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RESEARCH ARTICLE

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Susceptibility of non-cereal crops to *Fusarium graminearum* complex and their role within cereal crop rotation as a source of inoculum for Fusarium head blight

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Abstract

Fusarium graminearum, the cause of Fusarium head blight (FHB), is an important cereal pathogen. Moreover, some non-graminaceous crops are also known to be susceptible to *F. graminearum* infection. This study assessed the presence of *F. graminearum* species complex on non-cereal plants, grown in a cereal crop rotation and evaluated its pathogenicity to non-cereal plants *in vitro* and to spring wheat under field conditions. The relative density of *Fusarium* species isolated from oilseed rape, pea, potato and sugar beet plants was assessed in 2015 and 2016. A total of 403 isolates of *Fusarium* spp. were obtained from non-cereal plants and only 5% of the isolates were identified as *F. graminearum*. The pathogenicity test revealed that isolates of *F. graminearum* from spring wheat and non-cereal plants caused discolourations on leaves of faba bean, fodder beet, oilseed rape, pea, potato and sugar beet. The pea was the crop most susceptible to *F. graminearum* isolated from spring wheat. The pathogenicity of *F. graminearum* from sugar beet, oilseed rape, pea and potato to the same hosts differed depending on isolate and inoculated plant. Under field conditions, *F. graminearum* isolates from pea, potato, oilseed rape and wild viola were able to cause typical FHB symptoms in spring wheat. Based on the information generated in this study, we conclude that under congenial conditions, growing faba bean, pea, sugar beet, fodder beet, oilseed rape and potato plants in a cereal crop rotation may serve as alternative or reservoir hosts for *F. graminearum* pathogens.

Additional keywords: *Beta vulgaris* var. *saccharifera*; *Brassica napus*; pathogenicity; *Pisum sativum*; *Solanum tuberosum*; *Viola arvensis*.

Abbreviations used: AUDPC (disease progress curve); BBCH (phenological development stage of the plant); DPI (days post inoculation); FHB (Fusarium head blight); LAA (leaf area affected); NKP (nitrogen, phosphorus and potassium); PCR (polymerase chain reaction); PDA (potato-dextrose agar medium); RD (relative density); SNA (Spezieller Nährstoffarmer agar medium).

Authors´ contributions: All authors performed the experiments. Collected the field samples: OT, SK and GK. Collected data: JK PS, SK & NR. Molecular analysis: DS & AI. Data analysis, and interpretation of the data: NR & SK. Coordinating the research project and obtaining funding: GK. Drafting and critical revision of the manuscript: NR, GK & SK.

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Introduction

Fusarium head blight (FHB) of small grain cereals, caused by *Fusarium graminearum* Schw. (teleomorph *Gibberella zeae* Schw, Petch), is a global problem. This pathogen is dominant in cereal growing areas and can cause significant losses in grain yield and quality. In infected grains, the fungus may produce various mycotoxins which are harmful to humans and animals. *F. graminearum* is the main species producing deoxynivalenol. The reduction of yield and contamination by mycotoxin makes FHB the main cereal disease (Wilcoxson *et al.*, 1992; Gonzalez *et al.*, 1999; Kumar *et al.*, 2011; Yang *et al.*, 2013; Purahong *et al.*, 2014; Vaughan *et al.*, 2016; Janaviciene *et al.*, 2018). *F. avenaceum, F. culmorum, F. poae* and some

other less significant species may also cause FHB. However, *F. graminearum* species complex is the most frequently isolated species in many cereal-growing regions (Parry *et al.*, 1995; Waalwijk *et al.*, 2003; Xu *et al.*, 2008). Over the last decades, this species has become prevalent in Northern Europe (Waalwijk *et al.*, 2003; Yli-Mattila, 2010; Nielsen *et al.*, 2012; Parikka *et al.*, 2012; Sakalauskas *et al.*, 2014; Supronienė *et al.*, 2016a,b).

The host plant residues remaining in the soil are the primary source of FHB infection. Meteorological conditions, such as frequent rainfall and high relative humidity enhance the production of inoculum on the residues and increase disease prevalence for the development of FHB epidemics (Pereyra *et al.*, 2004; Mourelos *et al.*, 2014). Extended periods of high relative humidity (≥ 90%) and warm temperatures (from 15 to 30 °C) during cereal anthesis facilitate the infection of plants (De Wolf *et al.*, 2003). Control strategies relied on breaking the disease cycle, by developing resistant host cultivars and reducing the severity of the disease through management strategies, since little can be done to manipulate the environment (Gilbert & Tekauz, 2011). The crop rotation along with non-cereals was found to reduce mycotoxin concentrations and *Fusarium* infestations in cereals (Bernhoft *et al.*, 2012).

