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Pathogenicity of different *Fusarium* species on six arable crop species in Finland

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In cereals, *Fusarium* species composition and associated mycotoxin risks are well studied in the Nordic countries, but the interactions between *Fusarium* populations and the legume crops faba bean and field pea and the increasingly cultivated new crops such as maize and oilseed hemp are unrevealed. In this study, two-year field experiments were carried out with spring wheat, oat and and those above-mentioned crops on small demonstration plots in 10 different fields in Central Finland. The aim was to analyse the severity of symptoms and prevalence of *Fusarium* species from the root and stem tissues of the field plants. While the legumes exhibited the most symptomatic plants, the prevalence of *Fusarium* species and symptoms in the samples varied considerably between the fields, *F. avenaceum* and *F. equiseti* being the most frequently detected species. In addition, the germination, growth and symptom development from *Fusarium* inoculated seeds of these arable crop species were examined in greenhouse conditions. *F. graminearum*, *F. culmorum*, and *F. avenaceum* were the most pathogenic *Fusarium* species in these experiments comparing up to 105 *Fusarium* isolate x crop species combinations.

Key words: root rot, crown rot, crop rotation

Introduction

Increasing costs of fertilisers, elevating growing degree days, and EU policies all encourage Nordic farmers to diversify their crop production. During the last two decades, the cultivation areas of the two legumes, faba bean (*Vicia faba*) and field pea (*Pisum sativum*), have increased by up to 10-fold of their previous areas in Finland (Luke 2025). Moreover, species such as oilseed hemp (*Cannabis sativa*) and maize (*Zea mays*) are also becoming more common on Finnish farms. Oilseed hemp (hereafter, hemp) is a crop with high potential in different products (Rehman et al. 2021). Maize cultivation is slowly increasing, especially in cattle feed production, and the warming climate will further increase the potential use of this C4 crop (Peltonen-Sainio and Jauhiainen 2020). Species diversification in crop rotation has positive effects on weed, pest, and disease control and soil properties, and it can even be more profitable for a farmer than crop rotation with traditional species (Jalli et al. 2021, Volsi et al. 2022).

The genus *Fusarium* collectively represents one of the most important groups of fungal plant pathogens, causing various diseases in most of the world's economically important plant species (Dean et al. 2012, Okungbowa and Shittu 2012). In addition to economic losses, the health hazards posed to humans and livestock by a diverse set of mycotoxins produced by various *Fusarium* species are of equal concern (Desjardins 2006, Jestoi 2008). In the years of severe Fusarium head blight (FHB) infection, up to 20% of oat (*Avena sativa*) lots are rejected in Finland because the crops exceed the EU threshold for deoxynivalenol (DON) mycotoxin contamination (Hietaniemi 2016). Globally, FHB in small grain cereals causes yield losses exceeding 50% in the worst cases (Parry et al. 1995) with annual economic losses over one billion dollars (Wegulo et al. 2015).

Besides DON-producing FHB species (*Fusarium graminearum* species complex and *F. culmorum*), *F. langsethiae* and T-2/HT-2 mycotoxins are considered a threat in cereal production. For example, in the British Isles these toxins are considered a major concern (Edwards 2009). T-2 producing *F. langsethieae* is commonly detected in the UK, Northern Europe and Russia (Imathiu et al. 2013, Hofgaard et al. 2016, Tanaka et al. 2022). Exposure to trichothecene mycotoxins, such as DON and even more toxic T-2/HT-2 mycotoxin, has various toxic effects, including growth retardation, feed refusal, vomiting, immunosuppression, and reproductive disorders. In large quantities T-2/HT-2 can even be lethal due to its stronger ability to distract ribosomal activity (Pinton and Oswald 2014, Adhikari et al. 2017).

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Fusarium species have a wide host range, and in addition to cereals, they are likely to persist in many plant species grown on Finnish fields such as legumes (Orina et al. 2020), onions (Haapalainen et al. 2016) and weed plants (Haapalainen et al. 2016, Sneideris et al. 2020). Currently, a large proportion of Finnish fields is used for growing feed, mostly grasses. The use of maize silage is increasing, and cultivation of maize has been shown to correlate with the incidence of high DON contaminations (Dill-Macky and Jones 2000). Moreover, *Fusarium* species such as *F. proliferatum* and *F. verticillioides* that produce fumonisins are also known to thrive in maize production abroad. Recently *F. verticillioides* was reported to be found in a Finnish winter wheat field, which indicates that the population of Finnish *Fusarium* fungi may be becoming more diverse and harmful (Gagkaeva and Yli-Mattila 2020). Furthermore, we have learnt that management strategies of FHB in cereals such as cultivar resistance may be species specific (Hofgaard et al. 2022).

The management of FHB in cereals requires an integrated disease management approach, including a crop rotation system, cultivar resistance, fungicide treatment, weed management, and soil tillage (Wegulo et al. 2015, Hietaniemi 2016). In addition, the post-harvest management of the harvested crop plays an important role in the prevention of mycotoxin accumulation (Magan and Aldred 2007). Several fungicides are registered to control the disease, but the timing of spraying is critical, and even correctly timed spraying may not protect the yield from infection. Continuous infection pressure exists from airborne spores (Keller et al. 2013) from other fields and crop residues (Sutton 1982).

In cereals, *Fusarium* species composition and mycotoxin risks are well studied, but the interactions between the legume crops faba bean and field pea and the increasingly cultivated new crops such as maize and oilseed hemp have not been revealed. The aims of this study were i) to investigate the potential field-to-field variation of the root and stem symptoms associated with *Fusarium* populations in Finnish fields, using 10 demonstration plots consisting of six different crop species; and ii) to test the harmfulness of different *Fusarium* species and their different isolates on the germination and growth of six different field crop species by greenhouse assays.

