Fusarium spp. Causing Ear Rot and Stalk Rot of Forage Corn and Their Characteristics in Japan

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Abstract

Ear rot and stalk rot are among the most hazardous diseases of corn due to their toxicity to livestock. Fusarium spp., causing ear rot, were isolated from forage corn kernels in ten Japanese prefectures. Through morphological and molecular analysis of the translation elongation factor 1α (TEF) gene, 41 isolates were identified as F. verticillioides, 36 as F. proliferatum, 27 as F. fujikuroi, 3 as F. graminearum, 2 as F. concentricum, and 2 as F. miscanthi. F. verticillioides, F. proliferatum, and F. fujikuroi produced fumonisin (FUM); F. graminearum produced deoxynivalenol (DON); F. concentricum and F. miscanthi did not produce either mycotoxin. Piercing inoculations of female ears using cultured toothpicks containing these isolates revealed that F. proliferatum, F. fujikuroi, and F. concentricum were highly pathogenic, whereas F. miscanthi showed weak pathogenicity. FUM-producing species, such as F. verticillioides, F. proliferatum, and F. fujikuroi, are believed to be the major fungi causing ear rot in Japan. F. graminearum was isolated from corn with stalk rot symptoms and showed distinct pathogenicity.

Discipline: Agricultural Environment

Additional key words: deoxynivalenol, fumonisin, geographical distribution, genetic phylogeny

Introduction

Corn is the primary forage crop in Japan, predominantly used for whole-crop silage or grain production to feed livestock. Various diseases significantly impact forage corn in Japan (PSJ 2024). Ear rot caused by the Fusarium graminearum species complex (FGSC) (Amarasinghe et al. 2019) and the F. fujikuroi species complex (FFSC) (Armer et al. 2024) is a critical issue affecting corn production in Japan due to mycotoxin contamination in kernels. The members of FGSC produce trichothecene mycotoxins, such as deoxynivalenol (DON) and nivalenol (Amarasinghe et al. 2019), while those of FFSC produce fumonisin (FUM). Both of these pose health risks when consumed by livestock. Furthermore, with the recent increase in the international price of corn kernels for animal feed, there has been a significant increase in the use of forage corn for kernel production in Japan, making ear rot, a disease of the kernels, a critical concern.

Corn ear rot initially appears as a white to pale red

or salmon flesh-colored mold on the kernels, which gradually transforms into purple-black, causing rot in both kernels and the cob (Nishihara 1959). The fungus often spreads from exposed bracts at the ear tip or from insect-damaged parts. The disease is widespread throughout Japan, and ear rot and damage are severe during serious outbreaks. In the early 20th century, Gibberella moniliformis and G. zeae were reported as pathogens (PSJ 2024) that are now considered species complexes in the current classification system. Recently, F. verticillioides (Saccardo) Nirenberg (Okabe 2010) and F. asiaticum O'Donnell, T. Aoki, Kistler & Geiser (Kawakami et al. 2015) were reported as pathogens; however, other members of the species complexes were thought to be involved in the outbreak of the disease because of the variety of symptoms. In this study, we collected ear rot-affected forage corn from various regions of Japan to identify the pathogen species and to assess their mycotoxin production and virulence in corn. Fusarium spp. have also been isolated from forage corn with stalk rot, and similar studies have been conducted.

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Materials and methods

1. Collection of the isolates

Fusarium spp. were obtained from diseased samples collected from ten prefectures north of the Kanto district and Kumamoto prefecture in the Kyushu district, southern Japan, between July and October of 2009 to 2015 (Table 1; Fig. 1A). Corn kernels displaying reddish or brownish rot were subjected to a series of treatments: soaked in 70% ethanol for 1 min, followed by 1% sodium hypochlorite for 2 min, washed twice with sterile water, and then placed on 1.5% water agar. The samples were irradiated under near-ultraviolet light (BLB fluorescent bulb, FL20S-BLB, Toshiba, Japan) for three days with a 12 h photoperiod, leading to the formation of Fusarium yellowish-white to pink slimy spore masses, which were

subsequently spread onto a potato dextrose agar (PDA, BD Difco Co., USA) medium for single-colony isolation. Each isolate was cultured on a PDA slant and stored at 4°C. When stalk rot symptoms were observed, moldy rotting parts inside the stems were excised and treated in the same manner as described above to obtain isolates.

2. Identification of fungi

The isolates were cultured on PDA at 25°C in the dark for three days. After incubation, the aerial mycelium was removed and subjected to near-ultraviolet light irradiation for three days. Morphological observations of the colonies were conducted in the media. Morphological characteristics of anamorphs, including conidia and phialides, were estimated on V8 juice agar (Campbell®V8 juice 200 ml, CaCO, 3 g/L) at 25°C under BLB as

Table 1. Representative isolates of Fusarium spp. causing ear rot and stalk rot of corn in Japan^a