The primary host plants of *F. graminearum* species complex include wheat, barley, rice, oats, triticale, rye, as well as maize, in which *F. graminearum* may cause ear and stalk rots. Nonetheless, the disease symptoms caused by this fungus extended and recently were found and reported in some non-graminaceous crops. *F. graminearum* is implicated as the cause of tap-root and yellowing of sugar beet, root and seedling roots of soybean and dry rot of potato in the USA, and in root rot of pea in Canada (Ali *et al.*, 2005; Hanson, 2006; Broders *et al.*, 2007; Burlakoti *et al.*, 2008; Bilgi *et al.*, 2011). The fungus has also been isolated from several symptomless weeds (Pereyra & Dill-Macky, 2008; Mourelos *et al.*, 2014). The observations of alternative hosts of *F. graminearum* have epidemiological implications in the persistence, spread and management of *F. graminearum* in cereals and non-cereal plants, considering they are frequently grown in crop rotation. Burlakoti *et al.* (2008) demonstrated substantial genetic exchange among populations of *G. zeae* across cereal and non-cereal hosts and across wheat cultivars. The genetic similarity among populations of *F. graminearum* from barley, wheat, potato and sugar beet could be part of a large overall population. Also, *F. graminearum* isolates from potato and sugar beet can induce additional FHB symptoms in wheat and produce different mycotoxins in wheat spikes and rice grain (Burlakoti *et al.*, 2008; Christ *et al.*, 2011).

Formerly, FHB used to pose minimal threat to cereals in Lithuania. An outbreak of this disease was observed only in 2012, and since then it has persisted as a severe problem (Mankevičienė *et al.*, 2014; Supronienė *et al.*, 2016a,b). Then, given that in Lithuania *F. graminearum* is a comparatively new pathogen in cereals, the ecological and epidemiological factors that play an essential role in the adaptation and survival of this fungus in the cropping systems are not yet well-defined. Variation between *F. graminearum* isolate aggressiveness has been observed (Purahong *et al.*, 2014; Vaughan *et al.*, 2016).

Therefore, in the current study, we focused on the survival of *F. graminearum* in cereal crop rotations during the years when cereals are not grown. The present study assesses the presence of *F. graminearum* species complex on non-cereal plants in the field. It also evaluates the pathogenicity of this fungus to non-cereal plants *in vitro* and to spring wheat under field conditions.

Material and methods

Field description and study site

The research was conducted from 2015 to 2018 at the Institute of Agriculture, Lithuanian Research Centre for Agriculture and Forestry, in the Central part of Lithuania (55°23′50″N; 23°51′40″E). The presence of *Fusarium* spp. was assessed in pea, potato, rapeseed and sugar beet, grown in four subsequent cereal crop rotations established in two trials in 2015 and 2016 (Table 1).

The soil in all fields is *Endocalcari-Epihypogleyic Cambisol*, according to the world reference base for soil resources (WRB) classification (IUSS Working Group WRB, 2015). Soil characteristics are presented in Table 2. All fields were conventionally tilled, and crops were managed based on the common agronomic practices and individual needs (*e.g.*, weed species, insect and disease occurrence).

Plant sampling, *Fusarium* spp. isolation and identification

Fifty plants per field were randomly collected in August of 2015 and 2016. The plants were taken to the laboratory, identified and processed. All the plants were visually symptomless of *Fusarium* spp. infection. The samples were thoroughly washed under running tap water, dried on paper towels at 20±2 ºC temperature and numbered. Then plants were divided into several segments: root, crown, stem and leaf. Samples of each

Table 1. Crop rotations (I, II, III and IV) and fields (A, B) selected for plant sampling.

	I-A	I-B	II-A	II-B	III-A	III-B	IV-A	IV-B
2013	S-Wheat	S-Rape	W-Wheat	Pea	Pea	S-Barley	W-Wheat	W-Wheat
2014	S-Barley	S-Wheat	S-Barley	W-Wheat	W-Wheat	Pea	Maize	W-Wheat
2015	Pea	S-Barley	S-Rape	S-Barley	Sugar beet	W-Wheat	Potato	Maize
2016	W-Wheat	Pea	S-Wheat	S-Rape	S-Wheat	Sugar beet	S-Barley	Potato
2017	S-Barley	W-Wheat	S-Barley	S-Wheat	S-Barley	S-Wheat	W-Wheat	S-Barley
2018	S-Rape	S-Barley	Pea	S-Barley	Pea	S-Barley	W-Rape	W-Wheat

S, spring; W, winter. Grey background: Sampled fields.

Table 2. Soil characteristics of experimental fields.

	I-A	I-B	II-A	II-B	III-A	III-B	IV-A	IV-B
Soil texture	Loam	Loam	Loam	Loam	Loam	Loam	Loam	Loam
Sand, %	51	52	46	43	48	47	43	52
Silt, %	36	36	33	38	35	35	41	35
Clay, %	13	12	21	19	17	18	16	14
Humus, %	1.3	1.4	2.2	2.1	1.9	2.2	3.0	2.6
pH_{KCL}	6.5	6.3	7.0	6.9	6.8	6.9	7.1	6.8
P_2O_5, mg/kg	142	211	225	153	304	195	237	140
K_2O, mg/kg	179	197	224	154	233	172	152	236

plant were cut to approx. 1.0 cm size, surface-sterilised in 2% NaClO for 3 min, rinsed three times in sterile distilled water and left to dry on sterile filter paper for 30 min. Three different plant part segments were placed on potato-dextrose agar (PDA) supplemented with 50 mg/L chloramphenicol and incubated for 2-4 days at 22 ± 2ºC in the dark. The chloramphenicol permits the formation of distinctive colonies of *F. graminearum* (Andrews & Pitt, 1986). *Fusarium* colonies isolated on PDA were transferred after 3-5 days on to Spezieller Nährstoffarmer Agar (SNA) (Nirenberg, 1976), and incubated under the same conditions until the formation of a macro-conidial mass.

