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Root rot suppression mechanisms in lentil promoted by organic intercropping

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Abstract

Intercropping a grain legume with a grain nonlegume is of increased interest by producers in the Canadian Prairies, especially under organic production where intercropping is an alternative to the lack of economic returns of green manure or summer fallow. Information on the impacts of intercropping on root rot, a significant challenge for legume crops, is needed. The objective of this organic study, conducted over 2 years (2017–2018) in the semiarid Canadian Prairies, was to determine how intercrops of lentil (*Lens culinaris* Medik.)–yellow mustard (*Sinapis alba* L.) and field pea (*Pisum sativum* L.)–oat (*Avena sativa* L.), at different seeding ratios, might affect in-season root rot development and associated fungal communities. This 2-year study showed that the impacts of intercropping varied between crop combinations and among fungal species. Multiple pathogens, as well as saprophytes, were associated with the intercrops and respective monocultures, with most being *Fusarium* species. For intercropped lentil, there was a >50% reduction in the mean root rot severity, and an 11% reduction in the isolation of total *Fusarium* species, compared to its monoculture. These results suggest disease suppression in the intercropped lentil, which might be attributed to allelopathy from mustard leading to an increase in fungi with biocontrol potential (antagonists). These antagonist fungi were 84% higher in lentil intercropped with a full mustard ratio than in its monoculture. In contrast, root rot in pea intercropped with oat was mostly higher than in the pea monoculture, attributed to the prevalence of similar species, including *Fusarium* pathogens, common to both crop species.

Plain Language Summary

Intercropping legumes with nonlegumes is increasingly being practiced by organic producers. Information on the impacts of this cropping system on root rot is needed.

Abbreviations: FHB, Fusarium head blight; ITC, isothiocyanate; SI, subcrown internode.

The objective of this study was to determine how intercrops of lentil–yellow mustard and field pea–oat affect disease development and fungal populations associated with belowground tissue in the semiarid Canadian Prairies. This study showed that intercropping impacts varied between crop combinations, and fungal species. There was more root rot in the lentil monoculture than in its intercrops with mustard, and lower isolation of *Fusarium* spp. in the latter, in addition to higher levels of fungi with biocontrol potential. These results suggest disease suppression due to allelopathy from mustard and the presence of biocontrol microorganisms.

1 | INTRODUCTION

Most of the crop diseases prevalent under nonorganic (conventional) production can be found under organic management, although their relative prevalence might differ. Crop diseases that are normally controlled chemically in conventional operations need to be mostly controlled through resistant cultivars and crop management under organic production (Government of Ontario, 2025).

Root diseases are generally less severe on organic than conventional farms, while no consistent differences between systems have been reported for foliar diseases (Van Bruggen & Finckh, 2016). Increased levels of soil microbial activity leading to increased competition and antagonism in the rhizosphere contribute to disease control in organic systems (Knudsen et al., 1995). Suppression of root diseases in organic cereal crops can also be due to enhanced competition by arbuscular mycorrhizae, which are generally more abundant in organic than in conventional crops due to lower available nitrogen (N) and phosphorus in organically managed soils (Oehl et al., 2004). In western Canada, diseases affecting legume roots, caused by *Fusarium* spp. and other pathogens, are usually present in both organic and conventional systems regardless of environmental conditions (Chatterton et al., 2019; Fernandez, 2007; Fernandez et al., 2022). Root/crown diseases of crops, caused by *Fusarium* pathogens, might not only be a cause of yield reductions but also of pathogen carryover to subsequently grown crops (Fernandez et al., 2009; Saskatchewan Pulse Growers, 2023).

A global meta-analysis by Barbieri et al. (2017) revealed that N-fixing crops are more abundant in organic than in conventional farming. Overall, they estimated that leguminous crops provided 2.6x more N to soils farmed organically than in conventional rotations. Legumes are therefore important crops in organic agriculture, especially when used as green manure, but also as grain legumes in diversified rotations. However, it is not recommended that grain legumes be grown frequently because of their susceptibility to root rot diseases (Fernandez, 2007; Saskatchewan Pulse Growers, 2023). In addition, most legume crops are not very competitive against weeds, which makes weed management difficult in organic farming.

Growing two or more grain crops in the same space and time, known as intercropping, is being increasingly practiced in organic production (Barbieri et al., 2017). Intercropping provides organic producers with an alternative to the lack of economic returns of legume green manures, and it could extend diversified crop rotations. It has been concluded that the economic and environmental benefits of intercropping would be particularly apparent under low soil nutrient conditions more typical of organic production (Bedoussac et al., 2015). Intercropping is becoming of increased interest to producers in the Canadian Prairies seeking to enhance resource use efficiency; improve soil health; diversify income streams; and mitigate risks, including those from pests and diseases, in a region characterized by variable climatic conditions. This was manifested by the publication of articles on intercropping in various media, specifically in the Canadian Prairies (Agriculture and Agri-Food Canada, 2021; Badea, 2021; Betkowski, 2024; Stockford, 2017), including under organic management (Fleury, 2021, 2022). Despite the lack of reliable statistics on the adoption of intercropping in this region, and given the general increase in organic production (COTA, 2025; Statistics Canada, 2022), it is inferred that interest in organic intercropping has also been on the rise. This has been further confirmed through anecdotal evidence from organic producers attending field events in the semiarid Canadian Prairies (Fernandez, unreported data).

When intercropped, grain legumes are typically grown with nonlegume grain crops, especially in organic and low-input conventional systems. The increased N availability in intercrops with N-fixing legumes is expected to benefit the companion nonlegumes, in addition to the growth of the subsequently grown crop (Pappa et al., 2012). Furthermore, given that grain legumes are weak competitors of weeds, intercropping with more competitive species would be expected to be of particular benefit under organic management (Fernandez, Lokuruge, Abdellatif, Waelchli, Leeson, Schellenberg, et al., 2025).

Most studies on disease development in intercrops have been done under more humid environments than what is

typical in semiarid regions. Studies reported to date from different regions have revealed that the impact of intercropping on aboveground crop diseases can vary depending not only on the particular disease and crop species, but also on the environment, among other factors. Many such studies on intercropping have reported a decline in aboveground diseases compared to the respective monocultures. Boudreau's (2013) review concluded that, in the vast majority of studies on intercropping, there was a reduction in diseases such as damping off and *Fusarium* wilt, while in 75% of the studies on leaf spot fungi in legume crops, there was a disease reduction due to intercropping. In nonorganic systems in Brazil, common bean (*Phaseolus vulgaris* L.) intercropped with maize (*Zea mays* L.) had less angular leaf spot [*Phaeoisariopsis griseola* (Sacc.) Crous & U. Braun] and anthracnose [*Colletotrichum lindemuthianum* (Sacc. & Magn.) Briosi & Cavara] on pods compared to monocultures (Vieira et al., 2009). Other diseases of cereals and legumes, caused by obligate pathogens, have also been found to decline in intercrops in both organic and nonorganic systems (Hauggaard-Nielsen et al., 2008; Zhang et al., 2019). Other such reports on intercropping with legumes include a study in Kenya where common bean grown with maize had 22% lower root rot compared to the sole crop (Morris et al., 2017), while in a study in China, intercropping with maize also significantly decreased soybean [*Glycine max* (L.) Merr] root rot over the monoculture (Chang et al., 2020). According to Gao et al. (2014), maize–soybean intercropping in China also suppressed red crown rot (*Cylindrocladium parasiticum* Crous, M.J. Wingf. & Alfenas) in soybean, while Zhang et al. (2019) reported that intercropping of cereals with faba bean (*Vicia faba* L.) was most effective for *Fusarium* wilt (*Fusarium oxysporum* Schltdl.:Fr.) in the latter, which was reduced by 72%.

The potential reduction in the incidence of diseases in crops such as grain legumes, when the companion crop(s) are not susceptible to the same pathogens affecting the legumes, was actually identified among the most important benefits of intercropping (Boudreau, 2013). Thus, control of crop diseases in organic and nonorganic systems might be sustainably accomplished with intercropping, in addition to diversified crop rotations. A reduction in host density by increasing heterogeneity through crop mixtures might have similar effects as a break between monocultures and thus might constitute an alternative means of disease control (Vilich, 1993).

However, no effects or detrimental effects on crop health from intercropping have also been reported, so the impacts of intercropping on crop diseases can vary significantly. Among studies showing no differences in aboveground disease levels between intercrops and sole crops, Naudin et al. (2009) reported that in organic trials in France, cereal intercrops with pea (*Pisum sativum* L.) did not generally affect diseases of heads [*Fusarium* spp., *Parastagonospora nodorum* (Berk.) Quaedvlieg, Verkley & Crous] and pods [*Didymella pinodes* (Berk. & A. Bloxam) Petr. (= *Ascochyta pinodes* L.K. Jones = *Mycosphaerella pinodes* (Berk. & A. Bloxam) Vestergr.)] compared to their respective monocultures. In contrast, others have reported increased aboveground disease levels in intercrops compared to their respective monocultures. In nonorganic studies, white mold [*Sclerotinia sclerotiorum* (Lib.) de Bary] was more severe on bean grown with maize than in sole bean in Kenya (Van Rheenen et al., 1981), while Carr et al. (1995) reported that "ascochyta" and "sclerotinia" in lentil (*Lens culinaris* Medik.) were more extensive in intercrops than sole crops in North Dakota.

