrops and respective monocultures, managed organically in a semiarid region. The previous crop(s) significantly impacted disease severity and fungal isolations. There was more root rot and *Fusarium* cereal pathogens in durum after oat and pea–oat than after mustard and lentil–mustard. Fungi with biocontrol potential (antagonists) had a combined isolation of 20% and were most common in durum after mustard and its intercrops. These were also most common in organic crops in previous studies. The prevalence of antagonists in mustard-containing treatments, and their negative correlation with disease, suggest a dual mechanism of disease suppression: pathogen inhibition through mustard's allelopathy and enhanced populations of indigenous microbial antagonists.

1 | INTRODUCTION

Intercropping, the practice of growing two or more crops simultaneously in the same field, is gaining increasing attention as a sustainable agricultural strategy. This is supported by popular publications on this cropping system (Agriculture & Agri-Food Canada, 2021; Betkowski, 2024), including under organic management (Fleury, 2021, 2022). Legumes fix atmospheric nitrogen (N); thus, growing them with other crop types could be an efficient strategy for improving crop productivity, especially under low N conditions. In turn, more competitive companion non-legume crops can offer benefits, such as weed control, among others (Bedoussac et al., 2015; Fernandez, Lokuruge, Abdellatif, Waelchli, Leeson, Schellenberg, et al., 2025).

Previous research evaluated the growth and yield of lentil (*Lens culinaris* Medik.)–yellow mustard (*Sinapis alba* L.) and field pea (*Pisum sativum* L.)–oat (*Avena sativa* L.) intercrops in the semiarid Canadian Prairies (Fernandez, Lokuruge, Abdellatif, Waelchli, Leeson, Schellenberg, et al., 2025). Subsequent work examined the legacy effects of these intercrops on a following sole durum wheat (*T. turgidum* L. var. *durum*) crop (Fernandez, Lokuruge, Abdellatif, Waelchli, Leeson, Zvomuya, et al., 2025) and showed that soil nitrate-N (NO_3^--N) concentration (>15 cm deep) and subsequent durum wheat biomass and grain yield were significantly impacted by the previous year's intercrop. Specifically, pea–oat intercrops resulted in higher durum wheat aboveground biomass and grain yield than lentil–mustard intercrops.

Beyond economic and environmental benefits, intercropping can also exert a significant influence on plant disease dynamics, often leading to reduced disease levels compared to monocultures (Boudreau, 2013). This suppression can be the result of mechanisms such as altered microclimates, allelopathy, and/or shifts in the soil microbial community toward antagonistic microorganisms (Boudreau, 2013; Chen et al., 2023).

Fernandez, Abdellatif et al. (2026) examined the impact of lentil–mustard and pea–oat intercrops at different ratios on root rot development and the abundance and diversity of fungi colonizing belowground tissue. This work, conducted in the semiarid Canadian Prairies where such studies are lacking, revealed multiple pathogens and weak pathogens/saprophytes in all crops. *Fusarium* species were commonly isolated from the roots or subcrown internodes (SIs) of all these crops. However, the impacts of intercropping on these fungi varied between the intercrop combinations. Lentil intercropped with mustard resulted in lower levels of *Fusarium* pathogens than in the lentil monoculture. In contrast, pea intercropped with oat had a higher number of fungal species, including *Fusarium* pathogens, that were more similar between the two crops than between lentil and mustard. This study also isolated fungal species not known to be pathogenic on the intercropped species (Fernandez, Abdellatif, et al., 2026), which aligns with Chen et al. (2023) and suggests that intercropping can lead to the development of diverse non-pathogenic fungal species with various ecological functions. Intercropping could also have significant effects in restricting the increase and spread of pathogenic fungal spores and the carry-over of soil-borne diseases to the subsequent year(s) (Stockdale et al., 2001). An examination of diseases in a sole cereal crop, grown after intercrops, in the semiarid region of the Canadian Prairies is lacking.

Root and crown rot, primarily caused by *Fusarium* species and *Cochliobolus sativus* (Ito & Kurib.) Drechs. ex Dast. [anamorph *Bipolaris sorokiniana* (Sacc.) Shoemaker], are widespread in many regions of the world (Bozoğlu et al., 2022; Özer et al., 2023; Shrestha et al., 2021). Root/crown diseases pose a significant threat to cereal production globally, leading to substantial yield losses in wheat and barley (*Hordeum vulgare* L.) (Al-Sadi, 2021; Xiong et al., 2023). Root infections by *C. sativus* in wheat might not only cause yield reductions (Tinline & Ledingham, 1979), but this pathogen could also cause other diseases, such as black point

and spot blotch (Al-Sadi, 2021). Furthermore, colonization of underground tissue by *Fusarium* pathogens, and their survival and multiplication in those tissues after harvest, might not only promote root rot development in the subsequent crop but might also affect the development of other important diseases, such as Fusarium head blight (FHB) (Fernandez et al., 2008, 2009). Infected crop tissues might be a reservoir for *Fusarium* inoculum when the environment is not conducive to the development of head/grain diseases. Root infections by *C. sativus* and *Fusarium* pathogens have been commonly found in spring wheat (*Triticum aestivum* L.) samples collected in field surveys and organic and non-organic research trials in Saskatchewan, Canada (Bailey et al., 2000; Fernandez & Jefferson, 2004; Fernandez et al., 2007, 2011, 2022).

Reductions in soil-borne disease and/or pathogen in various crops have been associated with *Brassica* species grown in crop rotations (Motisi et al., 2009; Muehlchen et al., 1990). This effect is largely attributed to the release of glucosinolate hydrolysis products, specifically isothiocyanates (ITCs), into the soil upon the breakdown of plant residues. These ITC compounds exhibit broad-spectrum fungistatic or fungicidal activity on soil-borne pathogens, including *Fusarium* species (Manici et al., 1997), which would depend on factors such as the *Brassica* species, method of incorporation, and soil conditions. Gimsing and Kirkegaard (2006) reported maximum total ITC concentrations after incorporation of plant tissue of 21.6 and 90.6 nmol g^{-1} for *Brassica napus* L. and *Brassica juncea*, respectively, while according to Morra and Kirkegaard (2002), maximum ITC concentrations could vary from near 1.0 nmol g^{-1} soil, measured immediately after tissue incorporation of *B. napus* and *B. juncea* Czern. & Coss, to concentrations of 40–75 nmol ITC g^{-1} soil after incorporation of tissue that had been subjected to freezing and thawing. The duration and efficacy of ITCs was also reported to be higher in soils with low, rather than high, organic matter (Matthiessen & Kirkegaard, 2006). These ranges would be sufficient to exert fungistatic or fungicidal effects on pathogens like *Fusarium* species (Ashiq et al., 2022; Sarwar et al., 1998). This potent, naturally occurring fungicidal activity could provide a strong mechanistic basis for the potential of *Brassica* in intercrops to suppress root rot diseases and modify the soil fungal community in the subsequent cereal crop beyond any impacts of organic management on beneficial soil microbes (Knudsen et al., 1995).

Given the role that intercrops can play in diversified crop rotations, an examination of how these systems might impact root rot development, and the levels of associated fungi in a subsequent sole grain crop, is needed. This research aimed to investigate the legacy effects of two intercrop combinations, lentil–mustard and pea–oat, established at different seeding ratios in a semiarid region (Fernandez, Lokuruge, Abdellatif, Waelchli, Leeson, Schellenberg, et al., 2025), on the severity of root rot and the composition of fungal communities associated with underground tissue of a subsequent durum wheat crop under organic management (Fernandez, Lokuruge, Abdellatif, Waelchli, Leeson, Zvomuya, et al., 2025). We hypothesized that intercropping legumes with non-legumes, particularly yellow mustard, would significantly reduce root rot in the subsequent durum wheat crop compared to the respective legume monocultures, legume green manure, or summerfallow. We further expected that intercropping would lead to a significant shift in the belowground fungal community of the subsequent durum wheat, including a decrease in pathogenic fungal species and an increase in the prevalence of fungi with biocontrol potential (also known as antagonists), thus supporting a biocontrol mechanism. Evaluation of root rot and associated fungal communities in the preceding intercrops and respective monocultures was reported by Fernandez, Abdellatif et al. (2026).

Core Ideas

- Most fungal species isolated from durum subcrown internodes were present in intercrops and monocultures the previous year.
- Less root rot and *Fusarium* cereal pathogens in durum wheat grown after yellow mustard and lentil–mustard than oat and pea–oat.
- Fungi with biocontrol potential (also known as antagonists) accounted for over 20% of all isolations.
- Antagonists were most common in durum wheat grown after yellow mustard and its intercrops with lentil.
- Preceding crop(s) had a significant and lasting impact on the composition of fungal communities in durum wheat.

2 | MATERIALS AND METHODS

2.1 | Study area and experimental design

These trials were conducted in the Brown soil zone, where the soil type is an Aridic Haploboroll (Orthic Brown Chernozem) with silt-loam texture, with soil organic matter of approximately 3.5%. Intercropping trials had been conducted south of Swift Current, SK, at the Agriculture and Agri-Food Canada, Swift Current Research and Development Centre (latitude: 50°17′ N, longitude: 107°48′ W, elevation 825 m) in 2017 and 2018 on adjacent fields that had been organically managed since 2015. In each of the fields, a mixture of a legume, an oilseed, and a cereal had been grown to flowering and incorporated using a tandem disk harrow (Fernandez, Lokuruge,

TABLE 1 Monocultures and intercrop combinations at different seeding ratios, in a study conducted in southwest Saskatchewan, Canada (2017 and 2018).