Spore suspensions of each isolate were spread onto 2% water agar, from which single-spore isolates were picked and subcultured on PDA and SNA. *Fusarium* spp. were identified as described by Leslie & Summerell (2006). Colonies showing identical features and isolated from the same plant were considered to be a single isolate. The relative density (RD) of the *Fusarium* species complex (expressed as percentage of species among isolates from the same genera) on non-cereal plants was calculated as follows (Gonzalez *et al.*, 1999):

$$RD = \frac{\text{No. of fungal isolates of a species}}{\text{Total no. of species isolated}} \times 100$$

F. graminearum was re-isolated from the infected tissue to confirm infection. All isolates used in this study were morphologically identified as *F. graminearum* and verified by species-specific PCR, using the protocol suggested by Demeke *et al.* (2005) and the primer pairs Fg16F (CTCCGGATATGTTGCGTCAA) and Fg16R (GGTAGGTATCCGACATGGCAA) suggested by Nicholson *et al.* (1998). Using a variable number of tandem repeat (VNTR) markers (Suga *et al.*, 2004), it was estimated that three *F. graminearum* isolates, 159L, 153S and 153P from wild viola (Table 3), were genetically distinct (Sneideris *et al.*, 2018).

F. graminearum isolates

The isolates identified as *F. graminearum* were randomly selected for pathogenicity tests to non-cereal plants. Table 3 shows that for *in vitro* tests the 17 isolates selected were: 3 from wild viola (*Viola arvensis*), sugar beet (*Beta vulgaris* var. *saccharifera*), and pea (*Pisum sativum* L.); and 4 from both oilseed rape (*Brassica napus* L.) and potato (*Solanum tuberosum* L.). For field experiments the 23 isolates randomly selected were: 3 from winter wheat (*Triticum aestivum* L.), spring wheat, spring barley, wild viola, and oilseed rape; and 4 from both potato and pea.

Before the pathogenicity tests, *F. graminearum* isolates were cultured on PDA at 25 ± 2ºC for 7 days in the dark. For field spring wheat inoculation, *F. graminearum* isolates were grown on SNA medium at 25 ± 2°C for 7 days. Spores were washed by adding 10 mL of sterile distilled water to each 9-mm Petri dish. The concentration of spores in the suspension was counted using a *Neubauer* cell counting

Table 3. The origin of isolates of *Fusarium graminearum* used for pathogenicity tests.

No.	Isolate code	Host	Plant part from which the isolate was obtained	Year of isolation
For pathogenicity *in vitro*				
1	4vkv4	Spring wheat	Head	2016
2	153 P	Wild viola	Crown	2015
3	153 S	Wild viola	Stem	2015
4	153 L	Wild viola	Leaf	2015
5	C4	Sugar beet	Leaf	2017
6	C8	Sugar beet	Leaf	2017
7	C1	Sugar beet	Leaf	2017
8	R2	Winter oilseed rape	Leaf	2017
9	R1	Winter oilseed rape	Leaf	2017
10	R3	Winter oilseed rape	Leaf	2017
11	R4	Winter oilseed rape	Leaf	2017
12	B42	Potato	Steam	2015
13	B41	Potato	Tuber	2015
14	B40	Potato	Tuber	2015
15	B43	Potato	Tuber	2015
16	Z38	Pea	Crown	2015
17	Z39	Pea	Steam	2015
18	Z36	Pea	Steam	2015
For pathogenicity in field				
1	425 L	Winter oilseed rape	Leaf	2015
2	98 P	Winter oilseed rape	Crown	2015
3	6rsL	Winter oilseed rape	Root	2015
4	Z36	Pea	Stem	2015
5	Z37	Pea	Crown	2015
6	Z38	Pea	Crown	2015
7	Z39	Pea	Stem	2015
8	B40	Potato	Tuber	2015
9	B41	Potato	Tuber	2015
10	B42	Potato	Steam	2015
11	B43	Potato	Tuber	2015
12	K2.1	Winter wheat	Head	2016
13	K3.2	Winter wheat	Head	2016
14	K1.1	Winter wheat	Head	2016
15	K4.1	Spring wheat	Head	2016
16	K5.1	Spring wheat	Head	2016
17	K5.46	Spring wheat	Head	2016
18	M6.1	Spring barley	Head	2016
19	M6.2	Spring barley	Head	2016
20	M6.3	Spring barley	Head	2016
21	153 L	Wild viola	Leaf	2015
22	153 P	Wild viola	Crown	2015
23	541 S	Wild viola	Stem	2015

chamber. The spore concentration was adjusted to 1.0×10^5 spores/mL.