Various mechanisms have been postulated to explain changes in disease levels when different crop species are grown together. Granzow et al. (2017) suggested that intercropping can lead to synergistic or antagonistic interactions among plants growing in mixed cultures. Direct or indirect inhibition of soil-borne pathogens in intercrops could be responsible for disease reduction (Hauggaard-Nielsen et al., 2012). Disease suppression in intercrops can also result from factors such as a lower availability of the host plant and modification of the microclimate, which would contribute to a reduction in disease incidence by reducing the spread of pathogens and their carryover to the following year(s) (Boudreau, 2013; Kinane & Lyngkjær, 2002; Lithourgidis et al., 2011; Schoeny et al., 2010). Furthermore, Bedoussac et al. (2015) suggested that the main role of cereals in intercrops with legumes would be to reduce the spread of diseases by providing a physical barrier, and in the case of legumes such as peas, by also providing mechanical support to avoid lodging, which might further contribute to disease development. However, crop species could also harbor pathogens

Core Ideas

- Impacts of intercropping on root rot varied between the lentil–yellow mustard and field pea–oat intercrops.
- Most of the fungi isolated from belowground crop tissue were *Fusarium* species.
- Root rot and *Fusarium* species were lower in lentil intercropped with yellow mustard than in its monoculture.
- Fungi with biocontrol potential were isolated at higher levels from the intercropped lentil than its monoculture.
- Intercropped mustard and oat had a greater effect on the fungal community structure than the intercropped lentil and pea.

with a wide host range (Fernandez, 2007), in addition to crop residues being a possible source of pathogens able to survive and reproduce in them after senescence/harvest of the crops (Fernandez et al., 2008), thus this might result in increased disease levels in intercrop systems.

Brassica species are well-known for producing glucosinolates, a class of secondary metabolites (Lazzeri et al., 2013). When living *Brassica* plant tissues are disrupted, through root exudation or other means, these glucosinolates are hydrolyzed into a variety of breakdown products, most notably isothiocyanates (ITCs) (Fahey et al., 2001). These volatile ITCs possess broad-spectrum biological activity, including antifungal properties. In vitro studies have demonstrated the fungitoxic effects of various ITCs against a range of soilborne pathogens, including *Fusarium* pathogens (Ashiq et al., 2022; Manici et al., 1997; Plaszkó et al., 2021; Sarwar et al., 1998; Smolinska et al., 2003). Concentrations and glucosinate profiles are expected to vary depending on environmental conditions and *Brassica* species, including plant tissue type (Bellostas et al., 2007). A field study of 13 Brassicaceae species, including *Sinapis alba* L., showed that the total plant glucosinolate production at mid-flowering ranged from 0.8 to 45.3 mmol m^{-2}, with roots contributing an average of 23.6% (range of 2%–81%) of the total plant glucosinolates, although not all of them yielded ITCs upon hydrolysis (Kirkegaard & Sarwar, 1998). This suggests that allelopathic effects, specifically the release of ITCs, from *Brassica* plants could play a direct role in suppressing root rot pathogens in intercropping systems.

Research on root disease development in intercrops of field crops in temperate regions is limited. To the best of our knowledge, there has been no research on such diseases in intercrops specifically within the semiarid Canadian Prairies, a region experiencing ongoing dry and stressful growing conditions, or on the following crop(s) (Fernandez, Lokuruge, Abdellatif, Waelchli, Leeson, Zvomuya, et al., 2025).

The overall objective of this study was to examine whether intercropping lentil with yellow mustard (*S. alba*) and field pea with oat (*Avena sativa* L.) at different seeding ratios under organic management in the semiarid Canadian Prairies could reduce in-season root rot of legumes compared to their respective monocultures. We also aimed to determine if this intercropping would alter the composition and diversity of the fungal community in the affected plant tissue, and especially if it would decrease pathogenic fungi while increasing beneficial fungi. We further hypothesized that the lentil–mustard and pea–oat intercrops would show different effects, specifically due to the allelopathic action of ITCs from the living mustard plants. An evaluation of root rot in the subsequently grown durum wheat (*Triticum. turgidum* L. var. *durum*) was presented by Fernandez, Abdellatif, et al. (2026).

2 | MATERIALS AND METHODS

2.1 | Study area and experimental design

This study was located at the Swift Current Research and Development Centre of Agriculture and Agri-Food Canada in Swift Current, Saskatchewan, Canada (Lat.: 50˚17′ N, Long.: 107˚48′ W, elevation 825 m) from 2017 to 2018 on land that had been organically managed (CAN/CGSB, 2021) for the previous 2 years. The soil type in this brown soil zone is an Aridic Haploboroll (Orthic Brown Chernozem) with silt-loam texture, with a soil organic matter of approximately 3.5%. The average annual and growing season precipitation is lower, while evapotranspiration and mean annual temperature are higher, than in the other soil zones in the Canadian Prairies (Fernandez et al., 2016). Meteorological data were collected at a meteorological station 1 km from the trial sites (Fernandez, Lokuruge, Abdellatif, Waelchli, Leeson, Schellenberg, et al., 2025).

The intercrop trials on which root diseases were evaluated were conducted in 2017 and 2018 on two different adjacent fields, which had been organically managed as described by Fernandez, Lokuruge, Abdellatif, Waelchli, Leeson, Schellenberg, et al. (2025). In the previous 2 years of each trial, the sites were seeded to a mixture of a legume, an oilseed and a cereal, which were then incorporated at flowering using a tandem disk harrow. Prior to seeding in each of the two trial years, the soil was worked with a cultivator with mounted harrows, and then the surface was leveled with a harrow packer.

Treatments consisted of two-crop intercrop mixtures, and their respective monocultures (Fernandez, Lokuruge, Abdellatif, Waelchli, Leeson, Schellenberg, et al., 2025). Each intercrop combination had a legume and a nonlegume crop at three different seeding ratios, consisting of lentil–yellow mustard and field pea–oat. Seeding rate was 25% higher than recommended for this region for nonorganic production. Table 1 shows the intercrop treatments, seeding ratios, and the expected number of seeds per unit area for each treatment. The experimental unit was the plot (6 m long × 4 m wide), each consisting of 12 rows that were 30.5 cm apart, with 0.5 m between plots. The experimental design for all trials was a randomized complete block with four blocks as the replicates.

All seeding was done with a custom-built plot seeder equipped with double disk openers, on May 23, 2017, and May 18, 2018. The two crops in each of the intercrop combinations were seeded together as mixed rows to maximize the interaction between the two crops and promote the exchange of N between them (Mariotti et al., 2009). The lentil–mustard intercrops and their respective monocultures were seeded at a depth of 1.3 cm (2017) or 1.9 cm (2018), while the pea–oat intercrops and their respective monocultures were seeded

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	Nonlegume	Legume	Nonlegume	Legume	Nonlegume
Lentil–mustard						
Lentil100	1	0	1.00	0.00	204	0
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
Mustard100	0	1	0.00	1.00	0	289
Pea–oat						
Pea100	1	0	1.00	0.00	150	0
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
Oat100	0	1	0.00	1.00	0	313

[a]Crop varieties: lentil, CDC Maxim; yellow mustard, AC Andante; field pea, CDC Meadow; oat, AAC Oravena.

[b]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.

[c]Seeding ratios based on the number of seeds per m^2.

at 2.5 cm (2017) or 3.2 cm (2018). The granular inoculant TagTeam was applied at a rate of 2 g per row.

2.2 | Sample collection and assessment of root rot

All crop sampling was done on both sides ("sampling area") of the middle four rows ("harvest area") of each plot. For assessment of root rot in oat, 40 plants with a well-developed subcrown internode (SI) (>2 cm) were carefully pulled up at random from the "sampling areas" in each monoculture and intercropped oat plot at the late milk-early dough stage (growth stage 77–84; Zadoks et al., 1974). A well-developed SI was selected to ensure sufficient tissue for accurate rating and subsequent fungal isolation. Plants were air-dried and stored at 4°C until rated and plated for fungal isolation. The SI from each oat plant was excised and rated for extent of dark brown to black discoloration. The percentage of plants with ≥50% SI discoloration was determined for each of the oat plots based on the total number of SIs collected and assessed from the plot. For assessment of root rot in the two legumes and in mustard at late flowering to early seed set, a total of 40 plants were carefully pulled up from about 15 randomly selected locations from the "sampling areas" in each plot. Tap roots were then thoroughly washed under tap water, air-dried at 40°C for 48 h, and kept in paper bags at 4°C until analyzed. The percentage of roots with ≥50% brown to black discoloration on the tap root was calculated for each lentil, pea, and mustard plot, based on the total number of roots collected and assessed from the plot.