Material and methods

The experiments performed in this study are summarized in Figure 1. The study included field trials in two years, focusing on the prevalence and severity of root and stem symptoms in six arable crop species, and the identification of *Fusarium* pathogens from collected plant samples. Two separate greenhouse experiments were also conducted to compare the impact of different *Fusarium* species and to assess variation in pathogenicity within *Fusarium* species on the same crops.

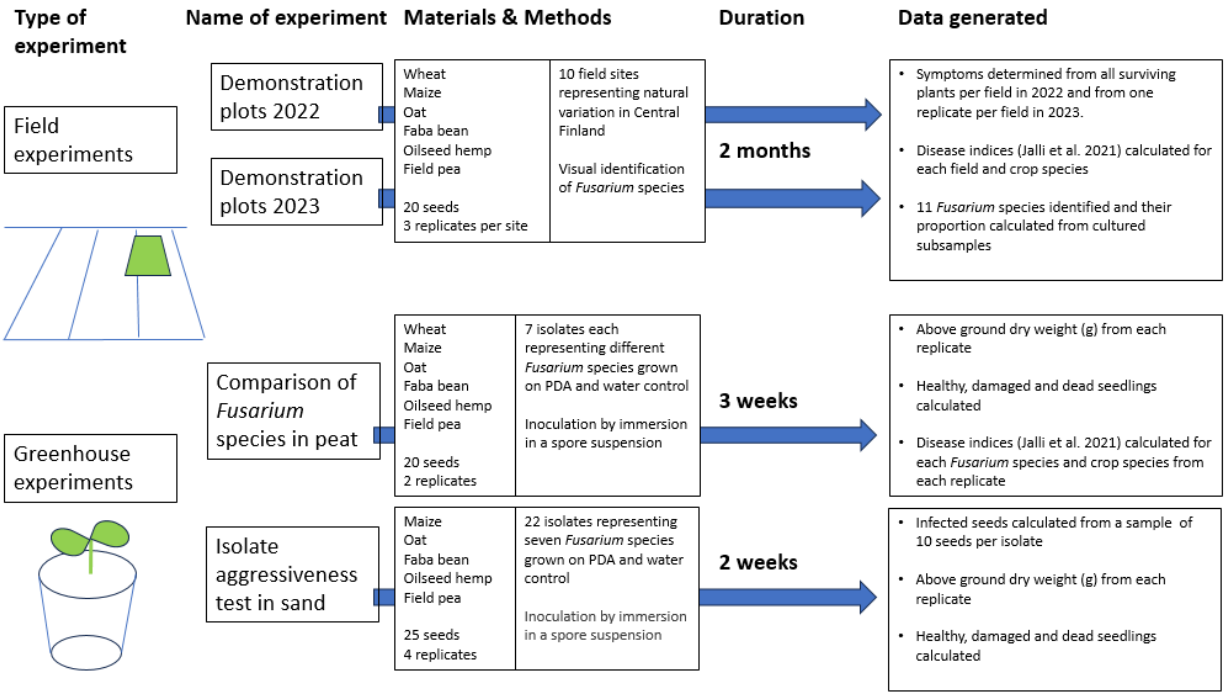

Fig. 1. Field and greenhouse experiment plans

Plant seed material

Six crop species, spring wheat (*Triticum aestivum* cv. Helmi), oat (cv. Belinda), faba bean (cv. Sampo), hemp (cv. Finola), maize (cv. Ambient), and field pea (cv. Astronaute), were selected to represent the variation of Finnish field crop production in the field and greenhouse experiments. Seeds were surface-sterilised by dipping in 70% ethanol for 10 seconds before they were used in the experiments. The seed material for oat was sourced from a greenhouse, and the maize seeds were bought as organic seed from Berner Ltd., Finland. The faba bean, wheat, and hemp seeds were harvested from field experiments conducted at Natural Resources Institute Finland's research station at Jokioinen in 2021.

Field experiments and sampling

In 2022 and 2023, 10 separate farmers' fields with different crop rotations in Central Finland were selected, and 10 separate demonstration (demo) plots were planted on them. Background information of the fields, farms and their crop rotations, tillage method, and soil type is presented as supplementary material (Suppl. Table 1). Table 1 describes the sampling seasons' weather conditions. The plots were planted after the farmer had sown the field (excluding the plot area) within a 2-week period between late May and early June in both years, and the plots were harvested just before the farmer was harvesting the main crop during the first two weeks of August, giving the plants approximately two months to germinate and grow. Within each plot, nine hill plots per m^2 were planted with six crops with a variable number of seeds per crop. The seed number varied from 20 seeds for oat, hemp, and wheat to 6–7 seeds for pea and faba bean, and five seeds for maize, depending on the crop's seed size. A set of 20 plants (1–4 hill plots) per crop, depending on the crop species, was planted in three replicates in a completely randomised design. Thus, each demo plot had 60 plants from each species. No additional fertilisation was applied for the demo plot area to what the farmer had applied. Besides removing weeds manually once, three to four weeks after planting, from each demo plot, no other plant protection was applied.

Table 1. The monthly mean temperature and precipitation in Central Finland (Jyväskylä airport) during the sampling periods. (Data retrieved from Finnish Meteorological Institute, 21.10.2024)

Month	2022 temperature, °C	2023 temperature, °C	Average temperature (1991–2020), °C	2022 rainfall, mm	2023 rainfall, mm	Average rainfall (1991–2020), mm
May	9	10	9.1	33	33.8	43
June	15.6	15.4	14	68.1	74.5	67
July	16.8	15.9	16.7	121.8	164.8	79
August	16.8	16	14.6	55.5	110.3	67

The number of harvested plants varied between years, demonstration plots and crop species (total number of plants collected per site over two years is shown in Table 3). The severity of root and stem disease symptoms were determined from all samples, and the disease index (DI) was calculated as follows: DI = (B+2*C+3*D+4*E)*100/4*(A+B+C+D+E) where A = number of plants with no symptoms; B = small spot (diameter less than half of the width of the stem) in coleoptile or damaged tissue in the basal of the stem or root tips (in case of dicots); C = larger spot or several spots on coleoptile or basal of the stem and clear darkening on roots; D = severe attack on coleoptile, stem basis and/or roots, plants stressed (more than 30%), and E = dead plants (applied from Jalli et al. 2021). Healthy plants had a clean white root system and no spots in their crown tissue. The types of symptoms varied, depending on the species, from blackened root hairs and black wounds in faba bean to brown spots on the surface of cereal stems. Maize rarely had any symptoms but in a case we observed some damaged mesocotyl tissue (between kernel and nodal roots), we categorized the plants to B. At the time of the sample collection the developmental stage of each crop varied according to the establishment of the field but generally all species except maize were at the flowering stage whereas maize was still in vegetative stage due to its long growing time requirement.