	Seeding ratio[b]		Seeding ratio[c]		Seeds m^{-2}	
Crop/intercrop[a]	Legume	Non-legume	Legume	Non-legume	Legume	Non-legume
Lentil–mustard						
Lentil100	1	0	1.00	0.00	204	0
Mustard100	0	1	0.00	1.00	0	289
Lentil100 + Mustard50	1	0.5	0.59	0.41	204	144
Lentil75 + Mustard75	0.75	0.75	0.41	0.59	153	217
Lentil50 + Mustard100	0.5	1	0.26	0.74	102	289
Pea–oat						
Pea100	1	0	1.00	0.00	150	0
Oat100	0	1	0.00	1.00	0	313
Pea100 + Oat25	1	0.25	0.66	0.34	150	78
Pea100 + Oat50	1	0.5	0.49	0.51	150	157
Pea75 + Oat75	0.75	0.75	0.32	0.68	113	235

[a]Crop varieties: lentil—CDC Maxim, yellow mustard—AC Andante, field pea—CDC Meadow, and oat—AAC Oravena.
[b]Seeding ratios based on monoculture seeding rates (lentil 76, mustard 15.3, pea 269, and oat 140 kg ha^{-1}).
[c]Seeding ratio based on the number of seeds m^{-2}.

Abdellatif, Waelchli, Leeson, Schellenberg, et al., 2025). The same selected intercropping treatments in 2017 and 2018 consisted of two combinations of a legume and a non-legume crop (lentil–mustard and pea–oat) at three different seeding ratios, in addition to their respective monocultures (Table 1). In addition, a "summerfallow" and a "forage pea manure" (cv. 4010) monoculture were included as checks. Treatments were arranged in a randomized complete block design with four blocks as the replicates. The experimental unit was the plot (6 m × 4 m), each consisting of 12 rows that were 30.5 cm apart, with 0.5 m between plots and a 15 m pathway between blocks (Fernandez, Lokuruge, Abdellatif, Waelchli, Leeson, Schellenberg, et al., 2025). All crops were harvested at maturity, while forage pea was terminated by mowing at flowering.

Durum wheat (cv. AAC Transcend) was seeded on the previously intercropped plots at a rate of 146 kg ha^{-1} on May 17, 2018 and May 13, 2019 (Fernandez, Lokuruge, Abdellatif, Waelchli, Leeson, Zvomuya, et al., 2025). Right before seeding the durum wheat, the soil was cultivated once at a depth of approximately 10 cm with a cultivator with mounted harrows, and the surface was leveled with a harrow packer.

Precipitation and air temperature were recorded daily throughout the year at a meteorological station located 1 km from the test sites (Table 2).

2.2 | Root rot assessment

For root rot assessment, 40 durum wheat plants with a well-developed SI (>2 cm) were dug up from each plot at the late milk-early dough stage of development (growth stage 77–84, Zadoks et al., 1974), air-dried, and then stored at 4°C. The SIs were excised from each plant and rated for extent of dark brown to black discoloration, indicative of diseased tissue, using a 0–3 scale, for which 0: no discoloration, 1: 1%–25% of the total surface area discolored (slight), 2: 26%–50% (moderate), and 3: >50% (severe) (Fernandez et al., 2014). The percentage of plants in the moderate or severe discoloration category, or the severe-only category, was determined for each plot based on the total SIs collected and assessed from the plot, and a mean percentage value was calculated per replicate.

2.3 | Fungal isolation and identification

For fungal isolations, a piece (1–2 cm) of tissue from each discolored SI was excised and surface disinfested for 1 min in 0.6% NaOCl and rinsed three times in sterile distilled water. Tissue pieces were then plated on modified potato dextrose agar (12 g of Bacto agar and 5 g of potato dextrose agar per liter of distilled water) amended with streptomycin sulfate (160 mg L^{-1}), chlortetracycline (60 mg L^{-1}), and dichloran (2,6_dichloro-4-nitroaniline; 6.5 mg L^{-1}) (Fernandez et al., 2014). Plates were incubated at 20–25°C under cool-white fluorescent and near-UV light (16 h light/8 h dark) for about 5–7 days. Fungi growing out of the tissue pieces were identified based on colony morphology and asexual and/or sexual reproductive structures using descriptions and keys in Leslie and Summerell (2006) and Watanabe (2002). Pure cultures of the isolates that could not be conclusively identified morphologically were transferred to half-strength V8-potato dextrose agar and sent to the University of Guelph Laboratory Services (Guelph, Ontario, Canada) for molec-

TABLE 2 Monthly total precipitation and average monthly air temperature at a study site in southwest Saskatchewan, Canada, 2018 and 2019. Long-term means are from 1981 to 2015.

Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	May–June–July	Total/mean
Precipitation (mm)														
2018	5.5	18.7	90.3	17.9	25.6	16.9	51.2	31.0	44.4	19.9	44.6	26.8	93.7	392.8
2019	11.5	38.1	1.4	31.7	13.3	156.0	11.1	42.6	117.4	25.7	28.3	15.8	180.4	492.9
Long-term mean	13.8	9.2	17.4	22.7	49.5	80.3	54.3	45.4	35.1	19.0	15.1	15.1	184.1	376.9
Air temperature (°C)														
2018	−8.5	−16.0	−5.7	1.1	14.6	17.1	18.8	18.7	9.3	3.9	−4.3	−5.9	16.8	3.6
2019	−7.7	−21.9	−4.8	5.6	9.5	15.8	17.7	16.8	12.3	1.8	−3.5	−7.0	14.3	2.9
Long-term mean	−10.4	−8.6	−2.7	4.9	10.8	15.3	18.4	18.2	12.5	5.4	−3.3	−9.5	14.8	4.3

ular identification. Genomic DNA was extracted and then amplified by polymerase chain reaction following the procedure described by Gardes and Bruns (1993) using the primers ITS1/ITS4. The sequences were analyzed using the ABI Prism Sequencing Analysis software and then aligned with published sequences in the National Center for Biotechnology Information database using the BLAST software (www.ncbi.nlm.nih.gov). The number of isolations of each fungal species from SIs relative to the total number of fungal isolations per plot was used to calculate their mean percentage isolation in each replicate. In addition, tissue pieces from a sample of up to five symptomless roots and SIs from each plot were also treated in the same manner as the discolored tissue.

2.4 | Statistical analysis

Data were subjected to analysis of variance using the generalized linear mixed model (GLIMMIX) procedure in SAS 9.4 (SAS Institute Inc., 2013), with treatment as a fixed effect and year and block nested within year (block[year]) as random effects. Diagnostic plots were constructed using the PLOTS = RESIDUALPANEL option of GLIMMIX to determine if the assumptions of normality of distribution and homoscedasticity were met. Root rot data were normally distributed. When the assumption of homoscedasticity was violated, the RANDOM _RESIDUAL_/GROUP = statement was included in the SAS code, along with DDFM = SATTERTHWAITE. When treatment effects were significant, means were compared by including the LINES and ADJUST = TUKEY (multiple comparison procedure) options in the LSMEANS statement. Treatment effects were assessed at $\alpha = 0.10$, which has been previously used for organic trials (Fernandez et al., 2022) due to their generally high inherent variability. Summary statistics for each crop and treatment were determined using PROC MEANS in SAS, and the relationships among response variables were evaluated via Pearson correlation analysis using the PROC CORR procedure (SAS Institute Inc., 2013).

Nonmetric multidimensional scaling ordination plots based on the Bray-Curtis distance matrix were generated to identify differences in crop root fungal community compositions using the metaMDS function. Statistical significance of differences in crop root fungal community compositions was assessed by permutational multivariate analysis of variance (PERMANOVA) based on the Bray–Curtis distance metrics with 999 permutations using the vegdist and adonis2 functions. Principal component analysis (PCA) was performed using the OriginPro 2024 software package (OriginLab Corporation) to further explore relationships among common root rot levels and percentage fungal isolations from durum wheat in each of the treatments. The PCA was performed on variables that were standardized by mean-centering (i.e.,

subtracting the mean from each variable) and scaling to unit variance (i.e., dividing each variable by the standard deviation). Principal component (PC) scores from the analysis were then plotted for individual observations relative to the first three PCs (PC1, PC2, and PC3) to generate biplots. The Shannon diversity index (Shannon & Weaver, 1949), an indicator of species diversity in a community, was calculated for fungal species and analyzed using the diversity function. These analyses were performed in R v.4.4.3 (R Core Team, 2025) using the "vegan" package v.2.6.10 (Oksanen et al., 2025).