Host range

The pathogenicity of *F. graminearum* was tested on the following crop plants: faba bean (*Vicia faba* L.), pea, oilseed rape, sugar beet, potato and fodder beet (*Beta vulgaris* L. subsp. *vulgaris* var. *crassa*). Plant seeds (or potato bulbs ~2.0 cm Ø) were planted in plastic pots (Ø 10 cm) filled with a soil mix having a pH of 5.0-7.0 with 14-16-18 nitrogen, phosphorus and potassium (NKP) (Durpeta, Lithuania). One seed (or tuber) per pot was sown at 2-3 cm depth. The pots were arranged in racks in a randomised complete block design with three replicates and placed in a growth chamber at 20/16°C day/night temperature and 16-h photoperiod. Fluorescent tubes (Luxline Plus, 840 Cool White) provided light in the growth chamber (Climacell 707, MMM Medcenter Einrichtungen GmbH). The pots were watered with distilled water three times per week until the end of the experiment.

In vitro inoculation

Pathogenicity tests were conducted in three separate experiments: i) inoculation of non-cereal host plant leaves with *F. graminearum* from spring wheat (4vkv4); ii) inoculation of non-cereal host plant leaves with *F. graminearum* from wild viola (153S, 153L and 153C) and iii) inoculation of non-cereal (sugar beet, oilseed rape, pea, potato) host plant leaves with *F. graminearum* from same non-cereal hosts (C4, C8, C1; R2, R1, R3, R4, B42, B41, B40, B43, Z38, Z39 and Z36). All experiments were conducted in a growth chamber. Each experiment was repeated twice.

The plants were inoculated without wounding the leaf using the agar plug technique, within 2-4 weeks after planting, at the 12–13 phenological development stage of the plant (BBCH) (Gargouri-Kammoun *et al.*, 2009). Two leaves were inoculated per plant with an agar plug (0.5 cm Ø) with mycelium, cut from the periphery of 7-day-old cultures. Five seedlings of each tested plant were inoculated with each *F. graminearum* isolate, in three replicates (total 15 plants per treatment). Control plants were not inoculated. Each plant was covered with a transparent plastic container. Plastic containers were removed 72 h after inoculation.

Evaluation of pathogenicity tests

Disease severity of each inoculated plant leaf was assessed 14 days post-inoculation (DPI) by calculating the percentage of leaf area affected (LAA): 1) 0% = no infection or no necrotic areas, 2) 5%, 3) 10%, 4) 25%, 5) 50% or more spots are present on the leaf (EPPO, 2002). Re-isolations of the pathogen were made from infected leaf tissue, to confirm infection by *F. graminearum*.

Field inoculation

For the inoculation of spring wheat cv. 'Triso' (moderately resistant to FHB) we selected 14 isolates (Table 3) of *F. graminearum* obtained from non-cereal crops: 3 isolates from oilseed rape and wild viola, 4 isolates from pea and potato; and 9 isolates from cereal crops (3 isolates from each spring wheat, winter wheat and spring barley) as positive controls. For the pathogenicity, spring wheat was grown in the crop rotation II-B after spring oilseed rape (Table 1). The floret of winter wheat was inoculated by injecting conidial suspension with an automatic pipette. Twenty microliters (10 µL/floret) of each isolate conidial suspension or sterile distilled water (negative control), were injected into two adjacent florets in the center of the spike (without wounding) at the middle of anthesis. The heads were covered to the entire spike with a polyethene bag (Fig. 1E) for 120 h to ensure constant high humidity (Purahong *et al.*, 2014). Each treatment consisted of 20 inoculated plants (5 plants × 4 replications).

Fusarium head blight evaluation

The FHB severity of each inoculated wheat head was evaluated after 7 (BBCH 69-71), 14 (BBCH 73) and 21 (BBCH 73-75) DPI according to the scale proposed by Engle *et al.* (2003). The FHB severity was used to calculate the disease progress curve (AUDPC): $AUDPC=\Sigma\ [(Y_{i+1} + Y_i) / 2]\ [t_i + 1 - t_i]$, where Y_i is FHB disease severity (%) at the *i*th observation and t_i are days of the *i*th observation (Madden *et al.*, 2007).

Statistical analysis

The data were analysed with the software ANOVA, from the package SELEKCIJA (Raudonius, 2017). Before further analyses, one-way ANOVA was performed to determine if trials could be combined. The means were compared by LSD multiple range tests at the probability level of $p>0.05$.

Results

A total of 403 isolates of *Fusarium* spp. were isolated from non-cereal plants: 184 in 2015 and 219 in 2016.