Identification of *Fusarium* species from field samples

Subsamples of approximately 5 mm in length from different symptomatic and non-symptomatic parts of the plants were surface-sterilised in 70% ethanol for 10 seconds, dried on sterile paper towel, and cultured on selective pentachloronitrobenzene (PCNB) medium (Nash and Snyder medium, Nelson et al. 1983). In 2022, 3–5 subsamples were cultured from healthy (A), and mildly (B) and severely (C, D) symptomatic plants, from each sample, whereas in 2023, two subsamples from healthy plants and two from severely infected plants were cultured from each sample (total number of samples per field site and total number of symptomatic samples per crop are shown in

Figure 3. *Fusarium* spp. cultures were further transferred to a potato dextrose agar (PDA) medium, and the fungal species were tentatively identified by the culture features and spore morphology according to the systematics by Gerlach and Nirenberg (1982).

Fusarium isolates used in greenhouse experiments

The impact of 22 different *Fusarium* spp. isolates (Table 2) on oat, maize, hemp, faba bean, and field pea was studied in inoculated pot experiments in greenhouse conditions. The fungal isolates were stored cryopreserved in 2 ml cryovials in an automated liquid nitrogen freezer at −150 °C, as part of the culture collection of Natural Resources Institute Finland (Luke). The identity of the *Fusarium* species was originally determined by the culture features and spore morphology, as described earlier, and confirmed by sequencing part of the translation elongation factor 1α (*TEF*) gene. Sequences were submitted to the NCBI sequence database, and their accession numbers are listed in Table 2. The isolates were grown on PDA at 25 °C, and their growth speed was monitored by measuring the area covered by mycelium calculated from three replicated cultures after three days of incubation (Table 2). Intensity of spore production was observed from four-week-old cultures.

Table 2. *Fusarium* isolates used in a greenhouse in a sand assay to study their impact on dry weight accumulation and germination, and in a peat assay (marked in bold) to study their impact on early symptom development in plants.

Isolate code	*Fusarium* species	Isolated from	Growth (mm^2)	Spore production	NCBI sequence database accession no
Fs06019	*F. sporotrichioides*	barley	8.8	strong	PQ561039
Fs06020	*F. sporotrichioides*	oat	10.2	strong	PQ561040
Fs06021	*F. sporotrichioides*	wheat	11.7	strong	PQ561041
Fs05003	*F. sporotrichioides*	wheat	15.1	strong	PQ561042
Fe06295	*F. equiseti*	wheat	6.9	weak	PQ561043
Fe05077	*F. equiseti*	oat	6.4	weak	PQ561044
Fe05079	*F. equiseti*	barley	8.2	weak	PQ561045
Fp06007	*F. poae*	barley	20.0	strong	PQ561046
Fp06009	*F. poae*	wheat	11.4	strong	PQ561047
Fp06008	*F. poae*	oat	20.8	strong	PQ561048
Ft41037	*F. torulosum*	carrot	2.5	average	PQ561049
Ft05097	*F. torulosum*	oat	2.2	average	PQ561050
Ft06040	*F. torulosum*	barley	2.8	average	PQ561051
Ft05065	*F. torulosum*	wheat	3.0	average	PQ561052
Fa06002	*F. avenaceum*	oat	5.7	average	PQ561053
Fa06003	*F. avenaceum*	wheat	7.2	weak	PQ561054
Fa41037	*F. avenaceum*	carrot	5.3	average	PQ561055
Fa05001	*F. avenaceum*	barley	4.7	average	PQ561056
Fg05011	*F. graminearum*	barley	3.4	average	PQ561057
Fc12004	*F. culmorum*	oat	4.4	average	PQ561058
Fc12011	*F. culmorum*	barley	6.9	average	PQ561059
Fc05015	*F. culmorum*	barley	5.9	average	PQ561060

To study the impact of *Fusarium* pathogens on early symptom development in plants, a peat assay was conducted with the following seven isolates from separate *Fusarium* species: Fs05003; Fe05079; Fp06007; Ft05065; Fa05001; Fg05011; and Fc05015 (Table 2). These isolates were growing well and the isolates Fs5003, Fa5001, Fg05011 and Fc5015 were also found to be the best mycotoxin producers in the paper of Kokkonen et al. (2010). To prepare the inoculum suspensions, fungal cultures grown on PDA for four weeks were suspended in 2ml ml sterile distilled water per plate and mixed with a blender. The resulting suspension was filtered through sterilized cheesecloth. For slowly sporulating fungi, such as *F. graminearum*, the inoculum was built from pieces of mycelium instead of spores. Density of spores or pieces of mycelia was counted and adjusted to 1.0×10^6 cfu ml^{-1} for inoculations. The seeds of five crop species were inoculated separately with each *Fusarium* isolate. The inoculation of the seeds