3 | RESULTS AND DISCUSSION

3.1 | Environmental conditions

The current study was conducted under drier conditions than the long-term average (Table 2). Most of the precipitation in 2019 fell in June (156 mm) with total precipitation in July of 11.1 mm, which is when the durum wheat would be maturing, being much lower than the long-term average for July and the total amount for July of 2018. Furthermore, the growing season in 2017, which was the first year of the intercrops, was also drier (67.3 mm) than the long-term average (Fernandez, Lokuruge, Abdellatif, Waelchli, Leeson, Schellenberg, et al., 2025). In the current study, mean temperature for May, June, July (MJJ) was higher in 2018 than 2019 and the long-term mean (Table 2) for a mean of 15.6˚C for the 2 years. Mean air temperature for MJJ (16.2˚C) was also somewhat higher in the intercrop year of 2017 than the long-term mean (Fernandez, Lokuruge, Abdellatif, Waelchli, Leeson, Schellenberg, et al., 2025).

Any variability in root disease levels and fungal populations observed in the current trials would be likely due, at least partly, to differences in environmental conditions between the 2 years of this study (Fernandez, Lokuruge, Abdellatif, Waelchli, Leeson, Zvomuya, et al., 2025), among other possible factors, which might have further affected any impacts of the intercrops. In field studies with non-pathogenic antagonists for their impacts on colonization of cereal substrates by *Fusarium* pathogens, results were reported not to be consistent for all sampling dates and between experiments (Luongo et al., 2005). In organic agriculture, due to the absence of synthetic chemicals for pest control, greater variability in observations than in intensive conventional agriculture would be expected. However, in the current study, there were commonalities in the data between years to reach some valid conclusions.

3.2 | Root rot in durum wheat

Root rot severity, assessed by the percentage of durum wheat SIs with moderate-to-severe or severe discoloration, varied significantly among the previous crop treatments (Table 3). Overall, root rot was rated moderate to severe in 80.5% of SIs and severe in 52.8% of SIs. These root rot levels were higher than in other organic studies previously conducted in the same area. In an organic cereal species study conducted in close proximity to the current study from 2010 to 2012, root rot in durum wheat preceded by field pea green manure for three consecutive years was present at an overall mean of 36.8% for moderate to severe SI discoloration and 16.0% for severe SI discoloration (Fernandez et al., 2014), lower than the levels observed in the current study. In addition, in an organic tillage-rotation study also conducted nearby, mean moderate to severe SI discoloration in spring wheat preceded by either forage pea manure or a grain legume was also lower at 38.4% in 2014 and 18.0% in 2015 (Fernandez et al., 2022) than in the current study (Table 3).

In our study, root rot levels in durum wheat grown after the checks, forage pea manure, or summerfallow were similar to each other (Table 3). In both cases, the percentage of severely discolored SIs was approximately 20% lower than in durum following the oat monoculture (Oat100) and most of its intercrops with pea. Oat monoculture and pea–oat intercrops had the highest percentages of severely discolored SIs. Conversely, durum grown after the mustard monoculture (Mustard100) exhibited significantly less severe discoloration than durum following the lentil monoculture (Lentil100) and the intercrop with a full ratio of lentil, by approximately 19%. These observations agree with the higher root rot in the in-season oat monoculture and its intercrops with field pea, and the lower root rot in the mustard monoculture and the lentil–mustard intercrops in 2017 and 2018 (Fernandez, Abdellatif, et al., 2026). Although there was no significant correlation between root rot levels in durum wheat (Table 3) and crop biomass or grain yield of this crop reported by Fernandez, Lokuruge, Abdellatif, Waelchli, Leeson, Zvomuya et al. (2025), the significant differences in disease severity among the previous crops highlight the impact of intercropping on soil health and disease pressure.

In addition to differences in the growth stage at which the previously grown legumes were terminated/harvested between the current study and previous organic trials nearby, differences in weather conditions among years are expected to have affected disease development in the following grain crop. Environmental conditions in this study were drier than for the studies conducted nearby a few years earlier. The years in which the durum and spring wheat crops were examined in Fernandez et al. (2014, 2022) had higher precipitation in MJJ than the years of the current trials. Total precipitation in MJJ was 313.8 mm in 2010, 252.2 mm in 2011, and 236.4 mm in 2012 for an average of 267.5 mm in the Fernandez et al. (2014) study, and 183.1 mm in 2014 and 125.2 mm in 2015 for an average of 154.2 mm in the Fernandez et al. (2022) study. For air temperature, the mean for MJJ was 13.6˚C in 2010, 14.1˚C

TABLE 3 Root rot in durum wheat grown after a year of intercrops, monocultures, forage pea manure, and summerfallow in an organic study conducted in southwest Saskatchewan, Canada (2018–2019).

Treatment[a]	Moderate to severe discoloration of subcrown internodes (%)	Severe discoloration of subcrown internodes (%)
Summerfallow	78.9a–c	48.6b–d
Forage pea manure	75.9bc	47.6cd
Lentil100	81.8ab	55.5ab
Mustard100	73.0c	44.7d
Lentil100 + Mustard50	79.8a–c	55.1ab
Lentil75 + Mustard75	83.6a	49.8b–d
Lentil50 + Mustard100	76.2bc	49.9b–d
Pea100	80.4ab	50.6b–d
Oat100	83.8a	59.0a
Pea100 + Oat25	84.8a	58.9a
Pea100 + Oat50	83.6a	54.6ab
Pea75 + Oat75	84.2a	59.5a
p value	<0.0001	<0.0001

Note: Values in a column followed by the same letter are not significantly different according to the Tukey multiple comparison test ($\alpha = 0.10$).

[a]Seeding ratios based on monoculture rates (lentil 76, mustard 15.3, pea 269, and oat 140 kg ha^{-1}): Lentil100 + Mustard50: 100% lentil + 50% mustard; Lentil75 + Mustard75: 75% lentil + 75% mustard; Lentil50 + Mustard100: 50% lentil + 100% mustard; Pea100 + Oat25: 100% pea + 25% oat; Pea100 + Oat50: 100% pea + 50% oat; and Pea75 + Oat75: 75% pea + 75% oat. Seeding rate for forage pea: 196 kg ha^{-1}.

in 2011, and 15.5˚C in 2012, for a mean of 14.4˚C for the 3 years of the Fernandez et al. (2014) study, and 14.3˚C in 2014 and 15.5˚C in 2015, for a mean of 14.9˚C for the 2 years of the Fernandez et al. (2022) study. In the current study, the lower total precipitation and higher mean temperatures during crop growth (Table 2) could have resulted in greater plant stress than in the durum or spring wheat grown in previous years in the nearby trials. These conditions might explain, at least partially, the higher root rot levels in the current study than in the previous studies, agreeing with observations by Shrestha et al. (2021), who found higher root rot in spring wheat in a warm and dry year in North Dakota.

3.3 | Fungal populations in belowground tissue of durum wheat

Similar to what was observed in the preceding intercropping trials (Fernandez, Abdellatif, et al., 2026), fungal species known to be pathogenic or weak pathogens/saprophytes were isolated from the discolored SIs of durum wheat in both years. A total of 32 fungal species or genera were isolated and identified from the durum wheat SIs, with *Fusarium* species collectively accounting for the largest proportion of isolates (mean 69.7%). Most of these fungi were also found occasionally in symptomless SIs, although in most cases none of these yielded any fungi (data not presented).

For both years combined (2018–2019), there were a total of 15 *Fusarium* spp. isolated from durum wheat SIs, plus unidentified *Fusarium* isolates (0.4%). Of all the species isolated from lesioned SIs, *Fusarium* was overall the most abundant genus at 69.7%, with the most frequently isolated species being *F. culmorum* (Wm.G. Sm.) Sacc. (12.2%), *Fusarium equiseti* (Corda) Sacc. (9.2%), *Fusarium oxysporum* Schltdl.:Fr. (8.8%), *Fusarium redolens* (Wollenw.) Sacc. (8.5%), *Fusarium avenaceum* (Fr.:Fr.) Sacc. (7.7%), and *Fusarium pseudograminearum* O'Donnell & T. Aoki (5.1%), followed by *Fusarium solani* (Mart.) Sacc. (4.9%), *Fusarium acuminatum* Ellis & Everh. (3.9%), *Fusarium sporotrichioides* Sherb. (3.1%), *Fusarium proliferatum* (Matsush.) Nirenberg ex Gerlach & Nirenberg (2.4%), *Fusarium torulosum* (Berk. & M.A. Curtis) Nirenberg (1.3%), and *Fusarium flocciferum* Corda (1.3%). Other *Fusarium* species isolated at ˂0.5% were *Fusarium tricinctum* (Corda) Sacc., *Fusarium poae* (Peck) Wollenw., and *Fusarium reticulatum* Mont.