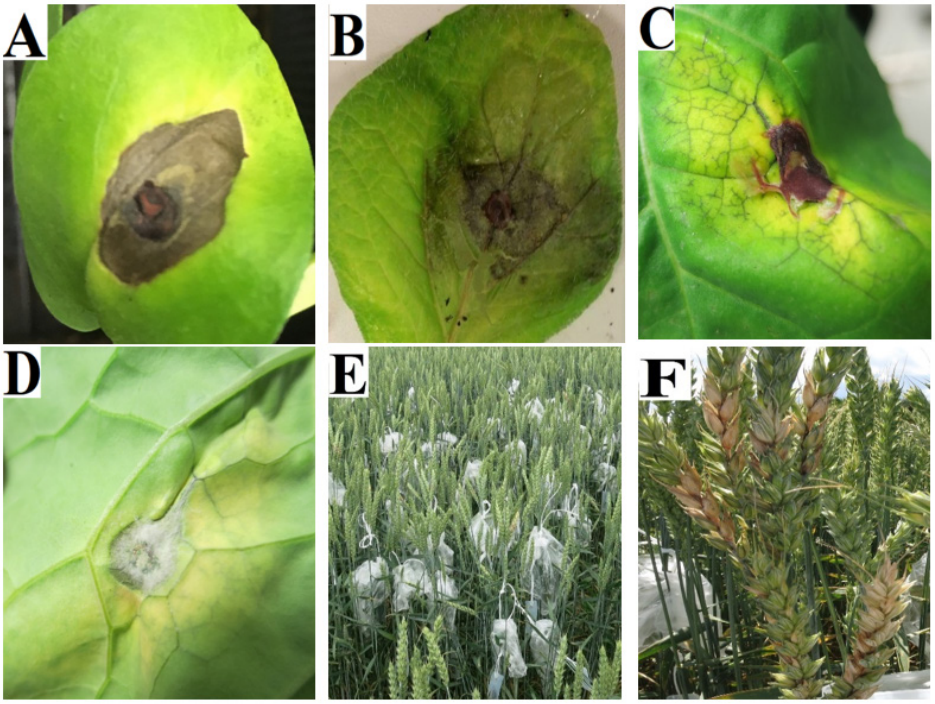

Figure 1. Symptoms of leaf discolorations caused by *F. graminearum* inoculation. A-D, agar plug inoculation and incubation at 20/16 °C day/night temperature and 16-h photoperiod in the growth chamber. E-F, conidial suspension injection to florets in the center of the spike. A, faba bean (7 days post-inoculation (DPI)); B, potato 7 DPI; C, D, oilseed rape 4 DPI (front and back sides, respectively); E, inoculated florets; and F, FHB symptoms in infected wheat 21 DPI.

The proportion of *Fusarium* spp. isolated from non-cereal plants is presented in Table 4. All FHB-associated *Fusarium* species were isolated in both experimental years. The prevalence of *F. graminearum* and other *Fusarium* spp. varied, depending on the year and plant species. The RD of *F. graminearum* ranged between 0 and 1.7%. In 2015, *F. graminearum* was detected only in pea (0.5%) and sugar beet (1.7%) plants, while in 2016, it was found in all the crop rotation plant species. *F. graminearum* RD ranged from 0.5 to 3.7%. The highest RD (3.7%) was on potato and the lowest (0.5%) on pea and sugar beet. The RD of *F. graminearum* species complex was relatively low compared with other *Fusarium* species. In *Fusarium* spp. RD ranged from 19.6 to 38.5% in 2015 and from 16.4 to 28.3% in 2016.

The pathogenicity of *F. graminearum* species complex isolates to non-cereal plants, which are usually grown in crop rotation with cereal crops in Lithuania, was evaluated. All *in vitro* tested *F. graminearum* isolates exhibited discolouration on leaves of all plant species. At the inoculation, pinpoint lesions first appeared and enlarged brown to dark brown necrotic lesions, which, in some instances, were surrounded by a yellow chlorotic or water-soaked area (Fig. 1A-D). In all cases after re-isolation, they were morphologically confirmed as *F. graminearum*. Negative control plants did not show any disease symptoms.

The pathogenicity of *F. graminearum* isolate 4vkv4 from spring wheat was tested to evaluate its

Table 4. Relative density of *Fusarium* species on non-cereal plants in 2015 and 2016.

Non-cereal plants	*F. graminearum*	Other *Fusarium* species	Total
	2015		
Pea	0.6	19.6	20.1
Oilseed rape	0	38.5	38.5
Sugar beet	1.7	19.0	20.7
Potato	0	20.7	20.7
Total	2.2	97.8	100
	2016		
Pea	0.5	23.7	24.2
Oilseed rape	0.9	28.3	29.2
Sugar beet	0.5	16.0	16.4
Potato	3.7	26.5	30.1
Total	5.5	94.5	100

pathogenicity on non-cereal crops (Table 3). Disease severity on non-cereal plants ranged from 36.5% up to 96.9% (on average 77.0%). Pea (96.9%), fodder beet (92.5%) and faba bean (89.3%) were more susceptible to *F. graminearum* 4vkv4 infection than sugar beet (69.8%) and oilseed rape (36.5%) (Fig. 2).

F. graminearum isolates from wild viola (153S, 153L and 153C) differed in their pathogenicity to non-cereal plants. Isolate from the stem (153S) showed less infection (on average 8.1%) in pea, sugar beet and fodder beet, compared to isolates from the crown (153P, on average 17.0%) and leaf (153L, on average 13.7%) (Table 5). Contrary to the first experiment, the oilseed rape was the most susceptible to all wild viola isolates, while pea (on average 2.8%) and sugar beet (on average 6.1%) were least susceptible.