was as follows: either 40 or 100 dry surface-sterilised seeds (depending on the seed size) were put into 100 ml Erlenmayer flasks and covered with 40 ml of liquid fungal inoculum containing 1.0×10^6 cfu ml^{-1}. The flasks were shaken at 240 rpm for 30 min. The solution was then decanted, and the inoculated seeds were left on filter paper to dry for 10 min. Water treated seeds were used as a control. The infection percentage of inoculated seeds was calculated by culturing infected seeds on PDA for one week. For peat assay, two replicates of 20 seeds were sown in a randomised order in three-litre pots filled with fertilised peat growing medium (Kekkilä Taimiseos, Kekkilä, Finland, pH 5.9) and sand mixture (¾ peat, ¼ sand). The hemp and oat seeds were sown at a depth of 2 cm, and the maize, field pea, and faba bean seeds at a depth of 5 cm. The pots were kept at a temperature of 18 °C/15 °C (day/night), and the light intensity was kept above 200 W m^{-2} for 16 h per day after one week from planting. The pots were covered with plastic for the first week after planting. Three weeks after planting, at the end of the experiment, the stem and root disease symptoms were observed, and the disease indices (0–100) were calculated from each pot using the same protocol as for the field samples (Jalli et al. 2021). Dry weight per pot (DW) was measured from harvested aboveground biomass and the germination rate was calculated based on the proportion of healthy seedlings in relation to the total number of planted seeds per pot.

The aggressiveness of different *Fusarium* species and isolates was compared by studying their impact on aboveground dry weight accumulation and germination ability with a sand assay. In the sand assay a total of 22 isolates from seven separate *Fusarium* species (Table 2) was used to inoculate the maize, oat, faba bean, field pea, and hemp seeds, as described above. Four completely randomised replicates of 25 seeds per treatment were sown in one-litre pots filled with sand (natural sand, particle size 0.5–1.6 mm) in similar greenhouse conditions as described for the peat assay above. The pots were watered so that the sand was moist and covered with plastic for one week to enhance germination. No fertilization was given to sand. Two weeks after inoculation and planting, the number of germinated plants was counted and categorised as healthy, damaged, and dead. Dry weight (DW) was also measured from harvested aboveground biomass.

For comparison of isolate aggressiveness the relative dry weight reduction (RDW) per plant was calculated for isolate comparisons by subtracting the sample dry weight (DW) per plant from the average dry weight per plant of the control samples and dividing it by the average of control sample DWs per plant and then multiplying by 100 per cent. RDW = (average DW of water controls – sample DW/average DW in water inoculated controls) × 100%.

The relative proportion of healthy germinated plants was calculated similarly by dividing the number of germinated seeds per pot by the average number of germinated seeds from water control treatments and then multiplying it by 100.

Statistical analysis

Pearson correlations were calculated for the isolates compared in both sand and peat experiments to determine the most informative traits. In the cases of disease indices and field trial locations, disease indices in peat and relative germination of healthy seedlings and plant dry weight reduction in relation to control treatments, linear mixed models using the Kenward-Roger calculation (SAS ad in Excel) were applied to calculate the statistical significance of the treatments and their interactions. Replicates were treated as random factors. Tukey tests were applied when pairwise comparisons were discussed in detail.

Results

Fusarium species associated with root and stem symptoms in the field

The establishment of the field demonstration plots was very variable between the field sites (Table 3). The hemp and wheat plots failed often in their establishment due to the extraordinary drought and warm temperatures of the early growing seasons and the weak germination rate of the seed, which was a problem especially with hemp seeds. The samples collected from different fields and their disease indices are presented in Table 3.

The disease indices/severities in field plots were not statistically impacted by the year of sampling ($p = 0.12$), but both the location of the trial and plant species significantly impacted them ($p < 0.001$). The interaction between the location of the trial and the crop species also had a significant impact on the disease indices, indicating that the ranking of the crops based on their symptoms depended on the location. For example, faba bean had higher DI than field pea in six field sites but not in all. Generally, the samples from hemp, maize, and oat were symptomless, whereas faba bean and field pea had many severe symptoms.

Table 3. Average stem and root disease index per crop and total number of plants (n) collected per site over 2 years and assessed for symptoms from each experimental field between 2022 and 2023

Crop	Haapamäki1	Haapamäki2	Koskenpää1	Koskenpää2	Laukaa1	Laukaa2	Laukaa3	Laukaa4	Uurainen	Viitasaari
Oat	0 (80)	0 (53)	0 (80)	0 (4)	0.4 (76)	2.2 (95)	0 (76)	0 (64)	0 (76)	2.4 (79)
Wheat	2.5 (66)	5.0 (35)	4.5 (77)	7.8 (24)	13.6(57)	16.7 (34)	0 (7)	0 (29)	7.8 (80)	8.3 (35)
Faba bean	12.0 (61)	8.3 (12)	22.9 (71)	35.0 (5)	22.3 (53)	34.5 (79)	31.4 (65)	28.1 (59)	53.1 (49)	29.9 (50)
Field pea	8.2 (80)	18.9 (57)	22.8 (80)	15.0 (24)	32.1(75)	18.7 (80)	43.8 (39)	17.6 (80)	56.0 (59)	27.9 (76)
Hemp	0 (75)	0 (41)	0 (50)	0 (10)	0 (31)	6.3 (23)	0 (71)	0 (36)	0 (28)	0 (33)
Maize	4.9 (80)	0 (22)	0.9 (96)	0 (3)	2.1 (80)	2.3 (54)	1.9 (49)	1.0 (46)	0.6 (48)	11.7(67)

Also, wheat had mild symptoms compared to faba bean and field pea (Fig. 1). The disease indices of field pea and faba bean varied especially much between trial sites, the Haapamäki sites having the healthiest plants (DI<13), whereas Uurainen had the most severe symptoms (DI>53). Koskenpää 2 was clearly a failed location, as only a few plants (Table 3) from the caraway field survived for sampling.