There were also 17 non-*Fusarium* fungal species isolated from SIs, plus unidentified non-*Fusarium* isolates (0.6%). The most frequent non-*Fusaria* isolated from durum wheat SIs were *Clonostachys* spp. (6.5%), the most common species of which was *Clonostachys rosea* (Link: Fr.) Schroers, Samuels, Siefert, and W. Gams at 50% of the isolations of this genus, with the rest being *Clonostachys miodochialis* Schroers (30%) and *Clonostachys epichloe* Schroers (20%). These were followed by the pathogens *C. sativus* (5.3%), *Didymella pinodella* (L.K. Jones) Qian Chen & L. Cai [=*Ascochyta pinodella* L.K. Jones = *Phoma pinodella* (L.K. Jones) Morgan-Jones & K.B. Burch] (2.1%), and by the weak pathogens or saprophytes *Rhizopus* spp. (2.6%), *Alternaria* spp. [mostly *A.*

alternata (Fries) Keissler] (2.3%), *Chaetomium* spp. (1.7%), *Acremonium* spp. (1.6%), *Microdochium bolleyi* (R. Sprague) De Hoog & Herm.-Nijh. (1.5%), *Stemphylium botryosum* Wallr. (1.4%), *Setophoma* spp. (1.1%), *Trichoderma* spp. (1.1%), and *Penicillium* spp. (1.0%). Other genera/species isolated at <1% were *Colletotrichum*, *Pythium*, *Cladosporium*, *Rhizoctonia solani* J.G. Kühn., and *Epicoccum nigrum* Link. The fungi most known for their biocontrol potential and further grouped as "antagonists," included *F. equiseti* and species of *Clonostachys*, *Acremonium*, *Chaetomium*, *Penicillium*, and *Trichoderma*, for a combined isolation of 21.1%.

Most of these species had been previously isolated from belowground tissue of durum or bread wheat in surveys and research trials at several locations across Saskatchewan, Canada (Bailey et al., 2000; Fernandez & Jefferson, 2004; Fernandez et al., 2007). Most of them were also among the species isolated from plant roots and crowns elsewhere, such as those collected in wheat surveys in North Dakota (Shrestha et al., 2021), Montana (Moparthi et al., 2021), Kazakhstan (Bozoglu et al., 2022), and Kyrgyzstan (Özer et al., 2023).

Most of the fungal species isolated from durum wheat SIs were also present in the previous year's intercrop trials (Fernandez, Abdellatif, et al., 2026), indicating a carry-over effect from the preceding crop. However, there were also species isolated in the previous intercrop year, although at low levels, but not present in the durum wheat SIs in the current trials, such as *Fusarium incarnatum*, *Fusarium lateritium*, *F. poae*, *Pythium* spp., and *Rhizoctonia* spp. Fungal species in our study were also similar to those isolated in other previous organic studies on root rot of durum or spring wheat conducted nearby (Fernandez et al., 2014, 2022). However, in the current study, the overall mean percentage isolation of *Fusarium* spp. in durum wheat grown after an intercrop year was around 70% (Table 4) versus 4.4%–15.4% in durum wheat in the nearby organic cereal study (2010–2012), which had been preceded by field pea green manure (Fernandez et al., 2014). Furthermore, in the nearby organic tillage-rotation study in 2014–2015 (Fernandez et al., 2022), the percentage isolation of *Fusarium* spp. from SIs of spring wheat preceded by forage pea manure or a grain legume was also lower, at 34.2%–40.4%, than in our current study.

Weather conditions in 2016, prior to the start of the intercrop trials (Fernandez, Lokuruge, Abdellatif, Waelchli, Leeson, Schellenberg, et al., 2025), might also explain the higher relative isolation of *Fusarium* spp. than in the organic and conventional studies conducted previously nearby and across Saskatchewan, Canada. At the Swift Current, SK, location, total precipitation in MJJ of 2016 was 346.9 mm, and mean air temperature was 15.5˚C. The abundant precipitation in MJJ of 2016 led to significant flooding of fields, resulting in a higher than expected development of Fusarium seedling blight in legume plants, including those seeded for green manure in the land where the intercrop trials were conducted in 2017 and 2018 (Fernandez, unreported observations). Thus, environmental conditions prior to the start of the intercrop trials, which preceded the current durum wheat trials, are expected to have increased *Fusarium* inoculum in the soil and crop residues and would explain, at least partly, the more frequent isolations of *Fusarium* spp. in the current durum wheat study than in previous ones nearby (Fernandez et al., 2014, 2022), despite the fact that the years in which the current trials were conducted were drier than in the previous studies.

In contrast, the main cereal root rot pathogen, *C. sativus*, was present at lower levels (mean of 5.3%) in this study compared to 38.1%–43.3% in durum wheat in the organic cereal study conducted in a nearby field in 2010–2012 (Fernandez et al., 2014) and 32.5%–46.1% in spring wheat in the organic tillage-rotation study conducted in a nearby field in 2014–2015 (Fernandez et al., 2022). In organic studies conducted in Poland, Baturo (2007) also reported that *B. sorokiniana* was isolated in smaller numbers than *Fusarium* spp. from disinfected stem bases of barley at tillering and dough stages, at 15.5% and 15.2%, respectively, for *B. sorokiniana* versus 58.7% and 54.5%, respectively, for *Fusarium* spp.

3.4 | Treatment effects on fungal populations in durum wheat SIs

In organic agriculture, due to the absence of synthetic chemicals for pest control, greater natural variability in observations than in intensive non-organic agriculture would be expected. In non-organic field studies with non-pathogenic antagonists for their impacts on colonization of cereal substrates by *Fusarium* pathogens, results were also reported not to be consistent across different sampling dates and experiments (Luongo et al., 2005). However, in the current study, our data showed commonalities between the 2 years, allowing for a number of valid conclusions.

Fungal species with an overall isolation of ≥1% are presented by treatment in Table 4. In most cases, non-*Fusarium* spp. had an individual mean percentage isolation across all treatments of <3%, except for *C. sativus* (mean of 5.3%) and *Clonostachys* spp. (mean of 6.5%). In turn, most of the *Fusarium* spp. isolated from durum SIs were present in all or most treatments, including the checks, summerfallow, and forage pea manure, with a mean percentage isolation of ≥5% (Table 4). The most frequent *Fusarium* pathogens of cereals were *F. avenaceum*, *F. culmorum*, and *F. pseudograminearum*, which were also commonly isolated from durum or spring wheat in previously conducted surveys in Saskatchewan, Canada (Fernandez & Jefferson, 2004; Fernandez et al., 2007), and in Montana (Moya-Elizondo et al., 2011), and were considered highly aggressive on wheat in Montana (Moparthi et al., 2021). Some of the other

TABLE 4 Percentage isolation (and standard error) of the most common fungal species from subcrown internodes of durum wheat grown after intercrops, monocultures, forage pea manure, and summerfallow in an organic study in southwest Saskatchewan, Canada (2018–2019).

Variable	Mean % isolation (%)	Summer-fallow (%)	Forage pea manure (%)[a]	Lentil 100 (%)	Lentil100 + Mustard50 (%)	Lentil75 + Mustard75 (%)	Lentil50 + Mus-tard100 (%)	Mustard100 (%)	Pea100 (%)	Pea100+ Oat25 (%)	Pea100 + Oat50 (%)	Pea75 + Oat75 (%)	Oat100 (%)
Fusarium species													
total *Fusarium* spp.	69.7	67.7	69.0	76.6	71.6	65.3	64.1	66.1	70.7	72.2	65.3	73.2	74.3
standard error		4.1	2.3	4.7	4.2	4.2	3.0	3.2	4.9	2.7	2.8	3.0	3.1
F. acuminatum	3.9	2.9	3.5	2.5	4.5	0.7	5.3	7.8	3.5	5.7	4.6	3.1	3.2
standard error		1.4	1.4	1.8	1.6	0.7	1.4	1.0	1.6	1.5	1.8	1.2	1.4
F. avenaceum	7.7	6.3	16.9	5.9	5.3	4.2	1.8	1.2	7.6	12.7	9.3	12.4	8.4
standard error		2.0	3.1	1.2	1.6	1.5	0.9	0.8	1.6	1.1	2.4	2.1	0.8
F. culmorum	12.2	9.2	14.4	9.5	11.7	6.0	4.6	10.9	15.8	13.3	14.1	18.2	19.0
standard error		2.6	3.0	2.3	1.3	1.5	0.7	1.4	2.2	1.6	2.0	2.1	1.6
F. equiseti	9.2	11.4	5.7	11.6	8.3	11.4	14.9	17.5	8.3	6.1	7.0	3.9	4.1
standard error		1.8	2.4	1.7	2.2	2.7	1.5	1.7	1.5	1.7	1.4	1.2	1.0
F. flocciferum	1.3	0.0	0.0	2.3	0.6	5.7	1.3	4.6	0.5	0.0	0.0	0.0	0.0
standard error		0.0	0.0	1.1	0.6	3.4	0.9	1.2	0.5	0.0	0.0	0.0	0.0
F. oxysporum	8.8	4.5	12.4	14.1	11.1	10.9	9.1	1.9	9.6	7.7	9.7	8.9	5.6
standard error		1.5	1.5	0.3	2.6	1.8	2.5	1.0	2.4	1.0	2.6	1.6	1.7
F. proliferatum	2.4	1.3	0.0	0.0	3.2	4.3	4.6	1.9	0.0	4.4	2.9	2.7	3.9
standard error		0.9	0.0	0.0	1.7	1.9	1.5	0.9	0.0	1.1	1.6	1.9	1.3
F. pseudograminearum	5.1	10.0	0.0	2.7	3.6	1.2	2.1	0.6	4.5	6.5	3.2	11.2	15.3
standard error		2.1	0.0	1.4	1.5	0.8	1.0	0.6	1.9	1.6	1.3	1.8	1.4
F. redolens	8.5	8.9	7.9	11.8	7.1	10.4	5.6	7.0	13.5	8.9	9.4	6.2	5.6
standard error		2.8	3.2	1.8	1.8	2.0	1.5	0.7	2.0	0.8	1.3	1.1	1.1
F. solani	4.9	2.2	4.8	13.3	10.6	4.7	7.6	2.1	5.1	3.2	1.9	1.6	2.0
standard error		1.1	1.5	2.0	2.2	1.9	2.2	1.5	2.0	1.3	1.3	1.1	0.8
F. sporotrichioides	3.1	6.1	2.5	2.3	2.2	1.9	2.8	1.3	1.5	3.1	2.5	4.3	7.2
standard error		2.1	1.3	1.1	1.1	0.9	1.6	0.8	0.8	0.9	0.9	2.0	2.1
F. torulosum	1.3	0.0	0.0	0.0	2.8	2.7	3.4	7.0	0.0	0.0	0.0	0.0	0.0
standard error		0.0	0.0	0.0	1.5	1.0	1.4	1.3	0.0	0.0	0.0	0.0	0.0
Non-*Fusarium* species													
Acremonium spp.	1.6	0.7	1.0	0.6	1.6	0.0	2.0	1.3	1.1	1.3	4.1	1.8	4.1
standard error		0.7	1.0	0.6	1.1	0.0	1.0	0.8	0.7	0.8	1.7	1.2	1.1