2.3 | Fungal populations in belowground discolored crop tissue

For fungal isolations, a piece (1–2 cm) of tissue from each discolored SI, or a 1 cm^2 piece of discolored tissue from each tap root, was excised and surface disinfested for 1 min in 0.6% NaOCl, and rinsed twice 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 sulphate (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 18°C–22°C under cool-white fluorescent and near-UV lights (16 h light/8 h dark) for 7–10 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 as in Fernandez et al. (2014). Isolates that could not be conclusively identified morphologically were grown on half strength V8-potato dextrose agar and submitted to the University of Guelph Laboratory Services (Guelph, Ontario, Canada) for molecular 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 PrismTM Sequencing Analysis software and then aligned with published sequences in the NCBI database using the BLAST software (www.ncbi.nlm.nih.gov). 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.

Percentage isolation of each fungal species in each crop was calculated by plot based on the number of its isolations relative to the total number of fungal isolates for the same crop in each plot. These values were then used to calculate the average percentage isolation of each fungal species per crop and treatment in each replicate.

2.4 | Statistical analysis

The GLIMMIX procedure of SAS 9.4 (SAS Institute Inc., 2013) was used for the analysis of variance of root rot severity data. The DIST = beta option was included in the MODEL statement of PROC GLIMMIX to account for the beta distribution of the data. The data were analyzed separately for each crop, with treatment modeled as a fixed effect and year and block nested within year as random effects. Differences among the means were compared using the Tukey multiple comparison test at $\alpha = 0.10$, which has been used for previous organic (Fernandez et al., 2019, 2022), as well as nonorganic (Iheshiulo et al., 2024), field studies. This α level was chosen given the inherent biological variability in organic field studies, especially in a semiarid environment, whose primary aim is to detect effects that might not be apparent at a more stringent α level. Relationships among response variables were evaluated via Pearson correlation analysis using the CORR procedure (SAS Institute Inc., 2013).

Fungal species data for each crop and treatment were also analyzed for summary statistics using the MEANS procedure in SAS 9.4 (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 *metaMDS* function. Statistical significance of differences in crop root fungal community compositions were assessed by permutational multivariate analysis of variance (PERMANOVA) based on the Bray–Curtis distance metrics with 999 permutations using the *vegdist* and *adonis2* functions. Shannon diversity indices (Shannon & Weaver, 1949) were calculated using *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 weather data for the study period were presented by Fernandez, Lokuruge, Abdellatif, Waelchli, Leeson, Schellenberg, et al. (2025). For the growing season (May−August), there was low precipitation in 2017 (67.3 mm) and 2018 (93.7 mm), representing 40.6% and 56.5% of the long-term average (165.8 mm), respectively. Substantially lower precipitation in May and June of 2017 and 2018, and in July of 2017, resulted in moderate drought conditions, especially in 2017, while precipitation in July of 2018 helped to somewhat ameliorate the drought in that year. The mean growing season temperature in 2017 and 2018 (15.6˚C–16.8˚C) was higher than the long term average (14.9˚C), especially in 2018 when the higher than average temperatures in May and June resulted in stressful growing conditions for the first half of the growing season (Fernandez, Lokuruge, Abdellatif, Waelchli, Leeson, Schellenberg, et al., 2025).

3.2 | Root rot severity in monocultures and intercrops

The analysis of root rot for each of the legume and nonlegume monocultures and their respective intercrop ratios showed a significant effect of these treatments (Table 2). However, differences in root rot between the monocultures and their respective intercrops varied between the two intercrop combinations. Root rot in lentil was most associated with the lentil monoculture (Lentil100). The treatments with the highest mustard ratio, Lentil75 + Mustard75 and Lentil50 + Mustard100, had the lowest root discoloration, with all three intercrop ratios representing a >50% reduction compared to the lentil monoculture (Table 2). For mustard, root rot was lowest, or among the lowest, in its monoculture (Mustard100), with levels in the intercrop ratios representing a mean increase of around 27% relative to its monoculture. In contrast to lentil, root rot in pea was least associated with its monoculture (Pea100), with root discoloration in the intercrop ratios having the highest levels, a mean increase of around 62% over its monoculture. For oat, the percentage SI discoloration in its monoculture (Oat100) was among the highest and that in Pea100 + Oat25 was the lowest, with the mean for all intercrop ratios being 15% lower than in the monoculture.

Regardless of root rot levels, for each of the crops in all treatments, there was no significant correlation between mean root rot severity and the crop biomass collected before harvest, or grain yield reported by Fernandez, Lokuruge, Abdellatif,

TABLE 2 Effect of monocultures and intercrops on discoloration of roots of lentil, yellow mustard, and field pea, and subcrown internodes of oat, in organic field trials in southwest Saskatchewan, Canada. Means averaged over 2 years (2017–2018).

Monoculture/intercrop	Discoloration of belowground crop tissue[a]	
	%	
	Lentil	**Yellow mustard**
Lentil100	14.1a[b]	
Lentil100 + Mustard50	6.1b	33.7a
Lentil75 + Mustard75	1.0c	35.3a
Lentil50 + Mustard100	2.2bc	31.2ab
Mustard100		26.2b
p value	<0.0001	0.02
	Field pea	**Oat**
Pea100	5.7b	
Pea100 + Oat25	19.0a	28.5b
Pea100 + Oat50	11.9a	36.1a
Pea75 + Oat75	13.7a	32.9ab
Oat100		38.2a
p value	<0.0001	0.006

[a]Percentage of lentil, field pea, and mustard roots with ≥50% area discolored, and percentage of subcrown internodes of oat with ≥50% area discolored.
[b]Values in a column followed by the same letter are not significantly different according to the Tukey multiple comparison test ($\alpha = 0.10$).

Waelchli, Leeson, Schellenberg, et al. (2025), indicating that root disease was not a limiting factor in crop productivity. Other factors, such as the dry growing conditions, were likely more influential on crop growth during the study period.

3.3 | Fungal populations in the monocultures

Multiple fungi known to be pathogenic, host-specific or with a wide-host range, as well as weak pathogens/saprophytes, were isolated from lesioned roots or SIs of the legume and nonlegume crops. Most of the fungi isolated from discolored belowground tissue were also found occasionally in symptomless roots or SIs, although in most cases none of these yielded any fungi (data not presented).

There is expected to be variation in pathogenicity (Fernandez & Chen, 2005), virulence (Chittem et al., 2015), and aggressiveness (Baćanović-Šišić et al., 2018) among isolates of some of the most common pathogens isolated in this study. It is also likely that their pathogenicity might be affected by the surrounding abiotic and biotic environment (Zarattini et al., 2021). Therefore, given the positive identification of most isolates and the objectives of this study, no further pathogenicity tests of any of the isolates were conducted.

Identification of the isolated fungi revealed that overall, for all monocultures combined, most of the fungal species isolated from roots and SIs belonged to the genus *Fusarium*, constituting a total of 17 identified *Fusarium* species, with a mean percentage fungal isolation of 69.5%, including 1.6% of unidentified *Fusarium* species. The most frequently isolated *Fusarium* spp. from the monocultures were *F. oxysporum* Schltdl.:Fr. (13.2%), *Fusarium solani* (Mart.) Sacc. (10.7%), *Fusarium culmorum* (W.G. Sm.) Sacc. (8.2%), *Fusarium avenaceum* (Fr.:Fr.) Sacc. (8.1%), *Fusarium equiseti* (Corda) Sacc. (5.8%), and *Fusarium redolens* (Wollenw.) Sacc. (5.2%). Species isolated at an overall percentage of 1%–<5% were *Fusarium acuminatum* Ellis & Everh., *Fusarium pseudograminearum* O'Donnell & T. Aoki, *Fusarium lateritium* Nees:Fr., *Fusarium proliferatum* (Matsush.) Nirenberg ex Gerlach & Nirenberg, *Fusarium sporotrichioides* Sherb., *Fusarium torulosum* (Berk. & M.A. Curtis) Nirenberg, and *Fusarium tricinctum* (Corda) Sacc., while fungal species isolated at 0.5%–<1% each were *Fusarium flocciferum* Corda and *Fusarium poae* (Peck) Wollenw. *Fusarium* species isolated occasionally (<0.5%) were *Fusarium hostae* Geiser & Juba and *Fusarium incarnatum* (Desm.) Sacc.

The number of *Fusarium* species and their percentage isolation from the monocultures varied among crops (Table 3). Overall, the total number of identified *Fusarium* spp., regardless of their frequency and including those isolated occasionally (not presented in Table 3), was highest in lentil (13), followed by mustard (11) and oat (10), with pea having the lowest number (7). The percentage isolation of all *Fusarium* spp. in the monocultures was highest in oat (78.1%) and lentil (75.3%), followed by pea (67.1%), and was lowest in mustard (49.5%).

TABLE 3 Percentage isolation of the most common Fusarium species from monocultures and intercrops grown in southwest Saskatchewan, Canada (2017–2018).