Fig. 2. Typical severe symptoms in faba bean (a) and field pea (b); healthy hemp plants (c)

The number of subsamples taken from the field samples and the *Fusarium* species determined from them are presented in Figure 3. Two *Fusarium* species, *F. avenaceum* and *F. equiseti*, were prevalent the root and stem samples collected from different crops and fields (Fig. 3a and 3b). In addition, *F. culmorum* and *F. oxysporum* were often detected, and they were associated with symptomatic plants (Fig. 3b). The dominant *Fusarium* species differed in different field locations. The frequencies of observed *Fusarium* species were quite stable between the observation years and field sites, but some fluctuations were also detected (Fig. 3). Especially, the detection frequence of *F. equiseti* and *F. culmorum* had high changes from year to year. Interestingly, *F. avenaceum* was not detected from the Koskenpää location in 2023.

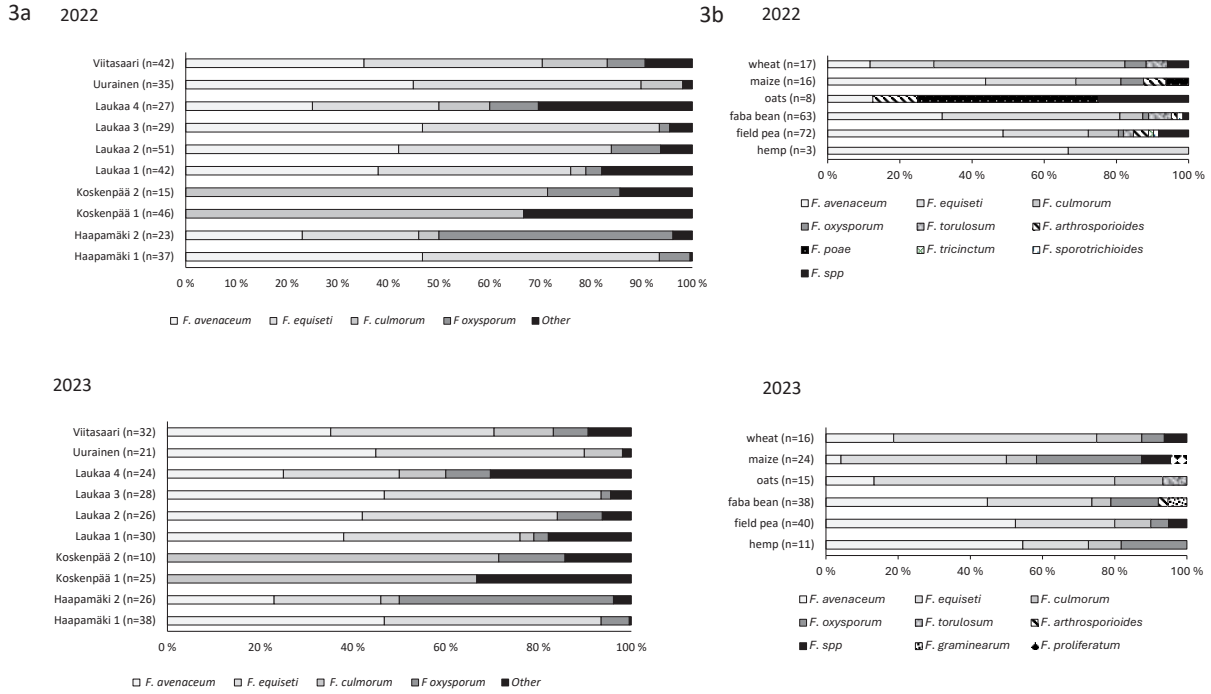

Fig. 3. Observations of different *Fusarium* species identified by morphological features from symptomatic and asymptomatic plant samples collected from 10 separate fields (a) in Central Finland and species detected from symptomatic tissue collected from 6 different plant species (b) in 2022–2023. Number of samples = (n).

Comparison of *Fusarium* species based on growth *in vitro*, and plant germination and symptom development in greenhouse

Twenty-two *Fusarium* isolates from seven different species (Table 2) were used in the greenhouse tests. In the *in vitro* growth tests F. poae isolates had the largest growth area (5.8±0.8 mm2 d^{-1}, mean±SD per day) in three days, whereas *F. torulosum* isolates had the smallest growth area (0.9±0.04 mm^2 d^{-1}) (Table 2). *F. sporotrichioides* and *F. poae* had the most efficient spore-production among the studied isolates.

The infection percentage of inoculated seeds was found to be 100 for all the isolates. Selected *Fusarium* isolates were compared in a peat assay (Table 4). Statistical analysis confirmed that both isolate and plant species significantly impacted the symptom development, and there was also significant interaction between them ($p< 0.001$). According to the symptoms observed after three weeks, hemp was the least affected by the *Fusarium* pathogens [DI<7.4]), while field pea exhibited the most severe symptoms (DI up to 90.9). *F. graminearum* and *F. culmorum* caused severe symptoms in cereals and in field pea (DI between 27.7 and 67), but the symptoms were much milder in hemp plants and faba bean (DI<7.4). *F. avenaceum* isolate caused very strong symptoms in field pea and significant symptoms in oat, maize, and faba bean (DI from 9.9 up to 90.9), but again, the symptoms in hemp plants were less severe (DI=2.9). *F. equiseti* caused severe symptoms only in faba beans. Shoot dry weights of the plants and germination were also measured from the peat assay. Field pea growth and germination and faba bean growth were both most impacted by *F. avenaceum whereas F. culmorum* and *F.graminearum* had the most distinctive impact on wheat and oats. Hemp growth and germination in peat assay was also impacted by most of the *Fusarium* species and especially *F. graminearum* treated seeds had less than half of the above-ground biomass (3.3 g vs 7.2g) compared to water control.

Table 4. *Fusarium* species comparison in peat assay. Average dry weight (DW), disease index (DI) and germination percentage (G) of 2 replicated pots for 7 isolates and water control and six crops are presented.