The pathogenicity of *F. graminearum* isolates from sugar beet, oilseed rape, pea and potato were evaluated in the same host plants. The 14 isolates caused similar *F. graminearum* symptoms on leaves and showed differences in disease severity and behaved differently on different host plants (Table 6). Disease severity on potato plants ranged from 16.5% up to 78.3% (on average 46.1%). The average disease severity on potato as host plant among *F. graminearum* isolates recovered from the same host was: potato 46.8%, pea 28.4%, sugar beet 44.8% and oilseed rape 59.6%. The isolates most pathogenic on potato plants (78.3%) were two *F. graminearum* from oilseed rape (R2 and R3). The pathogenicity test on pea showed that the most pathogenic (82.0%) isolate was R2, from oilseed rape (Fig. 1C), but the least pathogenic one (42.2%) was R1, another oilseed rape isolate. Disease severity on pea plants ranged from 42.2% up to 82.0% (on average 62.8%). The average disease severity in pea plants was recovered from potato (57.2%), pea (68.6%), sugar beet (64.7%) and oilseed rape (62.7%). The highest disease severity differences on pea (from 12.5% to 76.0%) were observed in *F. graminearum* isolates from sugar beet.

The average disease severity in sugar beet plants among *F. graminearum* isolates was 55.7% from oilseed rape, 55.8% from pea, 73.7% from sugar beet and 37.3% from potato. Disease severity on inoculated sugar beet plant ranged from 12.5% up to 76.0% (average of 54.3%).

The disease severity on oilseed rape plants among *F. graminearum* isolates was 34.3% from potato, 35.7% from pea, 25.2% from sugar beet and 44.5% from oilseed rape. Disease severity on oilseed rape plants ranged from 16.8% up to 58.5% (average 35.6%). *F. graminearum* pathogenicity tests indicated that all isolates were able to cause *F. graminearum* infection on all plant hosts but differed among the plant species (Table 6). The most pathogenic on potato and oilseed rape plants were isolates recovered from oilseed rape. However, pea and sugar beet plants were most susceptible to isolates from the same host (from pea and sugar beet).

The pathogenicity of *F. graminearum* isolates to spring wheat cereal was tested in the field (Table 7). All the 23 *F. graminearum* isolates were able to cause typical FHB symptoms in spring wheat. The infected florets were observed during the first evaluation at BBCH 69-71 (Fig. 1F). Data in Table 7 show that

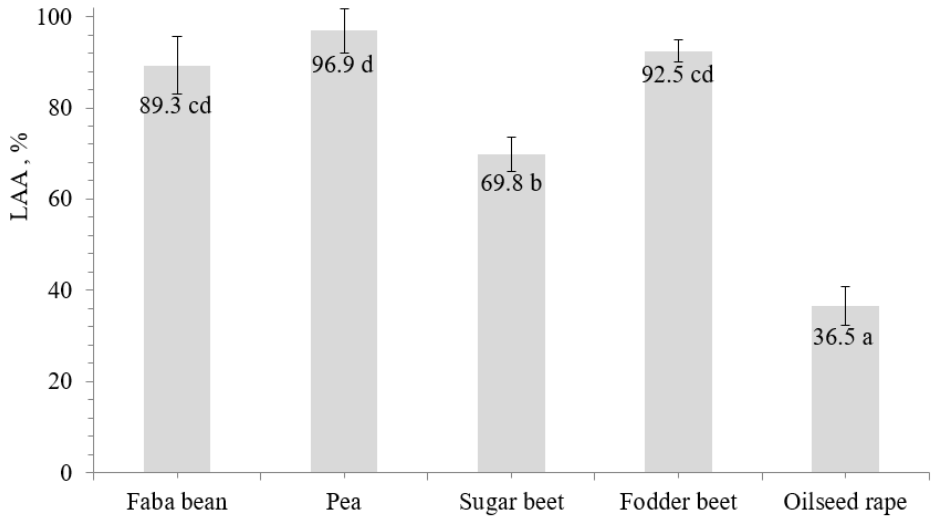

Figure 2. Disease severity expressed as a percentage of leaf area affected (LAA) in non-cereal plants inoculated with *F. graminearum* isolate 4vkv4 from cereal. Means followed by the same letter are not significantly different in each experiment (p>0.05).

Table 5. Percentage of leaf area affected (LAA) in non-cereal plants, inoculated with *Fusarium graminearum* isolates 153S, 153L and 153C recovered from *Viola arvensis*.

Crop (factor A)	*F. graminearum* isolate (factor B)			Average A (p=0.001)
	153S	153P	153L	
Faba bean	15.4±3.71	5.6±0.94	10.9±2.98	10.7
Pea	2.5±0.78	2.8±0.81	3.3±0.92	2.8*
Sugar beet	3.5±0.92	1.1±0.63	13.8±3.88	6.1*
Fodder beet	3.8±0.40	22.9±6.57	14.9±4.77	13.9
Oilseed rape	20.3±4.13	45.3±7.31	24.6±4.50	30.0**
Potato	10.5±2.71	13.0±3.84	12.1±3.10	11.8
Average B (p=0.045)	8.1*	17.0	13.7	12.9

*,**: statistically significant difference at p<0.05 and p<0.01, respectively. Data are presented as the mean of two trials having similar variance.

all isolates under field conditions were pathogenic to spring wheat cultivar 'Triso'. No symptoms of FHB infection were detected in the negative control. The range of *F. graminearum* severity among the isolates causing FHB to spring wheat varied between isolates. The FHB severity ranged from 0% to 10.4% (average of 2.3%) (Table 7). AUDPC ranged from 92.0% to 264.0%. Isolate Z37 from pea caused the least disease severity and had the lowest AUDPC compared to the other isolates used in the present study. The highest FHB severity differences (from 4.0% to 10.4%, average of 6.4%) were observed among potato isolates. The most pathogenic isolate was B41 from potato. In general, all the isolates were pathogenic and caused FHB symptoms (Fig. 1F). These results suggest that *F. graminearum* isolates from different host plants cause FHB but differ in disease severity.