Crop/ monoculture/ intercrop[a]	Total *Fusarium* isolates	*Fusarium acuminatum*	*Fusarium avenaceum*	*Fusarium culmorum*	*Fusarium equiseti*	*Fusarium flocciferum*	*Fusarium lateritium*	*Fusarium oxysporum*	*Fusarium proliferatum*	*Fusarium pseudograminearum*	*Fusarium redolens*	*Fusarium solani*	*Fusarium sporotrichioides*	*Fusarium torulosum*	No. of species[b]	Total % isolation
	%															
Lentil																
Monoculture	80.1	3.4	8.6	0.7	3.2	0.6	0.0	23.1	0.0	0.0	7.7	21.1	1.9	0.0	13	75.3
SE	4.7	2.2	3.1	0.7	1.6	0.6	0.0	4.3	0.0	0.0	2.3	3.2	0.9	0.0		5.5
Intercrop	71.1	2.3	8.5	1.2	3.3	0.4	0.0	21.0	0.2	0.0	13.0	13.5	1.2	0.0	13	68.4
SE	3.6	0.8	2.0	0.6	1.1	0.3	0.0	2.6	0.2	0.0	1.8	2.8	0.6	0.0		3.6
Mustard																
Monoculture	49.5	0.0	4.0	0.0	6.0	2.0	7.5	7.1	2.3	0.0	1.3	5.9	0.0	11.7	11	49.5
SE	1.0	0.0	1.4	0.0	1.4	1.0	0.8	0.8	0.9	0.0	0.8	0.6	0.0	2.4		1.0
Intercrop	56.6	0.0	8.1	0.0	7.4	1.5	7.4	9.7	4.1	0.0	0.3	4.2	0.0	11.1	11	56.6
SE	0.5	0.0	0.8	0.0	0.9	0.4	1.0	0.8	0.7	0.0	0.2	0.8	0.0	1.3		0.5
Pea																
Monoculture	68.9	9.6	13.7	1.1	5.0	0.0	0.0	12.0	0.0	0.0	11.4	12.4	0.0	0.0	7	67.1
SE	1.1	1.6	2.8	0.7	2.2	0.0	0.0	0.8	0.0	0.0	1.5	1.3	0.0	0.0		1.8
Intercrop	70.9	6.2	16.5	2.3	4.3	0.0	0.0	15.1	0.0	0.0	11.8	13.5	0.0	0.0	7	70.7
SE	1.7	0.8	1.9	0.7	0.9	0.0	0.0	1.2	0.0	0.0	1.1	1.2	0.0	0.0		1.7
Oat																
Monoculture	79.4	2.7	5.7	30.9	9.2	0.0	0.0	10.5	2.1	4.6	0.6	3.6	6.4	0.0	10	78.1
SE	4.4	1.1	1.9	5.7	2.2	0.0	0.0	1.2	1.7	1.2	0.6	1.4	1.4	0.0		5.6
Intercrop	73.2	2.4	2.6	25.5	9.5	0.0	0.0	7.8	3.9	3.4	4.1	5.0	5.6	0.0	10	72.8
SE	1.8	0.6	0.7	1.3	1.7	0.0	0.0	0.8	1.0	0.9	0.9	0.7	1.1	0.0		2.0
All monocultures	69.5	4.0	8.1	8.2	5.8	0.7	1.9	13.2	1.1	1.1	5.2	10.7	2.1	2.9		
All intercrops	68.0	2.7	8.9	7.3	6.1	0.5	1.8	13.4	2.0	0.8	7.3	9.1	1.7	2.8		
Overall mean	68.7	3.4	8.5	7.7	6.0	0.6	1.9	13.3	1.6	1.0	6.3	9.9	1.9	2.9		

[a]Mean of three ratios for each intercrop combination of lentil–yellow mustard and field pea–oat (see Table 1).

[b]This number includes all *Fusarium* species isolated from crops grown in monocultures or intercrops, even those isolated occasionally and not presented in this table.

The total of 17 *Fusarium* species and their overall percentage isolation in the monocultures (69.5%) are similar or higher than those reported from commercial pea and lentil crops in eastern Saskatchewan (Fernandez, 2007), across the Canadian Prairies (Chatterton et al., 2019), from organic diversified rotation-tillage trials (Fernandez et al., 2022), and nonorganic spring wheat (*Triticum aestivum* L.) grown in rotation with legumes (Fernandez & Zentner, 2005), in the same area as the current trials.

The most frequently isolated *Fusarium* spp. in this study that have been commonly identified as pathogenic on one or more of the crops are *F. avenaceum*, *F. culmorum*, *F. oxysporum*, and *F. solani* (Bhalla et al., 1992; Esmaeili Taheri et al., 2017; Summerell et al., 2010), which constituted a total percentage isolation of 39% in our study (Table 3). Most of the other *Fusarium* spp., constituting a total of approximately 26% of all isolations, are considered to be for the most part weakly pathogenic and/or saprophytic on roots or other plant parts of legumes or other crops (Chittem et al., 2015; Esmaeili Taheri et al., 2017; Fernandez, 2007; Munkvold, 2017; Rodrigues & Menezes, 2005; Safarieskandari et al., 2020; Xue et al., 2014; Zitnick-Anderson et al., 2020).

Overall, as expected, the legumes differed less between them in their associated *Fusarium* populations than from the nonlegume crops. Lentil and pea shared *F. oxysporum*, *F. solani*, *F. avenaceum*, *F. equiseti*, and *F. redolens* as the most common *Fusarium* species isolated from them, although these fungal species were found in all crops (Table 3). The observation that *F. avenaceum*, *F. oxysporum*, and *F. solani* were among the most frequent species isolated from the legumes in this study agrees with results from winter pea in Germany (Baćanović-Šišić et al., 2018), and field pea and lentil in North America (Chatterton et al., 2019; Chittem et al., 2015; Fernandez et al., 2022). The wide host range of these three species also agrees with previous studies (Baćanović-Šišić et al., 2018; Chittem et al., 2015; Fernandez, 2007; Safarieskandari et al., 2020). In addition to *F. avenaceum* having been isolated the most from roots and crop residues of legumes, especially pea, than of other field crops commonly grown in the Canadian Prairies (Fernandez, 2007; Fernandez et al., 2008), this fungus is among the most common pathogens in infected cereal heads and kernels in the same region (Fernandez et al., 2009).

In addition, the other well-known cereal head and root pathogens *F. culmorum* and *F. pseudograminearum* were more frequently isolated from oat than from any other crop in this study, with *F. pseudograminearum* being absent from all other crops (Table 3). Our observation that *F. culmorum* was present at high levels in oat agrees with results from a survey of commercial fields across Saskatchewan (Fernandez & Holzgang, 2009) where this pathogen was the most commonly isolated from SIs and crowns of oat crops. Results from a nonorganic crop residue survey in eastern Saskatchewan also showed that *F. culmorum* occurred at higher levels in crop residues of oat than in those of spring wheat or durum wheat crops (Fernandez et al., 2008).

Most of the *Fusarium* spp. isolated from the legumes and oat were present at lower levels, or absent, in mustard (Table 3). In turn, mustard had a different set of dominant *Fusarium* species that were only, or almost exclusively, isolated from it, and at higher levels than the other *Fusarium* species. These were *F. lateritium* and *F. torulosum* and to a lesser extent *F. flocciferum* and *F. proliferatum*, the latter also being isolated at similar levels from oat. *F. proliferatum* is a pathogen with a very broad host range (Proctor et al., 2009), while *F. torulosum* has been reported as pathogenic to barley (*Hordeum vulgare* L.) (Siahposh & Darvishnia, 2018), and *F. lateritium* as pathogenic to some weed species (Walker, 1981). None of these fungal species have been reported to be pathogenic to mustard, thus their role in the root health of mustard is unknown.

Overall, a total of 19 identified non-*Fusarium* genera/species were isolated from the roots and SIs of the monocultures in this study, although most of them were present at individual low levels (see most commonly isolated species in Table 4). There were also a few unidentified isolates (<1% of all non-*Fusarium* isolates). The most frequent non-*Fusarium* spp. in the monocultures were *Alternaria* spp. (9.7%), the most common of which was *Alternaria alternata* (Fries) Keissler, and *Clonostachys* spp. (5.3%), the most common of which was *Clonostachys rosea* (Link : Fr.) Schroers, Samuels, Seifert and W. Gams at 80% of all isolations of this genus, with the rest being *Clonostachys miodochialis* Schroers, *Clonostachys rhizophaga* Schroers, or *Clonostachys pseudochroleuca* Schroers. Isolated at 1%–<5% were *Didymella pinodella* (L.K. Jones) Qian Chen & L. Cai [= *Ascochyta pinodella* L.K. Jones = *Phoma pinodella* (L.K. Jones) Morgan-Jones & K.B. Burch], *Epicoccum nigrum* Link., *Rhizophagus* sp., *Stemphylium botryosum* Wallr., and *Trichoderma* spp. Other genera/species isolated at an overall 0.5%–<1% were *Penicillium* spp., *Pythium* spp., and *Rhizoctonia solani* J.G. Kühn., while those isolated at <0.5% were *Acremonium* spp., *Aspergillus* spp., *Cladosporium* spp., *Cochliobolus sativus* (Ito & Kurib.) Drechs. ex Dast., *Microdochium bolleyi* (R. Sprague) De Hoog & Herm.-Nijh., *Minimedusa polyspora* (Hotson) Weresub & P.M. Le Clair, and *Nigrospora sphaerica* (Sacc.) E.W. Mason, with *Arthrinium* spp. and *Chaetomium* spp. being isolated occasionally. The number of genera/species of the non-*Fusaria* present in the monocultures varied less among crops than their percentage isolation (Table 4). Overall, the highest number of these fungal genera/species was observed in mustard, pea, and oat (eight each), followed by lentil (six), while their overall percentage isolation was highest in mustard (49.5%), followed by pea (28.0%), with the lowest percentage isolation observed in the lentil (18.3%) and oat (20.6%) crops.