Treatment	Hemp			Faba bean			Field pea		
	DW (g)	DI	G (%)	DW (g)	DI	G (%)	DW (g)	DI	G (%)
F. avenaceum (Fa05001)	5.5	2.9	62.5	3.9	10.7	92.5	0.7	90.9	60.0
F. culmorum (Fc05015)	5.6	4.5	55.0	5.2	3.2	75.0	4.3	41.5	80.0
F. equiseti (Fe05079)	4.9	0.0	47.5	5.0	10.2	92.5	5.9	2.1	95.0
F. graminearum (Fg05011)	3.3	7.4	32.5	5.3	1.3	90.0	5.0	38.5	97.5
F. poae (Fp06007)	6.5	0.0	70.0	4.7	0.7	90.0	5.5	0.6	100
F. torulosum (Ft05065)	5.7	0.0	57.5	4.6	1.3	95.0	6.4	0.0	97.5
F. sporotrichioides (Fs05003)	4.2	0.0	37.5	5.9	0.0	95.0	4.6	0.8	82.5
Water control	7.2	0.0	72.5	5.2	1.4	87.5	5.8	0.0	97.5
	Maize			Spring wheat			Oats		
	DW (g)	DI	G (%)	DW (g)	DI	G (%)	DW (g)	DI	G (%)
F. avenaceum (Fa05001)	6.5	14.8	97.5	2.1	15.1	67.5	3.4	9.9	95.0
F. culmorum (Fc05015)	4.4	40.2	75.0	1.2	51.8	40.0	1.9	27.7	57.5
F. equiseti (Fe05079)	8.3	0.6	100	2.2	0.0	52.5	3.7	0.0	92.5
F. graminearum (Fg05011)	5.5	44.4	90.0	0.9	42.8	32.5	0.5	67.0	60.0
F. poae (Fp06007)	10.2	2.5	100	2.2	0.0	47.5	4.2	0.6	97.5
F. torulosum (Ft05065)	8.6	2.5	100	3.0	3.3	75.0	4.2	0.0	97.5
F. sporotrichioides (Fs05003)	8.7	1.3	97.5	2.1	0.0	50.0	4.0	0.0	97.5
Water control	9.5	2.5	100	2.8	9.5	62.5	4.7	2.5	97.5

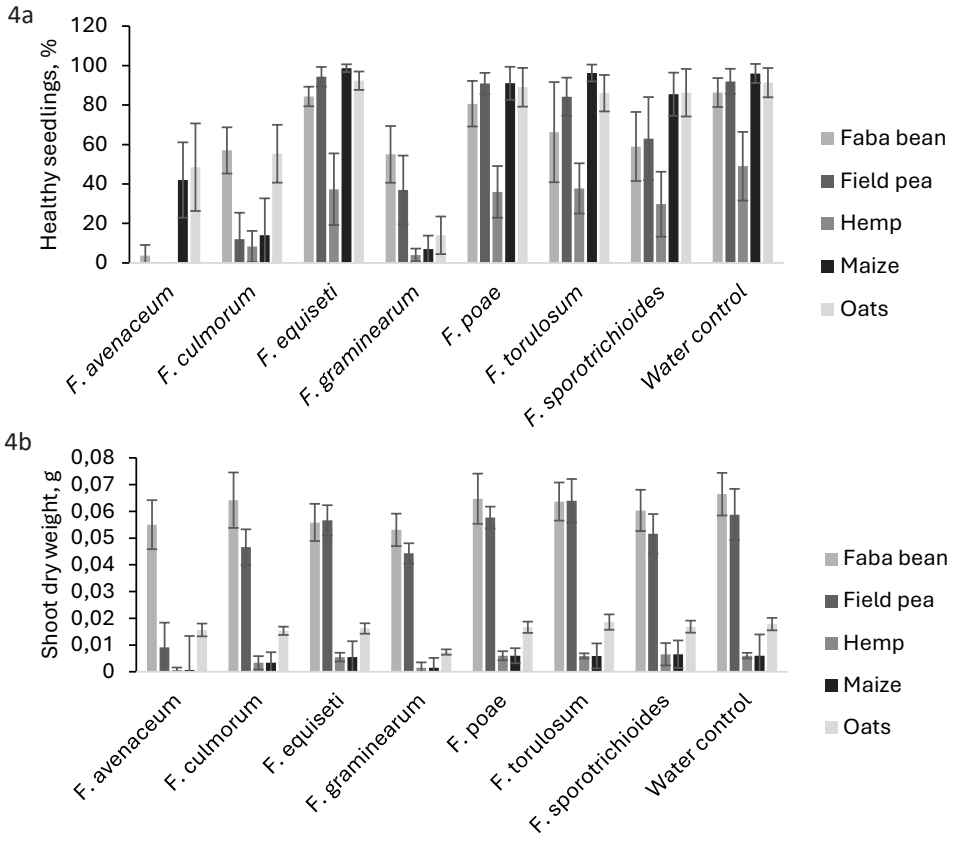

Fig. 4. The impact of different *Fusarium* species on germination of healthy seedlings (a) and on shoot dry weight development per plant (b) at 14 days post-inoculation. Both figures present average values and standard deviations.

The correlation between the disease indices in the peat assay and the reductions of shoot dry weight in sand assay was -0.56 (p= 0.0002, n=40), and the corresponding correlation for germination (proportion of healthy seedlings) was 0.55, (p= 0.0002, n=40). Figure 4 describes the impacts of different *Fusarium* species on crop germination and growth (dry weight accumulation). As shown in Table 3, the number of isolates representing each *Fusarium* species varied from 1 to 4. *F. avenaceum, F. culmorum*, and *F. graminearum* had the most severe impact on growth and germination (Figs. 4a and 4b), but the impact of different fungal species depended on the crop species (p< 0.0001, df=28, F-values 9.91 for the weight, and 8.43 for the germination). Faba bean especially was shown to be more tolerant to DON-producing species (*F. graminearum* and *F. culmorum*) but not against *F. avenaceum*. *F. equiseti* and especially *F. poae* had either neutral or even a growth-promoting impact on maize in both assays. Hemp germination was heavily impacted by all *Fusarium* species, whereas hemp growth was especially impacted by *F. graminearum*, *F. avenaceum* and *F. culmorum*.