Discussion

For a better understanding of *F. graminearum*, associated diseases in cereal and non-cereal crops were investigated. Our study demonstrated that the main FHB-associated *Fusarium* species occurred in the internal tissue of spring oilseed rape, pea, sugar beet and potato plants without causing visible symptoms of *Fusarium* spp. infection. Our results indicate that 2015-2016 was not favourable for *F. graminearum* development, but despite *F. graminearum* being the least frequently detected species, it was able to survive on all non-cereal species tested. Results show that the RD of *F. graminearum* was low in comparison with other *Fusarium* species, but despite climate change, the distribution and pathogenicity may change. Our findings illustrate that *F. graminearum* and other *Fusarium* fungi may persist in the plants mentioned above, but the lack of symptoms observed on plants suggest that the infection of these hosts by *Fusarium* species may be endophytic. This finding contrast with Ali *et al.* (2005) and Hanson (2006), who found that *F. graminearum* might cause distinct disease symptoms in sugar beet and potato. The FHB-related *F. graminearum* population is relatively 'new' in Lithuanian fields because the first outbreak of this pathogen was observed in 2012 and, hence, the pathogen may require more time to adapt to the new

Table 6. Disease severity expressed as a percentage of leaf area affected (means ± standard errors) in pea, sugar beet, oilseed rape and potato plants inoculated with *Fusarium graminearum* recovered from the same hosts.

Host	Isolate	Inoculated plant							
		Potato		O. rape		S. Sugar beet		Pea	
Sugar beet	C4	74.2±7.4	fgh	38.3±10.5	abcde	70.3±7.2	efg	52.2±9.2	abc
Sugar beet	C8	20.0±8.6	ab	16.8±6.6	a	74.7±5.9	fg	65.8±8.4	abcde
Sugar beet	C1	40.2±10.5	abcde	20.5±8.4	a	76.0±4.4	g	76.2±8.7	bcde
Oilseed rape	R1	26.3±8.1	abcd	47.3±11.2	bcde	73.7±5.1	fg	42.2±9.6	a
Oilseed rape	R2	78.3±8.0	h	25.5±8.3	ab	50.8±5.6	cde	82.0±6.5	e
Oilseed rape	R3	78.3±7.1	gh	58.5±8.5	e	25.0±6.6	ab	55.5±7.8	abcde
Oilseed rape	R4	55.5±10.6	efgh	47.2±9.6	bcde	73.2±4.8	fg	71.2±10.3	bcde
Pea	Z38	47.3±8.7	cdef	28.8±7.0	abc	38.0±8.7	bc	75.7±9.6	bcde
Pea	Z39	21.5±7.9	abc	25.3±8.6	ab	62.3±6.0	defg	79.3±8.6	cde
Pea	Z36	16.5±6.2	a	53.0±9.8	cde	67.0±6.6	defg	50.7±10.3	ab
Potato	B42	41.7±8.6	bcde	27.0±6.8	abc	50.3±5.6	cd	42.8±7.4	a
Potato	B40	48.2±10.9	def	28.7±7.5	abc	58.0±9.7	defg	70.2±9.5	bcde
Potato	B41	47.8±10.0	def	28.5±5.5	abc	12.5±3.7	a	51.0±10.2	ab
Potato	B43	49.7±9.1	defgh	53.0±9.7	cde	28.5±5.3	ab	64.8±9.7	abcde

*Means followed by the same letter are not significantly different in each experiment (p>0.05 and 0.01).

Table 7. The pathogenicity (means ± standard errors) of *Fusarium graminearum* isolates from non-cereal and cereal hosts to spring wheat, 2017.