(Continues)

TABLE 4 (Continued)

Variable	Mean % isolation (%)	Summer-fallow (%)	Forage pea manure (%)[a]	Lentil 100 (%)	Lentil100 + Mustard50 (%)	Lentil75 + Mustard75 (%)	Lentil50 + Mus-tard100 (%)	Mustard100 (%)	Pea100 (%)	Pea100+ Oat25 (%)	Pea100 + Oat50 (%)	Pea75 + Oat75 (%)	Oat100 (%)
Alternaria spp.	2.3	2.4	2.5	3.5	2.1	3.4	6.2	5.3	0.5	0.6	0.8	0.0	0.0
standard error		1.3	1.3	1.4	1.0	1.3	1.7	1.7	0.5	0.6	0.8	0.0	0.0
Chaetomium spp.	1.7	1.0	2.2	0.7	1.4	0.7	1.6	1.5	2.5	0.0	2.0	3.8	3.3
standard error		1.0	1.4	0.7	0.9	0.7	1.0	1.0	1.3	0.0	1.0	1.2	1.3
Clonostachys spp.	6.5	3.7	3.3	3.3	6.3	10.5	15.1	13.5	4.3	5.1	5.5	4.9	2.7
standard error		1.5	1.7	1.4	2.0	2.3	1.9	1.4	1.5	1.7	2.1	1.7	1.1
Cochliobolus sativus	5.3	10.7	7.7	3.6	4.0	2.7	3.4	3.4	7.5	5.0	5.3	4.6	5.3
standard error		3.8	2.0	1.2	2.0	1.0	1.6	1.4	2.5	1.6	1.9	2.3	1.5
Colletotrichum spp.	0.7	0.0	0.0	2.4	0.8	0.0	2.0	1.2	1.1	0.0	0.0	0.4	0.7
standard error		0.0	0.0	0.9	0.8	0.0	1.5	0.8	0.7	0.0	0.0	0.4	0.7
Didymella pinodella	2.1	1.0	5.9	1.7	0.0	0.0	0.0	0.0	5.9	2.5	4.3	3.6	0.0
standard error		1.0	1.4	1.1	0.0	0.0	0.0	0.0	1.1	1.0	1.4	1.1	0.0
Microdochium bolleyi	1.5	0.5	1.5	0.5	0.0	0.0	0.7	0.7	2.8	2.5	2.2	2.7	4.4
standard error		0.5	1.0	0.5	0.0	0.0	0.7	0.7	1.2	1.0	1.1	1.1	1.5
Penicillium spp.	1.0	1.3	1.5	0.6	2.1	1.9	0.6	0.0	0.0	1.2	1.2	1.1	0.7
standard error		0.9	1.0	0.6	1.1	0.9	0.6	0.0	0.0	0.8	0.8	0.7	0.7
Rhizopus spp.	2.6	1.8	1.0	2.6	3.7	3.4	2.7	4.4	1.4	3.2	3.0	3.1	1.0
standard error		0.9	1.0	1.4	1.7	1.0	1.7	1.4	0.9	1.7	2.0	1.6	0.7
Setophoma sp.	1.1	3.8	1.4	0.6	0.0	0.7	0.0	1.3	1.2	0.6	0.0	2.1	1.8
standard error		1.2	0.9	0.6	0.0	0.7	0.0	0.9	0.8	0.6	0.0	1.6	0.9
Stemphyllium spp.	1.4	1.4	0.6	1.8	5.0	2.0	0.5	0.0	0.5	4.4	0.8	0.0	0.0
standard error		0.9	0.6	0.9	2.3	1.0	0.5	0.0	0.5	1.1	0.8	0.0	0.0
Trichoderma spp.	1.1	1.5	1.0	0.8	0.6	1.5	1.1	0.6	0.6	1.3	1.9	0.7	1.1
standard error		1.0	1.0	0.8	0.6	1.0	0.7	0.6	0.6	0.8	1.0	0.7	0.7
Antagonists[b]													
Total	21.1	19.5	14.7	17.6	20.4	26.1	35.2	34.3	16.8	15.0	21.8	16.3	16.1
standard error		2.8	2.7	1.8	3.4	3.1	2.3	2.6	2.0	3.2	1.4	1.8	1.7

[a]Seeding ratios based on monoculture seeding rates (lentil 76, mustard 15.3, pea 269, and oat 140 kg ha-1): Lentil100: 100% lentil, Mustard100: 100% mustard, Lentil100 + Mustard50: 100% lentil + 50% mustard, Lentil75 + Mustard75: 75% lentil + 75% mustard; Lentil50 + Mustard100: 50% lentil + 100% mustard; Pea100: 100% pea, Oat100: 100% oat, Pea100 + Oat25: 100% pea + 25% oat; Pea100 + Oat50: 100% pea + 50% oat; and Pea75 + Oat75: 75% pea + 75% oat. Seeding rate for forage pea: 196 kg ha^{-1}.

[b]Antagonists include *F. equiseti* and species of *Clonostachys*, *Acremonium*, *Chaetomium*, *Penicillium*, and *Trichoderma*.

species, including *F. equiseti*, which was among the most commonly isolated *Fusaria*, are generally considered weak pathogens or saprophytes. *Fusarium equiseti* was among the least pathogenic of the *Fusarium* spp. tested by Fernandez and Chen (2005).

Among the fungal populations in the durum wheat SIs (Table 4), the isolation levels of *F. avenaceum*, *F. culmorum*, *F. oxysporum*, *F. redolens*, and *D. pinodella* were among their highest after forage pea manure. These levels were similar to or higher than those after the other two legume monocultures, but in most cases, higher than after summerfallow. In contrast, *F. solani* was most prevalent after the lentil monoculture and its high-ratio intercrop, while *F. flocciferum* and *F. torulosum* were found primarily after the lentil–mustard intercrop and the mustard monoculture. The main *Fusarium* cereal pathogens in this study were isolated at higher levels after the oat monoculture than the mustard monoculture (by 7x for *F. avenaceum*, 1.7x for *F. culmorum*, and 25.5x for *F. pseudograminearum*) and higher after the pea–oat intercrops than the lentil–mustard intercrops (by 3x for *F. avenaceum* and *F. pseudograminearum*, and 2x for *F. culmorum*).

Our data also showed that the percentage isolation of antagonists, which included *F. equiseti* and species of *Clonostachys*, *Acremonium*, *Chaetomium*, *Penicillium*, and *Trichoderma*, was highest in the SIs of durum wheat grown after the mustard monoculture and its intercrop with a full mustard ratio (Lentil50 + Mustard100) (Table 4). Total antagonist isolation after the mustard monoculture was 2x higher than after the oat monoculture. Isolation of the most frequently isolated antagonists was 5x higher for *Clonostachys* spp. and 4.3x higher for *F. equiseti* after the mustard monoculture than the oat monoculture, while these fungi were 2x higher after the lentil–mustard intercrops than the pea–oat intercrops. Furthermore, the mean percentage isolation of these antagonists was significantly and negatively correlated with root rot severity (*F. equiseti*: $r = -0.450$, $p < 0.001$; *Clonostachys* spp.: $r = -0.250$, $p = 0.014$), indicating their potential role in disease suppression.