Comparison of isolate aggressiveness

The aggressiveness of isolates from the three most prevalent *Fusarium* species from field samples, *F. avenaceum*, *F. culmorum* and *F. equiseti*, are compared in Figure 5 and with an analysis of variance. Averages from other isolates are attached as supplementary material (Suppl. Table 2 and 3). The interaction between isolates and crop species was found to be highly significant (p< 0.0001, df=36, F.= 6.85). Oat was the crop species where the group of studied *Fusarium* isolates had the lowest impact on germination rates while the dry weight accumulation of faba bean was least impacted. One of the studied *F. equiseti* isolates, Fe05079, impacted the growth of faba bean plants as much as *F. avenaceum* isolates, whereas *F. culmorum* had no significant impact on faba bean growth. The same *F. equiseti* isolate Fe05079 was also the most aggressive towards hemp and field pea. It also had a small impact on oat while maize seemed to be tolerant to all *F. equiseti* isolates. All the *F. avenaceum* isolates tested had a strong impact on hemp, field pea, and faba bean growth and germination (Fig. 5) but showed larger variation in their impacts on maize and oat traits: for example, isolate Fa05001 significantly differed from the other three isolates of *F. avenaceum*. All the *F. culmorum* isolates had a roughly similar effect on the tested crop species.

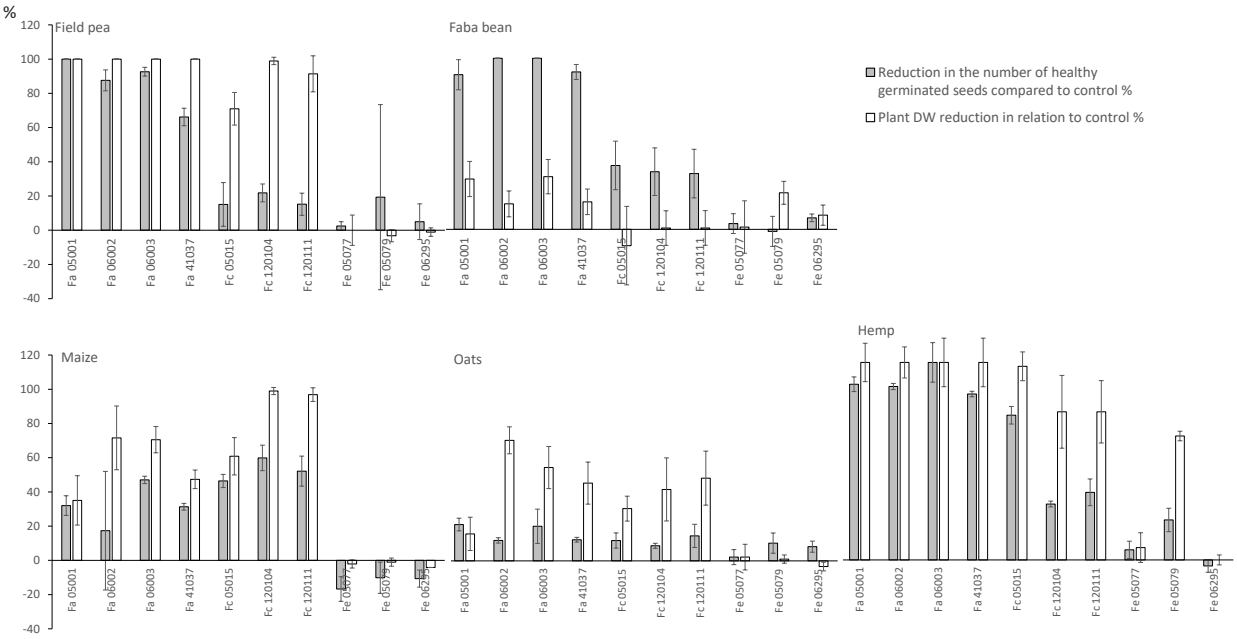

Fig. 5. Comparison of isolate aggressiveness of *F. avenaceum* (Fa), *F. culmorum* (Fc), and *F. equiseti* (Fe) isolates over five different crop species (faba bean, maize, hemp, field pea, and oat)

Discussion

The aim of this study was to better understand the risks related to mycotoxin producing *Fusarium* fungi in different field crop rotations by investigating the *Fusarium* species composition and symptom severity on different plant species in Finland on ten demofields and in greenhouse trials.

According to two years' field trials root and stem symptoms were found to be common in spring sown faba bean, field pea, and wheat, whereas oat, maize, and hemp appeared less susceptible, although they were found to harbour partly the same *Fusarium* species causing symptoms in other plants. Two *Fusarium* species (*F. avenaceum* and *F. equiseti)* were found to be highly prevalent and associated with symptom development. The most common *Fusarium* species found in Finnish cereal grains have been reported to be *F. avenaceum, F. culmorum, F. graminearum, F. poae, F. sporotrichioides*, and F. *langsethiae* (Hietaniemi et al. 2016). Interestingly, only few *F. graminearum* and no *F. langsethiae* were detected from the stem and root samples in this study, whereas the other species were common in the analysed plants. There can be several explanations for this. First of all, slowly growing *F. langsethiae* might be overgrown by other fungi before recognized. This does not however, explain the absence of *F. graminearum*. Either these species were not prevalent in the studied fields, or the conditions were not favourable for crown and root infections. Despite showing few symptoms in stems and roots many of these the species can still spread and damage flowers and grains (Divon et al. 2019, Nguyen et al. 2024). Nguyen et al. (2024) showed that different *Fusarium* species favoured different substrates in the wheat production cycle. For example, *F. poae* was only prevalent in grains, *F. avenaceum* was only found in residues, and *F. solani* only in soil, whereas *F. graminearum* was found in all of them. However, *F. graminearum*, despite being a diverse and adapting pathogen causing many kinds of symptoms in different plant tissues, is specialised mainly for heads (Walter et al. 2010, Kelly and Ward 2018).