Host	Isolate	FHB severity, %						AUDPC
		BBCH 69-71		BBCH 73		BBCH 73-75		
O. rape	425 L	0.1±0.1	abcde	1.9±0.3	abc	5.0±0.8	abcde	168.0
O. rape	98 P	0±0.1	abc	1.9±0.6	abc	3.9±0.4	ab	128.0
O. rape	6rsL	0.2±0.1	abcde	1.9±0.6	abc	3.7±1.8	ab	133.3
Pea	Z36	0.1±0.1	abcde	1.9±0.3	abc	5.9±0.9	abcde	189.3
Pea	Z37	0±0.0	a	1.3±0.3	ab	2.0±0.5	a	92.0
Pea	Z38	0.3±0.2	bcde	2.5±0.7	bcde	5.3±0.7	abcde	178.7
Pea	Z39	0.0±0.1	ab	1.3±0.2	ab	3.5±1.4	ab	106.7
Potato	B40	0.2±0.1	abcde	1.8±0.6	abc	5.7±1.5	abcde	133.3
Potato	B41	0.1±0.1	abc	1.9±0.4	abc	9.9±2.3	e	264.0
Potato	B42	0.2±0.1	abcde	3.9±0.5	e	9.6±2.9	cde	230.7
Potato	B43	0.0±0.0	a	1.1±0.4	ab	3.5±1.1	ab	125.3
W. wheat	K2.1	0.1±0.1	abc	1.2±0.2	ab	4.4±0.4	ab	142.7
W. wheat	K3.2	0.0±0.0	a	1.7±0.5	abc	4.5±1.3	abc	172.5
W. wheat	K1.1	0.1±0.1	abc	1.3±0.5	ab	3.9±1.0	ab	129.3
S. wheat	K4.1	0.1±0.1	abc	2.0±0.5	abc	4.8±1.3	abc	140.0
S. wheat	K5.1	0.1±0.1	abcde	3.2±0.7	cde	7.1±0.6	bcde	236.0
S. wheat	K5.46	0.1±0.1	abc	1.0±0.2	ab	3.6±0.8	ab	125.3
S. barley	M6.1	0.1±0.1	abc	1.0±0.4	ab	6.0±3.4	abcde	166.7
S. barley	M6.2	0.2±0.1	abcde	1.9±0.8	abc	5.0±1.9	abcde	173.3
S. barley	M6.3	0.1±0.1	abc	0.8±0.1	a	2.8±0.6	ab	104.0
Wild viola	153 L	0.2±0.1	abcde	1.1±0.5	ab	3.7±1.0	ab	120.0
Wild viola	153 P	0.4±0.2	e	1.2±0.6	ab	5.1±0.7	abcde	148.0
Wild viola	541 S	0.4±0.2	cde	3.4±1.3	cde	6.1±1.7	abcde	165.3

***** Means followed by the same letter are not significantly different in each experiment (p>0.05 and 0.01).

environment. However, contrary to this presumption, Harris *et al.* (2016) demonstrated the genomic flexibility of *F. graminearum* to adapt to a range of hosts. Therefore, our observations are more likely due to the relatively low amount of *F. graminearum* inoculum in the studied fields and insufficiently favourable environmental conditions for severe infections in non-cereal crops. Moreover, the *in vitro* tests of our study proved that under controlled condition all *F. graminearum* isolates from asymptomatic oilseed rape, pea, sugar beet and potato were able to cause disease symptoms not only on the primary host plants but also on the other non-cereal plants tested as well on wheat in the field.

The isolates of *F. graminearum* used in this study were found variable in their pathogenicity. The pathogenicity tests, conducted under controlled conditions, confirmed that isolates of *F. graminearum*, regardless of the plant from which they had been recovered (spring wheat, sugar beet, oilseed rape, pea, potato or wild viola), were able to infect faba bean, pea, sugar beet, fodder beet, oilseed rape and potato plants. The disease severity in inoculated non-cereal plants, both within isolates and host plants, varied considerably. These findings concur with previously published data (Chongo *et al.*, 2001; Burlakoti *et al.*, 2007; Pereyra & Dill-Macky, 2008; Ilic *et al.*, 2012). The capability of *F. graminearum* isolates from FHB-infected spring wheat heads and isolates from the wild viola, oilseed rape, pea, sugar beet and potato cause necrotic and chlorotic lesions on non-cereal plant leaves, confirms that this fungus is a broad host-pathogen.

Previously *F. graminearum* isolated from non-cereals was considered as residue saprophyte than a pathogen (Chongo *et al.*, 2001; Vaughan *et al.*, 2016). The present study demonstrates an ability of *F.*

graminearum isolates from non-cereal to cause FHB in cereals. A limitation of our data is that the isolates were tested only on a single spring wheat cultivar, but the experiment was conducted with a sufficient number of replicates. Our data indicate that all tested *F. graminearum* isolates were able to cause typical FHB symptoms under field conditions in spring wheat. Other researchers support this presumption, showing that *F. graminearum* isolates from potato, sugar beet (Burlakoti *et al.*, 2007; Christ *et al.*, 2011), sunflower, graminaceous weeds (Pereyra & Dill-Macky, 2008) and non-graminaceous weeds (Ilic *et al.*, 2012) could induce the typical FHB symptoms in wheat.

The host still plays an essential role in disease development, but climate changes accompanied by biological and genetic modifications can alter cereal susceptibility to infection and cereal-*Fusarium* interactions (Vaughan *et al.*, 2016).

Based on the information generated in this study, we conclude that under congenial conditions, growing faba bean, pea, sugar beet, fodder beet, oilseed rape and potato plants in a cereal crop rotation may serve as alternative or reservoir hosts for *F. graminearum* pathogens. The *in vitro* pathogenicity test results revealed that all isolates of *F. graminearum* complex from spring wheat and non-cereal plants caused discolourations on leaves of faba bean, fodder beet, oilseed rape, pea, potato and sugar beet. Disease severity varied considerably among the isolates and host plants. Under field conditions, *F. graminearum* complex isolates from pea, potato, oilseed rape and wild viola were able to cause typical FHB symptoms in spring wheat. Considering the relatively low relative density of *F. graminearum* in spring rape, pea, sugar beet and potato plants in the fields, we assume that these crops are still safe to grow in cereal rotations in Lithuania. However, bearing in mind the overall information of this study and the findings obtained in other countries, we must continue to remain vigilant. Our research was focused only on *F. graminearum*, but as several *Fusarium* species may also cause FHB, it would be important to evaluate other FHB associated pathogens.

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