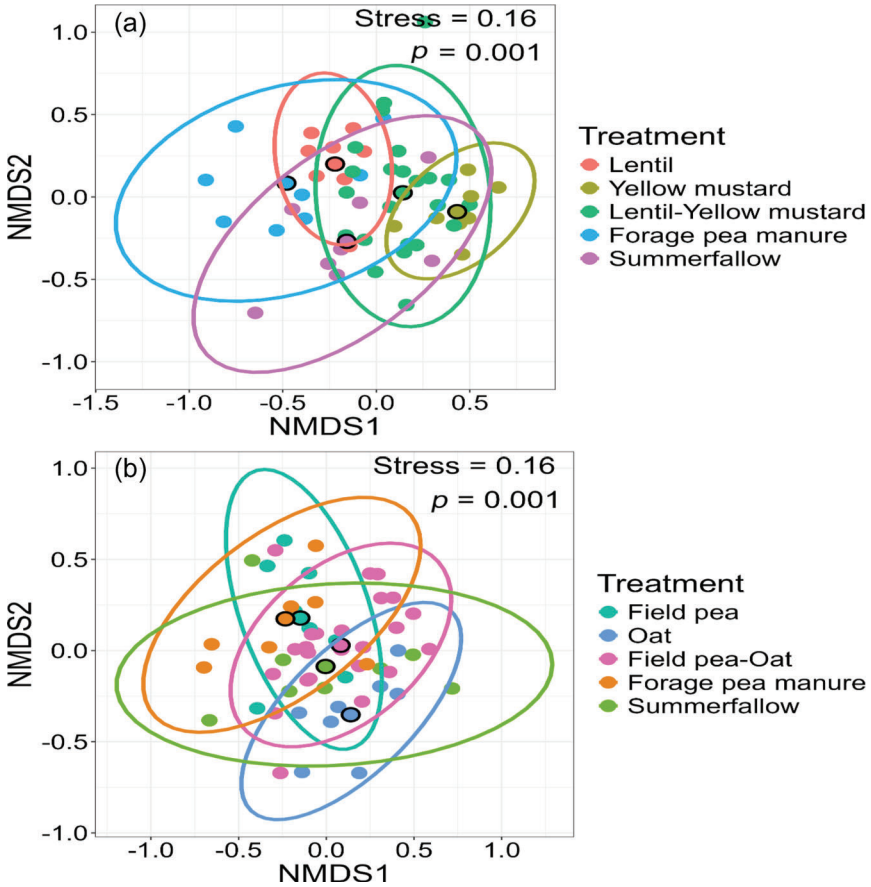
The higher root rot levels (Table 3) and isolation of *Fusarium* spp. (Table 4) from durum wheat grown after oat and its intercrops with pea than after the other treatments are a reflection of the observations made in the intercrop phase where overall *Fusarium* spp. and some of the non-*Fusarium* spp. were isolated at higher levels from the pea–oat than the lentil–mustard intercrops (Fernandez, Abdellatif, et al., 2026). These observations confirm that the two intercrop combinations have distinct legacy effects on the fungal communities of a subsequent crop.

None of the fungi associated with the durum wheat SIs, including *Fusarium* species (Table 4), were significantly correlated (not shown) in their percentage isolation with grain yield or crop biomass of this crop reported by Fernandez, Lokuruge, Abdellatif, Waelchli, Leeson, Zvomuya, et al. (2025). Thus, the observation that *Fusarium* spp. were the most commonly isolated fungi from SIs suggests that these species did not likely affect crop growth. However, colonization of belowground and/or ground-level plant tissue by *Fusarium* pathogens, and their subsequent survival in those tissues after harvest (Fernandez et al., 2007, 2008), might play a role in the development of important diseases, such as FHB, in subsequently grown cereals. Those tissues, in addition to other crop residues, might be a reservoir for *Fusarium* inoculum when the environment is not conducive to the development of head/grain diseases in the same year, such as under the dry conditions that these intercropping and following cereal crop studies were conducted (Fernandez, Lokuruge, Abdellatif, Waelchli, Leeson, Schellenberg, et al., 2025; Fernandez, Lokuruge, Abdellatif, Waelchli, Leeson, Zvomuya, 2025).

3.5 | Impact of intercropping on fungal communities: PERMANOVA, PCA, and Shannon diversity index

The PERMANOVA analysis confirmed that the preceding crop treatments had a significant legacy effect on the fungal community composition in the subsequent durum wheat SIs ($p = 0.001$, R^2: 0.17). This significant difference was evident when comparing the fungal communities from most crop treatments to the checks (summerfallow and forage pea manure), indicating that cropping history, as opposed to no cropping or crops terminated for green manure, profoundly influenced the soil fungal community.

The most substantial shifts in the fungal community were observed in treatments involving yellow mustard. The pairwise comparison between the forage pea manure and mustard monoculture had the highest R^2 value (0.423, $p = 0.001$), indicating that over 42% of the fungal community variation was due to the difference between these two treatments (Figure 1). This was followed by the lentil monoculture versus yellow mustard monoculture, where the R^2 value of 0.398 shows that nearly 40% of the community variation was explained by the difference between these two monocultures. These results are consistent with the hypothesis that the biofumigation effect of mustard, through the breakdown of glucosinolates into antifungal ITCs, affected the soil microbiome by creating a fundamentally different fungal environment. In contrast, the weakest but still significant effect was found between the lentil monoculture and the lentil–mustard intercrop (R^2: 0.065, $p = 0.006$) (Figure 1). This very low R^2 value suggests that while the addition of mustard caused a detectable shift in the fungal community, this shift accounted for only about 6.5% of the total variation, indicating that the effect of this intercrop combination was minor compared to the strong effect of the yellow mustard monoculture. However,



Comparison	R^2	p value
Summerfallow vs Forage pea manure	0.176	0.002
Lentil-Mustard Intercrops		
Summerfallow vs Lentil monoculture	0.188	0.002
Summerfallow vs Yellow mustard monoculture	0.272	0.003
Summerfallow vs Lentil+Mustard intercrop	0.112	0.001
Forage pea manure vs Lentil monoculture	0.197	0.002
Forage pea manure vs Yellow mustard monoculture	0.423	0.001
Forage pea manure vs Lentil+Mustard intercrop	0.159	0.001
Lentil monoculture vs Yellow mustard monoculture	0.398	0.002
Lentil monoculutre vs Lentil+Mustard intercrop	0.065	0.006
Yellow mustard monoculture vs Lentil+Mustard intercrop	0.101	0.001
Pea-Oat Intercrops		
Summerfallow vs Field pea monoculture	0.107	0.077
Summerfallow vs Oat monoculture	0.152	0.004
Summerfallow vs Pea+Oat intercrop	0.093	0.002
Forage pea manure vs Field pea monoculture	0.081	0.279
Forage pea manure vs Oat monoculture	0.307	0.001
Forage pea manure vs Pea+Oat intercrop	0.081	0.003
Field pea monoculture vs Oat monoculture	0.243	0.001
Field pea monoculture vs Pea+Oat intercrop	0.048	0.120
Oat monoculture vs Pea+Oat intercrop	0.094	0.002

FIGURE 1 Nonmetric multidimensional scaling (NMDS) ordination plots showing the effect of different seeding ratios of intercrops and respective monocultures grown the previous year on the fungal community composition in belowground tissue of durum wheat: (a) lentil and yellow mustard monocultures and their intercrop ratios, and (b) field pea and oat monocultures and their intercrop ratios. The stress value for each ordination indicates a good fit to the data. The accompanying table presents the permutational multivariate analysis of variance (PERMANOVA) results for each crop, including the R^2 and p values.

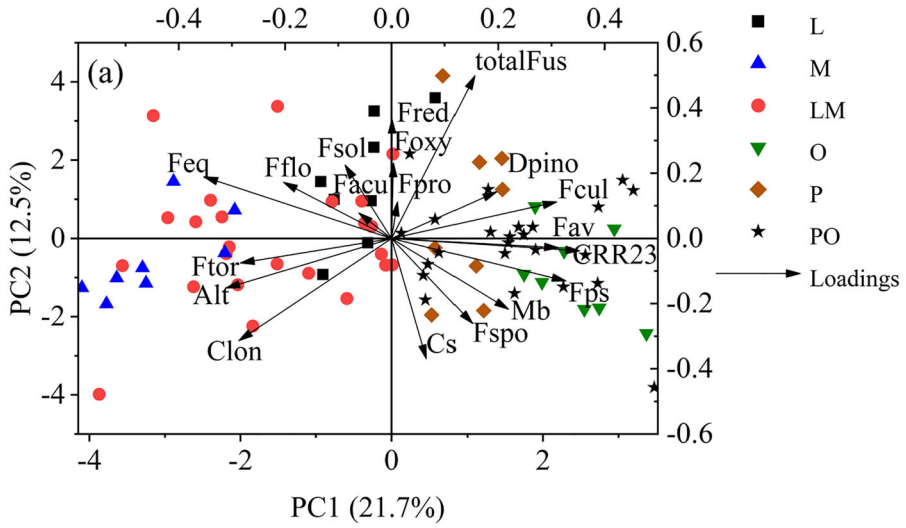


FIGURE 2 Biplots from the principal component analysis of isolation from durum wheat subcrown internodes grown after monocultures and intercrops grown the previous year, in an organic intercropping study in southwest Saskatchewan, Canada (2018–2019). The most prevalent isolates are plotted as vectors, and the monocultures and intercrops are plotted as points. Percentages of variance explained by the first two redundancy analysis axes are in brackets. CRR23, moderate to severe discoloration of subcrown internodes; L, lentil; P, pea; M, mustard; O, oat; LM, lentil-mustard intercrops; PO, pea-oat intercrops. Fungal isolates: totalFus, total *Fusarium* spp.; Alt, *Alternaria* spp.; Clon, *Clonostachys* spp.; Cs, *Cochliobolus* sativus; Dpino, *Didymella pinodella*; Fav, *Fusarium avenaceum*; Facu, *F. acuminatum*; Fcul, *F. culmorum*; Feq, *F. equiseti*; Fflo, flocciferum; Foxy, *F. oxysporum*; Fpro, *F. proliferatum*; Fps, *F. pseudograminearum*; Fred, *F. redolens*; Fsol, *F. solani*; Fspo, *F. sporotrichioides*; Ftor, *F. torulosum*; Mb, *Microdochium bolleyi*.

this small but significant change was seemingly sufficient to selectively suppress the pathogens responsible for root rot, leading to a reduction in root disease severity (Table 3). The results also showed significant differences among the field pea and oat treatments. The strongest difference in this group was between the field pea and oat monocultures (R^2: 0.243, $p = 0.001$) (Figure 1), but the field pea monoculture and the pea–oat intercrop were not significantly different from each other. This may be due to the high proportion of shared fungal species between field pea and oat, as discussed before, which prevented a major shift in the community when these crops were grown together in an intercrop. Thus, overall, the PERMANOVA results clearly indicate that the preceding crop treatments had a significant and lasting impact on the composition of the fungal communities in the subsequent durum wheat SIs.