The results from our greenhouse study show that hemp and faba bean are less susceptible to *F. graminearum* than cereals. This indicates that crop rotation has a limited impact on disease severity. However, the significant differences between the fields in the prevalence of the three most common *Fusarium* species encourage us to further study the possibilities of pathogen control caused by soil type and management practices. Kaukoranta et al. (2019) modelled the impacts of cereal intensity to oat mycotoxin accumulation in different regions of Finland, and in certain regions, they found both DON and T-2/HT-2 mycotoxins in harvested oats to increase with the number of preceding years of cereals, especially in cases where the field was not ploughed. Each *Fusarium* species likely has its own optimal growing conditions and both the local rainfall and temperatures impact as well as soil types and tillage methods may have their impacts. Within this study the methods varied between the demonstration plots and they are presented in Supplementary Table 1. The number of observations is however too small to make any conclusions from these variables.

F. oxysporum, which is globally the most common *Fusarium* pathogen associated with wilt diseases, and which infects a wide range of species (Rana et al. 2017), was detected in most fields, but usually in low frequencies. It was the dominant species only in the case of Haapamäki2 in 2023. *F. oxysporum* was not included in the greenhouse tests because it had many species-specific strains (Laurence et al. 2014). Interestingly, *F. avenaceum* was not detected from Koskenpää location in 2023. Within this study the fungal species were determined by culturing plant samples on selective medium, but this method may not show all fungal species due to competition occurring on the medium.

This is the first report of *F. equiseti* causing root rot in faba bean in Finland, although it has been shown to cause severe symptoms in a Mediterranean environment (Haddoudi et al. 2021). The results from greenhouse tests confirmed that *F. equiseti* was especially pathogenic to faba bean. The results also support the trends from field trials, where *F. culmorum* was found to be the dominant species from a field with severe symptoms. Also, in the field where maize had the most severe symptoms, the plant samples contained a high proportion of *F. culmorum*. The results of Fg05011 where this isolate reduced the germination of oat seeds clearly more than the germination of the seeds of the other studied crop species are in agreement with those of Yli-Mattila et al. (2022), according to which Finnish *F. graminearum* isolates are adapted to oats. It was interesting that *F. sporotrichioides* was not pathogenic or was only very slightly pathogenic to all crops, while in the previous studies it has been easy to inoculate *F. sporotrichioides* conidia to cereals. It is important to note that in our experiment we used one or few selected isolates per species. Having more isolates could have given a better picture from the virulence of a certain *Fusarium* species. For example, Bugingo et al. (2025) isolated more than 700 *Fusarium* isolates when they investigated the diversity and pathogenicity of seedborne *Fusarium* species affecting lentil crops in the Northern Great Plains. Large differences in virulence were detected. Interestingly, *F. equiseti* was among the most predominant species in that study but *F. sporotrichioides*, *F. graminearum*, and *F. oxysporum* were among the most virulent.

When peat and sand assays are compared it appears that the pathogens that impact on germination can be more severe on sand, e.g. *F. avenaceum* led to high germination loss in all crops, but on the other hand the one-week longer growing time in peat might actually show more symptoms developed and be better to distinguish impacts occurring in nature. E.g. *F. equiseti* did not clearly differentiate from the water control in sand assay but in peat

it had clearly higher disease index. It is, however, also good to note that due to limited resources we only had one isolate per species in peat assay whereas in the sand assay we had 1 to 4 isolates per species. Thus, the peat assay is not as representative of the species.

The results from the greenhouse tests also suggest that in some field plots the weak germination of plants could be associated with the existing micro-organisms, as *F. avenaceum* and *F. culmorum* both strongly impacted the germination ability of hemp, for example. If the plant has died soon after germination, there is no sample to be collected two months after planting. The greenhouse tests also indicate that there is variation within the *Fusarium* species, encouraging to the utilisation and comparison of the most aggressive isolates in disease management and functional pathogenicity studies.

While our study pointed out connections between symptoms and *Fusarium* fungi also other abiotic and biotic factors may have a role here. E.g. we observed that faba bean plant tissue especially was prone to acquiring a dark colour after they were extracted from the soil, probably due to phenolic compounds reacting within the tissue. Thus, assessment was done immediately after rinsing the roots. The role of other pathogens was not studied, but it can be significant in field samples. Root rots and wilts (*Aphanomyces euteiches*, *Phytophthora pisi* sp. Nov.) in pea and faba bean thrive best in wet soil (Hossain et al. 2012, Heyman et al. 2013). Meanwhile, *Fusarium* infections are more common if the early summer is hot and dry (Borgström et al. 2019), as it was during our experimental years. Pea wilting may also be solely due to soil compaction and water management issues (Grath and Håkansson 1994).

Only one cultivar was applied per crop and there is very limited information available from the cultivar resistance against these *Fusarium* species even from wheat and oats and even less from these minor crops. Thus, in further studies applying of several genotypes simultaneously would be recommendable.

Conclusions

There was clear variation in the prevalence of *Fusarium* species and the associated root and stem symptoms between the different demonstration fields and six studied crop species. Based on our results *F. culmorum, F. avenaceum* and *F. graminearum* were the three most pathogenic *Fusarium* species in causing root and stem symptoms in the studied crop species. Moreover, *F. culmorum and F. graminearum* were more pathogenic to oats and wheat whereas *F. avenaceum* was more pathogenic to legumes*. F. avenaceum* was the most commonly detected *Fusarium* pathogen in the studied soils of Central Finland. *F. equiseti* was shown to be a common fungus in the soils, causing root and stem symptoms especially in faba beans, which supports previous findings from other parts of the world. Our results suggest that crop rotation can have a limited impact on the management of *Fusarium* diseases. Better understanding especially of legume diseases caused by different *Fusarium* species is needed. In future studies we recommend sampling of different crop species, soil, crop residue, and several plant parts in order to increase our understanding of *Fusarium* fungal populations in Nordic crop production.

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