TABLE 4 Percentage isolation of the most common non-*Fusarium* species from monocultures and intercrops grown in southwest Saskatchewan, Canada (2017–2018).

Crop/monoculture /intercrop[a]	*Alternaria* spp.	*Clonostachys* spp.	*Didymella pinodella*	*Epicoccum nigrum*	*Penicillium* sp.	*Pythium* sp.	*Rhizoctonia solani*	*Rhizophagus* sp.	*Stemphylium* sp.	*Trichoderma* spp.	No. of species[b]	Total % isolation
	%											
Lentil												
Monoculture	3.3	6.8	3.7	0.0	0.5	0.0	0.0	0.0	2.2	1.8	6	18.3
SE	1.1	2.1	1.3	0.0	0.5	0.0	0.0	0.0	1.7	0.9		4.2
Intercrop	4.4	6.4	2.6	0.8	0.4	0.4	0.0	0.0	2.9	5.8	12	25.3
SE	1.1	1.9	0.8	0.5	0.3	0.3	0.0	0.0	0.8	1.4		3.6
Mustard												
Monoculture	30.7	5.2	0.0	2.6	0.0	1.2	1.0	1.9	3.9	2.1	8	49.5
SE	2.9	0.9	0.0	1.1	0.0	0.8	1.0	0.9	1.3	1.4		2.2
Intercrop	26.3	2.5	0.2	3.0	0.9	0.6	2.2	1.8	2.7	1.5	9	42.1
SE	1.2	0.9	0.2	0.8	0.4	0.3	0.7	0.5	0.6	0.5		0.8
Pea												
Monoculture	4.9	2.3	11.8	4.2	0.0	0.0	0.0	1.6	1.0	1.7	8	28.0
SE	2.0	1.3	2.2	2.0	0.0	0.0	0.0	0.8	0.7	0.9		1.5
Intercrop	5.0	3.2	12.9	0.9	0.0	0.9	0.0	0.8	0.9	2.6	9	27.4
SE	1.3	1.1	1.9	0.5	0.0	0.6	0.0	0.5	0.6	0.9		2.0
Oat												
Monoculture	0.0	7.0	0.0	1.1	1.2	2.1	0.3	4.4	1.8	0.4	8	20.6
SE	0.0	3.0	0.0	0.7	0.8	1.3	0.3	1.3	1.3	0.4		4.4
Intercrop	0.1	6.9	3.1	2.2	1.2	1.8	0.6	2.5	1.4	2.1	12	25.8
SE	0.1	1.5	0.8	0.8	0.5	0.5	0.3	0.7	0.6	0.7		1.6
All monocultures	9.7	5.3	3.9	2.0	0.4	0.8	0.3	2.0	2.2	1.5		
All intercrops	9.0	4.8	4.7	1.7	0.6	0.9	0.7	1.3	2.0	3.0		
Overall mean	9.3	5.0	4.3	1.9	0.5	0.9	0.5	1.6	2.1	2.3		

[a]Mean of three ratios for each intercrop combination of lentil–yellow mustard and field pea–oat (see Table 1).

[b]This number includes all non-*Fusarium* species isolated from crops grown in monocultures or intercrops, even those isolated occasionally and not presented in this table.

In general, the majority of the non-*Fusarium* spp. had a higher host specificity than most of the *Fusarium* spp. isolated in this study (Table 4). Among the most commonly isolated non-*Fusaria*, the legumes shared *D. pinodella*, which was most frequent in pea. This agrees with observations on pea and lentil roots from a survey of nonorganic crops in eastern Saskatchewan, Canada (Fernandez, 2007). In organically grown winter pea in Germany, Baćanović-Šišić et al. (2018) reported that *D. pinodella* was the most frequently isolated pathogen (>70%) from roots, followed by *D. pinodes*.

The absence or low levels of the cereal pathogen *C. sativus* in the monocultures of pea, lentil, and mustard in our study agrees with those reported in roots of legume and oilseed crops (Fernandez, 2007). Its presence in oat (Table 4) in this study was lower than in spring wheat in a previous organic study in the same area (Fernandez et al., 2014), agreeing with findings from surveys of nonorganic commercial fields across Saskatchewan where levels of *C. sativus* in SIs were lower in oat than in wheat or barley (Fernandez & Holzgang, 2009; Fernandez et al., 2007). Similar observations were made in crop residues from nonorganic crops sampled in eastern Saskatchewan, Canada, where *C. sativus* was present at lower levels in oat than in barley, durum, or spring wheat tissues (Fernandez et al., 2008), and from a nonorganic rotation study under conservation tillage in southern Brazil (Fernandez & dos Santos, 1992) where this pathogen was present at lower levels in residues of *Avena* spp. than in those of wheat or barley.

The higher percentage isolation of the genus *Alternaria* from the roots of mustard than from those of the other non-*Brassica* crops, agrees with previous observations by Fernandez (2007) that *Alternaria* spp. were more frequent in roots of oilseed crops, including canola (*Brassica* spp.), compared to pulse crops.

3.4 | Treatment effects on fungal populations in intercrops of lentil–mustard and pea–oat and their respective monocultures

Overall, with the exception of a few fungal species present occasionally, there were no fungal species in any of the intercrop combinations that had not been isolated from their respective monocultures (Tables 3 and 4). Fungi that were present at higher levels in an intercrop than in its respective monoculture(s) might have been favored by the conditions and prevailing environment when grown with the companion crop, and/or the fungi might have been derived from its companion crop. The mixed-row seeding employed in this study, promoting closer root interactions between the crops, might have also contributed to our observations on root rot and associated fungi, as suggested by Gao et al. (2014) and Granzow et al. (2017) who reported that close root proximity enhanced suppressive effects and fungal diversity in mixed stands.

Our results indicate that the actual number of *Fusarium* species isolated from each of the monocultures did not change when these crops were grown in the intercrops (Table 3). However, total *Fusarium* species had a significantly higher isolation in mustard when intercropped than when grown as monoculture (by 14%), while in lentil the isolation of all *Fusarium* isolates was significantly lower in the intercrops with mustard than in its monoculture, representing a mean reduction of 11% compared to its monoculture (Table 3). In particular, in lentil *F. solani* decreased by 36% in the intercrops relative to its monoculture. The higher frequency of *Fusarium* spp. in the mustard intercrops appeared to be accounted for by *F. avenaceum*, *F. oxysporum* and *F. proliferatum*, with the relative abundance of *F. avenaceum* being double in the lentil–mustard intercrops compared to the mustard monoculture (Table 3). The fact that *F. avenaceum* and *F. oxysporum* were among the most commonly isolated fungi from lentil suggests a potential transfer of these fungi from lentil to mustard roots, resulting in an opportunistic or weak colonization of mustard, which did not translate into higher root rot levels in the latter (Table 2).

For the non-*Fusaria*, in all cases, especially in lentil and oat, there were more species isolated from the intercrops than the individual monocultures (Table 4), while their percentage isolation was in most cases similar between the monocultures and their respective intercrops, except for mustard in which these species were isolated at lower levels when intercropped than in its monoculture.

In contrast to the lentil–mustard intercrop combination, the observation that root rot severity in pea intercropped with oat was overall higher than in the pea monoculture (Table 2) might be attributed, at least partly, to the higher number of species, including *Fusarium* pathogens, that were similar between these two crops than between lentil and mustard. A mean of 76.5% of the most frequently isolated *Fusarium* species, and 67.0% of the non-*Fusarium* species, was similar between pea and oat, versus 52.9% and 58.3%, respectively, for lentil and mustard (Tables 3 and 4). This suggests that the pea–oat intercrop may have amplified inoculum for the shared pathogens. Despite the overall higher root rot in intercropped pea, root rot severity in oat was among the highest in its monoculture compared to when it was intercropped with pea, and was significantly higher in the monoculture than in the Pea100 + Oat25 treatment (Table 2). This might be attributed to a decrease in some of the *Fusarium* pathogens in the intercropped oat, although this was not always significant (Table 3). Conversely, *F. redolens* was present at higher levels in the intercropped oat than in its monoculture, suggesting a transfer of this species from pea to oat, potentially exacerbating disease development in the oat crop (Table 2).