A PCA was conducted for disease and fungal variables in durum wheat SIs in the intercrops and their respective monocultures. Relationships among root rot severity and percentage isolation of the most common fungi in durum wheat SIs are plotted in Figure 2. A scree plot of eigenvalues (Figure S1), used to visualize the amount of variance explained by each PC, showed a clear "elbow" after the first two PCs indicating that these two PCs accounted for the majority of the total variance in the dataset, explaining 21.7% and 12.5% of the total variance, respectively, for a combined total of 34.2%. This demonstrated that the two-dimensional ordination was a reliable representation of these data and further confirmed that the preceding crop treatments had a significant and lasting impact on the composition of the fungal communities.

The PCA results showed that moderate to severe SI discoloration (CRR23) was closely associated with the pea–oat intercrop ratios and the oat monoculture (Oat100) and least associated with the lentil–mustard intercrop ratios and the mustard monoculture (Mustard100) (Figure 2). Among the most commonly isolated fungi, *F. pseudograminearum*, *F. avenaceum*, *F. culmorum*, *D. pinodella*, *F. sporotrichioides*, and *M. bolleyi* were closely associated with the pea–oat intercrop, the oat monoculture (Oat100), and disease severity (moderate to severe SI discoloration). *Fusarium solani* and *F. oxysporum* were more closely associated with durum wheat grown after the legume monocultures (Figure 2), agreeing with their isolations from the legume monocultures in the previous intercrop years (Fernandez, Abdellatif, et al., 2026). *Cochliobolus sativus* was also more associated with pea–oat and the oat monoculture than with lentil–mustard and the mustard monoculture. In contrast, *F. equiseti* and *Clonostachys* spp., the most frequently isolated antagonists, in addition to *F. flocciferum*, *F. torulosum*, and *Alternaria* spp., were mostly associated with the mustard monoculture and the lentil–mustard intercrop.

The observations in the biplots (Figure 2) are supported by correlations among the various parameters measured. These showed that root rot severity (moderate to severe SI discoloration, CRR23) had a low to moderate positive correlation with some of the most common crop pathogens

associated with the SIs of durum wheat, such as *F. avenaceum* (r: +0.387, $p = 0.0001$) and *F. pseudograminearum* (r: +0.246, $p = 0.0159$), but there was no significant correlation between moderate to severe SI discoloration and *C. sativus*. This suggests that SI discoloration was mostly associated with the presence of some of the most important cereal *Fusarium* pathogens. Furthermore, the percentage total of *Fusarium* spp. was negatively correlated with *C. sativus* (r: −0.465, $p < 0.001$), an indication of the presence of some form of competition among these fungi. In contrast, in the tillage-rotation study previously conducted nearby, correlations between moderate to severe SI discoloration in spring wheat and percentage fungal isolations were positive and high for *C. sativus*, suggesting that this pathogen likely accounted for the root rot levels in that study (Fernandez et al., 2022). Observations of the potential biocontrol agents in the PCA (Figure 2) are also supported by negative correlations of root rot severity (moderate to severe SI discoloration) with *F. equiseti* (r: −0.450, $p = 0.000$) and, to a lesser extent, with *Clonostachys* spp. (r: −0.250, $p = 0.014$). There were also low to moderate negative correlations among fungal species. *Fusarium equiseti* was negatively correlated with the most commonly isolated pathogens, such as *F. avenaceum* (r: −0.473, $p = 0.000$), *F. culmorum* (r: −0.392, $p = 0.000$), *F. pseudograminearum* (r: −0.425, $p = 0.000$), *D. pinodella* (r: −0.249, $p = 0.015$), and *C. sativus* (r: −0.243, $p = 0.017$), while *Clonostachys* spp. were negatively correlated with *F. avenaceum* (r: −0.396, $p = 0.000$), *F. culmorum* (r: −0.299, $p = 0.003$), and *F. pseudograminearum* (r: −0.225, $p = 0.028$).

The Shannon diversity index analysis, which measures species richness and evenness within the fungal community, revealed no significant differences ($p > 0.10$) among any of the treatments (data not presented). Thus, while the preceding crops caused a significant change in the overall composition of the fungal community with fungal species becoming more or less prevalent due to their suppression or promotion, the overall number of species and their relative abundance remained largely unchanged across treatments.

3.6 | Mechanisms involved in the reduction of root rot and biocontrol of associated pathogens

Various international studies support the suppressive effect of *Brassica* species on subsequent crop diseases. For instance, non-organic intercropping or rotation of *Brassica* species, including brown mustard (*B. juncea*) and turnip rape (*B. rapa*), with radish (*Raphanus sativus* L.) in France and Germany was shown to reduce inoculum density and severity of *R. solani* in subsequent sugar beet (*Beta vulgaris* L.) crops (Kluth et al., 2010; Motisi et al., 2009). Similarly, in a US trial, a pea–white mustard (*S. alba*) rotation was reported to decrease root rot severity from *Aphanomyces euteiches* Drechs. in pea, which was confirmed by reduced pathogen propagules in bioassays (Muehlchen et al., 1990). Furthermore, incorporation of *B. juncea* residues in France increased suppressiveness against *F. oxysporum* wilt in flax (Friberg et al., 2009).

The reduced root rot severity (Table 3) and lower *Fusarium* cereal pathogen levels (Table 4) observed following the lentil–mustard intercrops and mustard monoculture suggest a disease-suppressive legacy effect from the previous year (Fernandez, Abdellatif, et al., 2026). This effect was likely due, at least partly, to the biofumigation potential of the mustard crop. The disease suppressiveness effect of *Brassica*-based green manure could result from the production of glucosinolates by *Brassica* species, hydrolyzed into volatile toxins like ITCs (Gimsing & Kirkegaard, 2006), which can inhibit soilborne pathogens (Sarwar et al., 1998). The lower isolation frequencies of cereal pathogens like *F. avenaceum*, *F. culmorum*, and *F. pseudograminearum* following mustard-containing than oat-containing treatments (Table 4) support this mechanism. In the previous intercrop year (Fernandez, Abdellatif, et al., 2026), the crop residues after harvest of the yellow mustard monoculture and its intercrop were not incorporated until the following spring just before seeding of the durum wheat, which potentially could reduce the impact of volatile compounds. However, the decomposition of the mustard roots and other crop residues over time would still release ITCs into the soil. This is consistent with previous research demonstrating the efficacy of *Brassica* residues in managing common root rot (*C. sativus*) and *Fusarium* foot rot of wheat (Campanella et al., 2020) or after incorporating residues of *Brassica* species, including *S. alba*, on diseases caused by *Fusarium* species and other pathogens (Friberg et al., 2009; Kluth et al., 2010; Motisi et al., 2009; Muehlchen et al., 1990).

Beyond this fungicidal effect, our results suggest that yellow mustard and its intercrop at its highest ratio, resulted in an increased presence of non-pathogenic, antagonistic fungi (Table 4), in the subsequent durum wheat. This suggests that yellow mustard might be playing a role in the biocontrol of pathogens and disease suppression in the subsequent durum wheat crop. The PCA biplots (Figure 2) reinforced these associations, showing the mustard treatments clustering with the increased abundance of these beneficial fungi and reduced root rot severity. These results agree with reports that shifting the balance of fungal communities in the rhizosphere and endosphere toward beneficial organisms can significantly enhance the suppression of crop root pathogens (Chen et al., 2023; Morsy et al., 2020).