Among the non-*Fusarium* species, *D. pinodella* was present at similar or lower levels in the roots of pea intercropped with oat than in the pea monoculture, while although at low levels, this pathogen was isolated more from the intercropped oat than from the oat monoculture (Table 4). These results partly agree with reports on ascochyta blight in aboveground tissue of field pea, where intercropping with other crops species reduced its development. When pea was intercropped with barley under organic management in Denmark, ascochyta blight (*Ascochyta pisi* Lib.) was significantly lower than in the pea monoculture (Kinane & Lyngkjær, 2002), while organic intercrop combinations of faba bean, barley, oat, triticale (*Triticosecale* Wittmack), or wheat with pea in Spain and Tunisia also resulted in a reduction in ascochyta blight (*D. pinodes*) in pea (Fernández-Aparicio et al., 2010). Under nonorganic management in France, Schoeny et al. (2010) reported that under moderate to severe disease pressure, ascochyta blight (mostly caused by *D. pinodes*) on pods and stems was reduced by 20%–50% in pea–cereal intercrops compared to the pea monoculture.

3.5 | Mechanisms involved in root rot development and fungal species differences

The observed root rot reduction in the intercropped lentil (Table 2) might be foremost attributable to decreased host density and/or to allelopathic effects from the mustard roots. Different types of mustards are known for their allelopathic potential (Farooq et al., 2011). As stated above, *S. alba* and other *Brassicas* produce glucosinolates which are hydrolyzed into ITCs upon tissue damage or root exudation (Fahey et al., 2001). While our study examined living intercropped plants rather than the biomass incorporation used in traditional biofumigation studies (Sarwar et al., 1998), the observed reduction in root rot and shifts in fungal communities may be attributed to a continuous, low-level release of ITCs from living mustard roots, which are known for their fungitoxic properties (Smolinska et al., 2003). Thus, in the intercrop with lentil, there was likely a release of ITCs from the mustard roots affecting the growth of *Fusarium* pathogens potentially infecting lentil roots (such as *F. solani*). The reduced isolation of *Fusarium* spp. from intercropped lentil roots relative to its monoculture supports this mechanistic link (Table 3). It is also plausible that pH differences among cropping systems might also have an effect on some of the mechanisms involved in pathogen suppression in this study. Rosa and Rodrigues (1999) concluded that alkaline or neutral conditions favored ITCs formation. The average pH down the soil profile where our organic trials were conducted was 7.03–8.01 at 0–15 cm, and 7.24–8.16 at 15–30 cm (Fernandez, unreported data), while the average pH in nonorganic soils adjacent to our organic trials was a mean of 6.31 at 0–5 cm, 6.05 at 5–10 cm, and 6.82 at 10–20 cm (Barbara Cade-Menun, unreported).

Some of the fungi isolated from roots and SIs in this study have also been identified as antagonists, or associated with biocontrol of crop pathogens. The most common of these in one or more monoculture and intercrop ratios are in Table 5, with less frequently isolated fungi with biocontrol potential being *M. polyspora*, *N. sphaerica*, and species of *Arthrinium* and *Chaetomium*. Overall, these antagonist fungi accounted for a total of 17.6% of all isolations in the monocultures (Table 5). Compared to the other crops, these species were present at their highest number and percentage isolation in oat.

Among the antagonist fungi isolated in this study (Table 5), species that have been shown to be effective in the biocontrol of crop pathogens in other studies include *C. rosea*, *C. miodochialis*, and *M. polyspora* (Abdellatif et al., 2022; Gromadzka et al., 2009; Lenc et al., 2015; Luongo et al., 2005); *E. nigrum* (Xu et al., 2012); *F. equiseti* (Šišić et al., 2017); and species of *Trichoderma* (Fernandez, 1992; Gromadzka et al., 2009; Lenc et al., 2015), *Acremonium* (Lenc et al., 2015; McGee et al., 1991), and *Penicillium* (Li et al., 2019). Mwakilili et al. (2021) reported that in maize-*Desmodium* spp. intercrops, the fungal microbiome was more diverse and species rich than in monoculture, with fungal groups enriched in intercropping including fungi not known for being crop pathogens, such as *Acremonium*, *Penicillium*, *Clonostachys*, and *Trichoderma*, among others, while fewer fungal genera were enriched in monocultures.

Clonostachys spp. were among the most commonly isolated non-*Fusarium* species in lentil, mustard, and oat (Tables 4 and 5). These species were most common in the lentil grown with the highest ratio of mustard, Lentil50 + Mustard100, where their percentage isolation was 74% higher than in the lentil monoculture (Table 5). *Clonostachys* species are endophytes also able to promote plant growth and drought tolerance (Sutton et al., 2008). Although present at lower levels, *Trichoderma* spp. were also higher in the intercropped lentil and intercropped oat than in their respective monocultures. Among the other fungi with biocontrol potential, *F. equiseti* was highest in oat, followed by mustard (Tables 3 and 5).

Thus, beyond allelopathy, the lentil–mustard intercrop appeared to have promoted a higher number and percentage isolation of fungi with biocontrol potential in the intercropped lentil than in its monoculture (Table 5). These observations suggest a synergistic effect of allelopathic compounds from mustard and increased populations of beneficial microorganisms, which likely contributed to the overall lower root rot observed in the intercropped lentil (Table 2).

TABLE 5 Percentage isolation of the most commonly-isolated fungi with biocontrol potential from monocultures and intercrops grown in southwest Saskatchewan, Canada (2017–2018).

Crop/monoculture/ intercrop ratio[a]	*Acremonium* spp.	*Clonostachys* spp.	*Epicoccum nigrum*	*Fusarium equiseti*	*Nigrospora sphaerica*	*Penicillium* spp.	*Rhizophagus* sp.	*Trichoderma* spp.	No. of species[b]	Total % isolation
	%									
Lentil										
Monoculture	0.0	6.8	0.0	3.2	0.0	0.5	0.0	1.8	4	12.2
SE	0.0	2.1	0.0	1.6	0.0	0.5	0.0	0.9		2.3
Lentil100 + Mustard50	0.0	5.4	0.6	3.6	2.0	0.7	0.0	4.7	6	17.0
SE	0.0	3.8	0.6	2.0	1.4	0.7	0.0	2.2		4.7
Lentil75 + Mustard75	0.0	2.1	0.5	3.6	0.5	0.5	0.0	6.9	7	15.1
SE	0.0	1.1	0.5	2.0	0.5	0.5	0.0	3.1		3.3
Lentil50 + Mustard100	0.0	11.8	1.4	2.8	0.7	0.0	0.0	5.7	5	22.4
SE	0.0	3.7	1.4	2.2	0.7	0.0	0.0	2.4		4.7
Mustard										
Monoculture	0.0	5.2	2.6	6.0	0.0	0.0	1.9	2.1	5	17.8
SE	0.0	0.9	1.1	1.4	0.0	0.0	0.9	1.4		8.3
Lentil100 + Mustard50	0.0	1.9	2.3	7.8	0.0	0.0	0.8	0.7	5	13.4
SE	0.0	1.3	1.5	1.6	0.0	0.0	0.8	0.7		1.8
Lentil75 + Mustard75	0.0	2.4	2.9	8.5	0.0	1.7	1.8	1.7	6	19.0
SE	0.0	1.6	1.2	1.8	0.0	0.8	0.9	0.8		1.6
Lentil50 + Mustard100	0.0	3.1	3.3	5.8	0.0	1.2	2.8	2.1	6	18.2
SE	0.0	2.0	1.8	1.5	0.0	0.8	1.1	1.2		2.5
Pea										
Monoculture	0.0	2.3	4.2	5.0	0.0	0.0	1.6	1.7	6	15.3
SE	0.0	1.3	2.0	2.2	0.0	0.0	0.8	0.9		1.5
Pea100+Oat25	0.0	2.6	0.0	5.5	0.0	0.0	0.0	1.3	3	9.4
SE	0.0	1.3	0.0	1.8	0.0	0.0	0.0	0.9		1.5
Pea100 + Oat50	0.0	4.0	1.1	3.9	0.0	0.0	0.0	2.7	4	11.7
SE	0.0	1.5	0.7	1.2	0.0	0.0	0.0	0.9		1.9
Pea75 + Oat75	0.0	3.2	1.7	3.5	0.0	0.0	2.3	3.7	5	14.3
SE	0.0	2.7	1.2	1.9	0.0	0.0	1.2	2.6		3.8

(Continues)

TABLE 5 (Continued)

Crop/monoculture/intercrop ratio[a]	*Acremonium* spp.	*Clonostachys* spp.	*Epicoccum nigrum*	*Fusarium equiseti*	*Nigrospora sphaerica*	*Penicillium* spp.	*Rhizophagus* sp.	*Trichoderma* spp.	No. of species[b]	Total % isolation
Oat										
Monoculture	0.0	7.0	1.1	9.2	0.0	1.2	4.4	0.4	7	25.2
SE	0.0	3.0	0.7	2.2	0.0	0.8	1.3	0.4		3.4
Pea100 + Oat25	1.9	7.5	1.6	7.4	0.0	1.2	3.0	3.7	7	26.3
SE	1.3	2.3	1.2	2.1	0.0	0.8	1.6	1.6		2.5
Pea100 + Oat50	2.1	6.3	1.5	10.9	0.0	0.4	3.1	1.3	9	29.2
SE	1.4	2.2	0.7	3.2	0.0	0.4	1.3	0.7		2.7
Pea75 + Oat75	0.0	7.0	3.6	10.3	0.0	1.9	1.6	1.2	7	27.1
SE	0.0	3.4	2.0	3.7	0.0	1.1	0.8	0.9		3.3

[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.

[b]This number includes all fungi with biocontrol potential isolated from crops grown in monocultures or intercrops, even those isolated occasionally and not presented in this table.

3.6 | Fungal communities—PERMANOVA and Shannon diversity index

A PERMANOVA analysis on Bray–Curtis dissimilarities revealed that intercropping significantly modified the belowground fungal microbiome, with significant differences in overall fungal community composition among monocultures and intercrops, as well as between the two intercrop combinations. The PERMANOVA model for pea and oat was highly significant ($p = 0.004$, R^2: 0.146), explaining 14.6% of the total variation in the fungal community composition (Figure 1). Pairwise comparisons showed significant differences among the treatments. The fungal community in the pea monoculture was significantly different from the oat monoculture ($p = 0.001$). Additionally, the pea and oat monocultures were significantly different from each of the pea–oat intercrop ratios ($p < 0.05$), while comparisons among each of the latter were not significant. The PERMANOVA model for mustard and lentil was also highly significant ($p = 0.002$), explaining 15.4% of the fungal community variation (R^2: 0.15389) (Figure 1). This indicates that the lentil–mustard intercrop also caused a significant shift in the overall fungal community structure. Pairwise comparisons revealed that the Lentil100 monoculture was significantly different from the Mustard100 monoculture ($p = 0.001$), and from each of the lentil–mustard intercrop ratios ($p < 0.05$).

Comparison of fungal communities in a monoculture versus the same crop grown in an intercrop (Figure 2) showed significant differences for mustard and oat. The fungal communities in the mustard intercrop were significantly different from those in the mustard monoculture ($p = 0.001$, stress: 0.12), forming two distinct, nonoverlapping clusters. Similarly, the oat fungal communities were significantly different between the intercrop and the monoculture ($p = 0.04$, stress: 0.11), with these clusters showing some overlap, but being distinct. In contrast, there was no significant difference in the fungal communities between the lentil monoculture and its intercrop ($p = 0.39$, stress: 0.12), with the two clusters showing a high degree of overlap (Figure 2). Similarly, the fungal communities in the pea monoculture and its intercrop treatments were not significantly different ($p = 0.31$, stress: 0.09), with the two groups also showing a large overlap.

Shannon diversity index calculations revealed no statistically significant differences in diversity among treatments for lentil ($p = 0.16$) and mustard ($p = 0.55$) (Table 6). In contrast, pea intercrop treatments showed significant differences in the Shannon diversity index ($p = 0.04$). Specifically, the pea monoculture and the Pea100 + Oat25 treatment exhibited the highest diversity, while a significant reduction in fungal diversity was observed when pea was intercropped with higher proportions of oat (Pea100 + Oat50 and Pea75 + Oat75) compared to its monoculture. Oat also showed signifi-

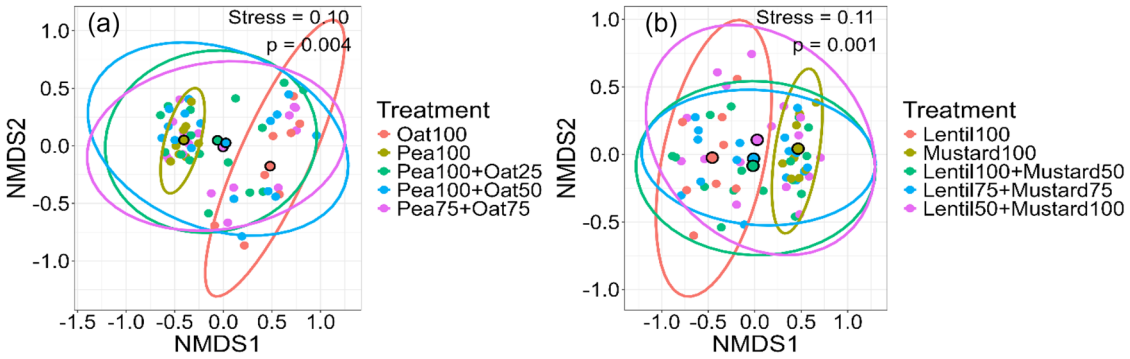


FIGURE 1 Nonmetric multidimensional scaling (NMDS) ordination plots showing the effect of different seeding ratios on the fungal community composition in intercropping systems: (a) Pea and oat monocultures and their intercrop ratios and (b) lentil and mustard monocultures and their intercrop ratios.

cant differences among treatments ($p = 0.06$), with the Pea100 + Oat25 and Pea100 + Oat50 ratios having the highest diversity.

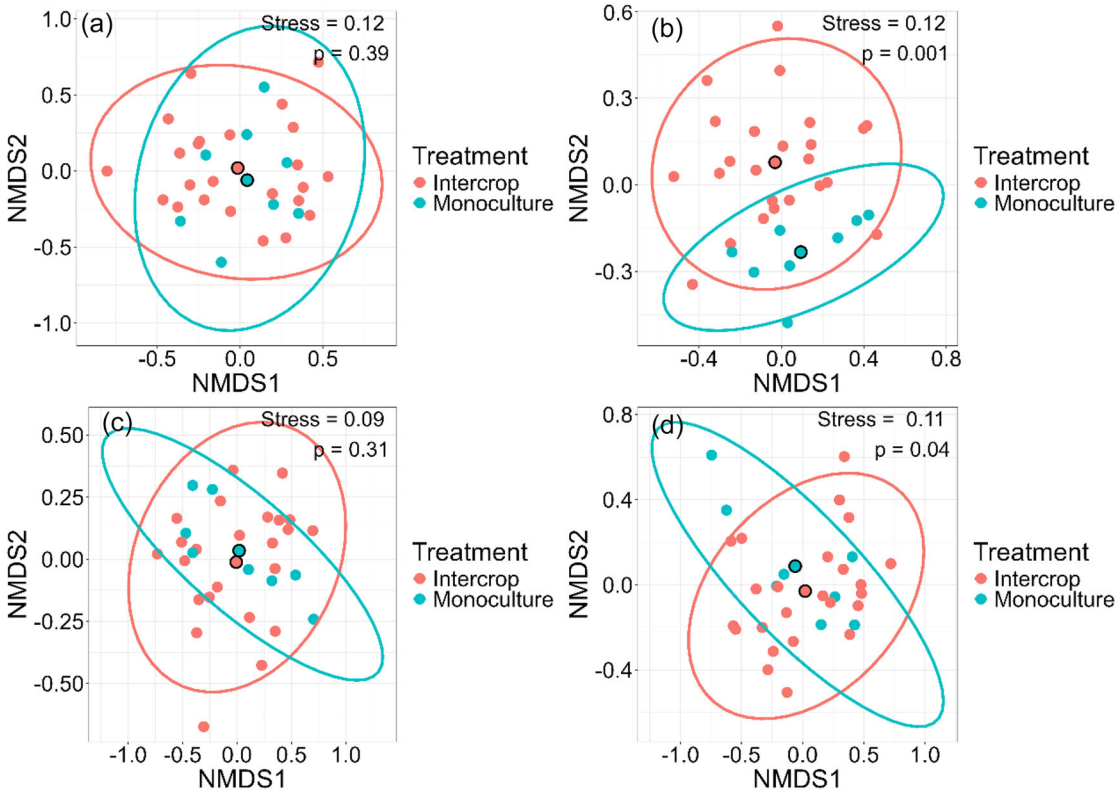
These findings indicate a significant change in the overall fungal community structure for both mustard and oat when intercropped with legumes. This suggests that the types and proportions of fungi were altered. The results from the PERMANOVA analysis complement the Shannon diversity index findings for mustard and oat, which showed no significant changes between the monocultures and intercrops, although the oat intercrops did show a significant difference when compared to the other oat treatments. This suggests that while the overall community structure changed, its richness remained similar. In contrast to the nonlegumes, for lentil and pea the PERMANOVA results showed that the overall fungal community structure was not significantly different between the monocultures and the intercrop treatments. This aligns with the Shannon diversity index results for lentil, which also showed no significant difference in the monoculture-intercrop comparison. While the pea monoculture-intercrop comparison showed a significant difference, the overall PERMANOVA analysis suggests the changes were not substantial enough to represent a significant difference in the community as a whole. Thus, the PERMANOVA analysis confirmed that the intercropped mustard and oat had a much more substantial and statistically significant effect on the fungal community structure than the intercropped lentil and pea.