These findings align with previous reports showing the biocontrol potential of the antagonist fungi against various pathogens. *Clonostachys* species are well-documented biocontrol agents, known for their mycoparasitic activity, competition for nutrients, and ability to induce host plant resistance (Abdellatif et al., 2022; Sutton et al., 2008; Xue et al., 2009). Some of the *Clonostachys* species isolated from

organic fields in southwest Saskatchewan, Canada, were able to control *Fusarium graminearum*, *F. avenaceum*, and *C. sativus* in in vitro tests (Abdellatif et al., 2022) and in preliminary field and controlled-environment trials (Abdellatif, unreported observations). In addition, some of these *Clonostachys* species were also able to control *A. euteiches* in in vitro studies (Fernandez, unreported observations). In other studies elsewhere, *C. rosea* also gave the best control of *F. culmorum* in winter wheat (Knudsen et al., 1995), reduced mycotoxin production by *F. graminearum* and *F. culmorum* in wheat (Gromadzka et al., 2009), suppressed sporulation of *F. culmorum* and *F. graminearum* on wheat straw and maize (*Zea mays* L.) stalks (Luongo et al., 2005), reduced mycotoxin production by *Fusarium verticillioides* (Sacc.) Nirenberg in maize (Samsudin et al., 2016), and was associated with a lower incidence of root and stem-base diseases of winter wheat (Lenc et al., 2015). *Clonostachys* spp. are endophytic fungi that, in addition to their biocontrol potential, can also promote plant growth and drought tolerance (Morsy et al., 2020; Sutton et al., 2008).

Similarly, *F. equiseti* can act as an endophyte, promoting plant growth and reducing root rot disease caused by pathogenic *Fusarium* species in various crops (Dawson et al., 2004; Horinouchi et al., 2007; Luongo et al., 2005; Sing et al., 2009; Šišić et al., 2017). Other species isolated in the current study known for their biocontrol potential against crop pathogens are isolates of *Acremonium* (Lenc et al., 2015), *Chaetomium* (Knudsen et al., 1995; Lenc et al., 2015; Yue et al., 2018), and *Trichoderma* spp. (Fernandez, 1992; Lenc et al., 2015; Villar et al., 2022). In addition, among other genera/species, Thambugala et al. (2020) also listed species of *Alternaria*, *Penicillium*, and *Paramyrothecium* as being potential biocontrol agents.

The higher root rot levels and increased populations of the main *Fusarium* cereal pathogens in the oat monoculture and pea–oat intercrops than in the mustard-containing treatments (Tables 3 and 4) are likely a reflection of the susceptibility of oat to cereal root rot pathogens (Fernandez & Jefferson, 2004) and its known lower allelopathic potential compared to mustard. Pea roots are also known to support some cereal root rot pathogens (Fernandez et al., 2022; Moparthi et al., 2021), thus contributing to their inoculum load in their intercrop with oat. While the pea–oat intercrop may be optimal for maximizing the growth of a subsequent durum wheat crop (Fernandez, Lokuruge, Abdellatif, Waelchli, Leeson, Zvomuya, et al., 2025), the current study demonstrated that growing a legume with a *Brassica* species, such as lentil–mustard, would be effective for controlling *Fusarium* and other pathogenic fungi in the subsequent cereal crop. However, this disease control benefit must be balanced against the potential negative trade-off of yellow mustard on soil N levels and the growth of the subsequent cereal (Fernandez, Lokuruge, Abdellatif, Waelchli, Leeson, Zvomuya, et al., 2025). To mitigate this, growing a legume after a monoculture or intercropped *Brassica* species would be expected to help restore soil N levels, especially when the companion legume grows poorly due to dry conditions (Fernandez, Lokuruge, Abdellatif, Waelchli, Leeson, Schellenberg, et al., 2025). Further research into the legacy impact of *Brassica* species and their intercrops on the health and N-fixing ability of subsequent legumes would be important for the development of a sustainable cropping system. Improving the health of an in-season or following grain legume would also be of great significance to the pulse industry given the continued prevalence of root rot (Chatterton et al., 2019; Fernandez et al., 2022) and the persistence of these pathogens in legume crop residues over time (Fernandez et al., 2008).

The significant reduction in root rot severity and pathogenic *Fusaria* following the yellow mustard monoculture and the lentil–mustard intercrops suggests a dual mechanism of biocontrol. The mustard (*S. alba*) residue contains high levels of glucosinolates, which upon hydrolysis, release ITC compounds that provide biofumigation, suppressing pathogenic fungi like *Fusarium* species in the soil (Manici et al., 1997). In addition, the microbial community analysis demonstrated that the mustard-containing treatments enhanced the populations of antagonistic fungi, especially *Clonostachys* spp. and *F. equiseti*. The synergistic effect of these chemical and biological suppression mechanisms provided a lasting reduction in pathogen pressure on the subsequent durum wheat crop, making this cropping system an effective disease-management tool.

3.7 | Promoting biocontrol under organic management

The data from our study and comparison with other local, regional, and international research provide a context for the effectiveness of intercropping in an organic system. Our results showed that specific intercrop selections can successfully promote the presence of biocontrol fungi within the context of organic management.

The presence of biocontrol organisms under organic management, even at individually low levels, has also been found in previous local and regional research. Nearby organic studies have also reported isolating *F. equiseti* and species of *Acremonium*, *Clonostachys*, *Chaetomium*, and *Penicillium* at individual low frequencies from belowground tissues of cereal and legumes (Fernandez et al., 2014, 2022). This contrasts with non-organic studies and surveys in this and other locations in Saskatchewan, Canada, where none of the fungi with biocontrol potential identified in the current study (Table 4) were isolated from SIs of spring or durum wheat (Fernandez & Jefferson, 2004; Fernandez & Zentner, 2005; Fernandez et al., 2007). This pattern is further supported by a comparative study in the Dark Brown soil zone of the Canadian Prairies, which reported that *F. equiseti* was most associated

with the organic system, while the pathogens *F. avenaceum* and *F. culmorum* were least associated (Fernandez et al., 2011).

The dual-mechanism approach of pathogen inhibition via biofumigation and the promotion of beneficial fungi, as demonstrated in this study, provides a useful strategy for managing diseases like *Fusarium* root rot, which is prevalent in durum wheat in Saskatchewan, Canada (Fernandez et al., 2007, 2014). The promotion of antagonists through intercropping or rotations with yellow mustard or another *Brassica* represents a practical and synergistic approach to disease management that leverages the inherent advantages of organic farming, which has proven to increase microbial diversity and activity, particularly of antagonistic microorganisms, compared to non-organic systems (Baturo, 2007; Knudsen et al., 1995; Lenc et al., 2015; Lori et al., 2017; Nam et al., 2023; Sivapalan et al., 1993). Within an organic environment, specific intercropping strategies can be considered a tool to further enhance the activity of biocontrol agents. This strategy not only provides disease control but may also promote crop growth and improve drought tolerance, as some of these beneficial fungi are known to provide these benefits (Sutton et al., 2008).

4 | CONCLUSIONS AND FURTHER RESEARCH

This study provided a better understanding of how intercropping can be used to manage root rot in a subsequent cereal crop under organic management in the semiarid Canadian Prairies, a region conducive to crop stress due to ongoing dry conditions. The varying effects of different intercrop combinations and seeding ratios on root rot and fungal communities highlight the importance of selecting appropriate species and proportions for specific disease management goals. The most significant finding of this study was the strong disease-suppressive effect of the yellow mustard-containing systems in the semiarid Canadian Prairies. Grain intercropping with yellow mustard (lentil–mustard) provided a practical strategy for managing root diseases in subsequent cereal crops. This is attributable to a dual mechanism where the synergistic effects of biofumigation from the mustard component and a larger community of beneficial antagonistic fungi provided an effective form of disease suppression.

Although the individual levels of the biocontrol fungi were low, their combined isolation percentage was over 20%, highlighting their collective importance. These results support the integration of *Brassica* intercrops, such as lentil–mustard, into organic rotations as a practical strategy for managing root diseases in subsequent cereal crops. This approach leverages the inherent advantages of organic farming to create a disease-suppressive environment while also selecting crops that enhance the populations of indigenous biocontrol agents. Repeating intercrops or rotations over time under organic or low-input management with crops that can promote the growth of these microorganisms would be expected to increase their levels and thus be of great value for crop health and resilience. In contrast, under intensive non-organic management, synthetic chemical inputs, particularly fungicides, can mask the impacts of biofumigation on fungal pathogens and/or directly suppress the development of a biocontrol fungal community, thus potentially obscuring the beneficial impacts of the latter on crop health.

The observed changes in fungal community structure and reductions in pathogen levels provide a basis for continued evaluation and adoption. More research is needed to further test the impact of crops on microorganisms with biocontrol potential of important pathogens in-season and in the subsequent crop(s) in order to identify all factors that might influence pathogen and beneficial microbial populations when crops are grown in mixtures at different ratios. In particular, during this study and in the previous intercrop years, there was lower-than-average precipitation during the growing season compared to the long-term means. Dry conditions may influence population sizes of both pathogenic and beneficial fungal communities and their interactions (Singh et al., 2009). Further research should investigate the impact of these intercropping systems across a broader range of environmental conditions relevant to the Canadian Prairies to determine the consistency and robustness of these disease suppression effects. This would provide a more comprehensive understanding of the long-term effectiveness, sustainability, and resilience of intercropping as part of an organic or low-input management system.

AUTHOR CONTRIBUTIONS

Myriam R. Fernandez: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; supervision; validation; writing—original draft; writing—review and editing. **Lobna Abdellatif**: Data curation; investigation; methodology; resources; supervision; validation; writing—review and editing. **Noe Waelchli**: Data curation; methodology; resources; validation; writing—review and editing. **Mervin St. Luce**: Writing—review and editing. **Clemence Muitire**: Data curation; formal analysis; software; validation; writing—review and editing. **Francis Zvomuya**: Formal analysis; writing—original draft; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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