Thus, our study showed that intercropping could be a tool for manipulating the belowground microbiome and driving it toward a more beneficial state. Our results partially agree with those of Jalloh et al. (2024) that intercropping significantly influenced the composition of belowground microbial communities, but while they also found that intercropping can increase microbial diversity and abundance, our results from the Shannon diversity index showed no significant differences in the overall fungal diversity between any of the previous lentil–mustard treatments, and some differences for the field pea intercrop. This means that even though the lentil–mustard intercrop did not increase the total number of species, it selectively enriched fungi with biocontrol potential leading to a reduction in root rot in lentil.

Our study not only showed differences among crop monocultures and intercrop combinations but also found that nonlegumes contributed significantly to microbial diversity. This appears to agree with previous studies. Venter et al. (2016) reported a positive effect of increasing crop diversity on soil microbial diversity and richness; however, the addition of legumes in rotation made no difference to total soil microbial diversity. The observation that nonlegumes contribute significantly to this diversity is also supported by Bainard et al. (2017), whose study in the same region found that continuous wheat and rotations with a single pulse crop maintained higher soil fungal richness and diversity than when there was increased intensification of pulses in rotation with wheat, suggesting that inclusion of nonlegumes is key to maintaining diversity.

The findings from this study on organic intercropping are consistent with a previous nearby study by Fernandez et al. (2022) on organic tillage and crop rotation, as both prove that agricultural management practices can significantly impact fungal diversity. The Fernandez et al. (2022) study demonstrated that a diversified crop rotation can lead to higher fungal diversity over time, particularly for spring wheat under more intensive tillage. Our findings complement this by showing that plant associations in an intercropping system can also drive changes in diversity with a crop-dependent outcome.

A comparison of both organic studies revealed that the fungal communities associated with the cereal crops (oat and spring wheat) were more responsive to changes in management than those associated with legumes. In the current study, fungal diversity in oat changed significantly with the different intercrop proportions. Similarly, Fernandez et al. (2022) found that fungal diversity in spring wheat was highly influenced by the tillage and rotation system. In contrast, while



Crop	R^2	F	*P*-value
Lentil	0.03	0.942	0.389
Mustard	0.105	3.513	0.001
Pea	0.026	0.813	0.313
Oat	0.044	1.378	0.039

FIGURE 2 Nonmetric multidimensional scaling (NMDS) ordination plots showing the effect of intercropping versus monoculture on the fungal community composition in belowground crop tissue: (a) lentil, (b) mustard, (c) pea, and (d) oat. 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, F, and p values.

forage pea manure diversity was not significantly affected by tillage or rotation (Fernandez et al., 2022), in the current study, field pea, but not lentil, diversity changed significantly with intercropping.

Furthermore, these fungal diversity effects might be more achievable in organic than nonorganic systems. Lenc et al. (2015) reported that species of *Acremonium*, *Clonostachys*, and *Trichoderma* isolated from winter wheat roots were also more common in the organic than nonorganic systems, while Sousa et al. (2008) found that *Brassica oleracea* L. var. *costata* DC samples from organic production exhibited higher total content of phenolics, which have an important role in plant health protection, than those from conventional practices.

A synergistic effect on the soil fungal community is plausible by combining intercropping and organic practices, which might be able to increase the overall richness of the fungal community. Fernandez et al. (2022) noted that reduced tillage and diversified rotations under organic management improved disease suppression by favoring beneficial, saprophytic fungi over pathogenic species. Thus, we further hypothesize that combining intercropping with other organic practices, such as diversified crop rotations, would further contribute to creating an environment that is less suitable to crop pathogens and more favorable to beneficial organisms. This integrated approach may lead to a more resilient and beneficial microbiome with greater fungal diversity than either monoculture or single-species rotations alone, which could offer superior suppression of plant pathogens, particularly *Fusarium* species, and better adaptation to environmental stresses.

TABLE 6 Effects of intercrops and respective monocultures on the Shannon diversity index in field pea, lentil, yellow mustard, and oat in an organic study in southwest Saskatchewan, Canada (2017–2018).

Treatment	Pea	Lentil	Mustard	Oat
Monoculture	2.21	2.00	2.16	2.02
Intercrop	2.02	1.91	2.16	2.20
p value	0.01	0.56	0.98	0.22
Treatment			**Shannon diversity index**	
Field pea				
Pea100			2.21a[a]	
Pea100 + Oat25			2.05ab	
Pea100 + Oat50			2.02b	
Pea75 + Oat75			2.00b	
p value			0.04	
Lentil				
Lentil100			2.00a	
Lentil100 + Mustard50			1.77a	
Lentil75 + Mustard75			2.02a	
Lentil50 + Mustard100			1.95a	
p value			0.16	
Yellow mustard				
Mustard100			2.16a	
Lentil100 + Mustard50			2.09a	
Lentil75 + Mustard75			2.21a	
Lentil50 + Mustard100			2.19a	
p value			0.55	
Oat				
Oat100			2.02b	
Pea100 + Oat25			2.31a	
Pea100 + Oat50			2.25a	
Pea75 + Oat75			2.05b	
p value			0.06	

[a]Means with the same letters within each crop, in the lentil–mustard and pea–oat intercrop combinations, are not significantly different ($p \leq 0.10$).

3.7 | Implications for pathogen carryover

Our findings are of significance given that legume roots can serve as a reservoir for *Fusarium* pathogens that affect a variety of crops, including those responsible for Fusarium head blight (FHB) in cereals (Fernandez, 2007). Regardless of any in-season impacts of intercropping on *Fusarium* pathogens, infected root and crown tissues can play an important role in the survival and carryover of this inoculum to subsequent growing seasons. Colonization by *Fusarium* pathogens of underground- and/or ground-level plant tissue, and their subsequent survival and multiplication in those tissues after harvest, might affect the future development of important crop diseases, such as FHB (Fernandez et al., 2009). Those tissues, in addition to other crop residues, might be a reservoir for *Fusarium* inoculum when environmental conditions are not conducive to the development of head/grain diseases. However, given the wide host range of *F. avenaceum*, an FHB pathogen commonly isolated in this and other studies, this species might not likely be suppressed to a great extent by intercropping with the nonlegume crops used in this study. Furthermore, our observations also suggest that mustard should not be regarded as an important source of the most common *Fusarium* pathogens of legume and cereal crops.

4 | CONCLUSIONS AND FUTURE RESEARCH

Our findings demonstrate that intercropping can significantly influence in-season root rot severity and associated

fungal communities, with the effects varying markedly between the lentil–mustard and pea–oat combinations, suggesting that each such combination should be treated as unique.

The fungi identified in all monocultures and intercrops included host-specific and wide-host range pathogens, as well as weak pathogens and saprophytes. While most were *Fusarium* species, some of which are responsible for FHB in cereals, we also identified several fungi with known biocontrol potential. Our results suggest that intercropping can promote these beneficial fungi, which may not only aid in disease management but also enhance crop growth and drought tolerance. This highlights the potential of intercropping as a disease management tool under organic management in the semiarid Canadian Prairies.

The nonlegumes in both the lentil–mustard and pea–oat intercrops seemed to have provided the highest microbial diversity. Intercropping legumes with crops like mustard offers a highly beneficial strategy for organic crop production, which depends on N-fixing crops for nitrogen supply, and to the pulse industry given the impact of *Fusarium* pathogens on legume crop growth, and persistence of populations of these pathogens in soil and crop residues over time. Given the lack of successful control through breeding alone, integrating intercrops, particularly legume–*Brassica* combinations, into cropping systems could be a valuable and sustainable management tool in the semiarid Canadian Prairies.

However, while our study highlights the potential for *Brassica* intercrops as a disease management tool in organic systems, certain limitations of this study should be considered. Notably, both years (2017 and 2018) experienced drier-than-normal growing conditions, especially during critical periods of crop development, which may have decreased disease pressure and altered the associated fungal communities. The fungal communities observed in this study could differ from those in years with more suitable growing conditions. Under wetter conditions, pathogen suppression effects might be more pronounced or differ in direction. The activity of allelochemicals like ITCs might also be affected by soil moisture. Climate change is expected to bring increased environmental variability, including shifts in precipitation patterns, making it vital to understand intercropping performance across a range of environmental conditions. Therefore, while our findings provide valuable insights into root disease management under semiarid conditions, more research is needed across diverse environments to evaluate the consistency of the results from this study. Identifying all factors that might affect pathogen populations when different crops are grown in mixtures at different ratios and under varying environmental conditions is critical for optimizing intercropping as a sustainable disease management strategy in the Canadian Prairies and beyond.

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; investigation; methodology; supervision; 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—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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