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Isolate	Fungal species	Isolation source	Geographical origin	Isolation date	MAFF	TEF	FUM	DON
CF23 (A) ^b	Fusarium concentricum	ear	Osaki, Miyagi	2010/9	511528	LC796843	_	_
Mo1588 (A)	Fusarium concentricum	ear	Nasushiobara, Tochigi	2012/7	511567			
Mo523 (B)	Fusarium fujikuroi	ear	Nasushiobara, Tochigi	2009/9	511563		+	
CF21 (B)	Fusarium fujikuroi	ear	Morioka, Iwate	2010/8		LC796844		
CF46 (B)	Fusarium fujikuroi	ear	Koshi, Kumamoto	2010/8	511525	LC796846	+	_
CF25 (B)	Fusarium fujikuroi	ear	Osaki, Miyagi	2010/9	511524	LC796845	+	_
Mo311 (C)	Fusarium graminearum	silage ^c	Morioka, Iwate	2012/9		LC796848		+
Mo914 (C)	Fusarium graminearum	silage	Daisen, Akita	2012/9		LC796847		+
CF32 (D)	Fusarium miscanthi	ear	Shinjo, Yamagata	2010/9	511529	LC796849	_	_
CF36 (D)	Fusarium miscanthi	ear	Fukushima, Fukushima	2010/9	511530	LC796850	_	_
CF3 (E)	Fusarium proliferatum	ear	Sapporo, Hokkaido	2010/9	511521	LC796851	+	_
CF8 (E)	Fusarium proliferatum	ear	Kuroishi, Aomori	2010/9		LC796852		
CF16 (E)	Fusarium proliferatum	ear	Daisen, Akita	2010/9	511522	LC796853	_	_
CF22 (E)	Fusarium proliferatum	ear	Morioka, Iwate	2010/9	511523	LC796857	+	_
Mo905 (E)	Fusarium proliferatum	silage	Senpoku, Akita	2010/9		LC796854	+	_
Mo961 (E)	Fusarium proliferatum	silage	Sapporo, Hokkaido	2010/9		LC796855	+	_
Mo1908 (E)	Fusarium proliferatum	ear	Takizawa, Iwate	2012/10	511585	LC796856	+	
CF5 (F)	Fusarium verticillioides	ear	Sapporo, Hokkaido	2010/9	511526	LC796858	+	_
CF30 (F)	Fusarium verticillioides	ear	Osaki, Miyagi	2010/9		LC796861		
CF43 (F)	Fusarium verticillioides	ear	Nasushiobara, Tochigi	2010/9		LC796862		
Mo899 (F)	Fusarium verticillioides	silage	Fukushima, Fukushima	2010/9		LC796859	+	_
Mo921 (F)	Fusarium verticillioides	silage	Kitakami, Iwate	2010/9		LC796860	+	_
CF44 (F)	Fusarium verticillioides	ear	Koshi, Kumamoto	2010/9	511527	LC796863	+	_
B4-1 (C)	Fusarium graminearum	stalk	Chitose, Hokkaido	2012/10		LC796864	_	+
No.50 (C)	Fusarium graminearum	stalk	Ishioka, Ibaraki	2015/8	511607	LC796865		
No.51 (B)	Fusarium fujikuroi	stalk	Ishioka, Ibaraki	2015/8	511608	LC796866		
No.54 (F)	Fusarium verticillioides	stalk	Ishioka, Ibaraki	2015/8	511611	LC796867		

^a The isolates used to analyze the *TEF* gene were chosen and deposited in the NARO Genebank with MAFF numbers (https://www.gene.affrc.go.jp).

^b The letters in the parentheses indicate the types of *Fusarium* spp. based on their morphology.

^c Silage, including corn grain, was used to isolate *Fusarium* spp.



Fig. 1. Natural symptoms of ear rot and stalk rot in corn and the inoculation methods

A: Natural symptoms of corn ear rot, B: Toothpick inoculation of corn ears, C: Natural symptoms of corn stalk rot, D: Toothpick inoculation of corn stems, and reproduced symptoms

described above using an optical microscope (n= 50). DNA was extracted from the mycelia scraped from the cultures using a previously reported method (Tsukiboshi et al. 2005). PCR amplification of the translation elongation factor 1α (*TEF*) gene was performed using the HS392 and HS393 primers, and amplification was performed as previously reported (Suga et al. 2014). The PCR products were purified and sequenced as previously described (Tsukiboshi et al. 2005). The sequence data were aligned and used to construct a molecular phylogenetic tree by the GENETYX ver. 10 software (Nihon Server Co., Tokyo, Japan). The obtained sequences of the TEF gene were registered in the DNA Data Bank of Japan with accession numbers LC796843-LC796867. Accessions associated with the Fusarioid ID (https://www.fusarium.org/) were utilized as standard strains for each species in the analysis.

3. Mycotoxin production test

Each isolate (Table 1) was incubated with 2 g of cornmeal, to which an equal volume of water was added. The cornmeal used in this study was prepared by grinding dried corn kernels (variety unknown) collected from a field in Nasushiobara, Tochigi Prefecture, Japan, in 2009. The isolates were then incubated for seven days at 25°C in the dark and subsequently tested for mycotoxin production by the detection kits RIDA®QUICK FUM (R-Biopharm, Germany, detection limit 2 ppm) and RIDA®QUICK DON (detection limit 1.5 ppm), following

the manufacturers' instructions. Cornmeal supplemented with sterile distilled water served as the control in this experiment.

4. Pathogenicity test

Four isolates were subjected to pathogenicity testing, specifically CF3 of F. proliferatum, CF46 of F. fujikuroi, CF23 of F. concentricum, and CF32 of F. miscanthi (Table 1). The isolates were initially grown on a PDA plate 9 cm in diameter at 25°C in the dark for three days. Subsequently, 20-30 of 6 cm wooden toothpicks previously dipped in potato dextrose broth (BD Difco Co.) were placed onto each colony and then incubated at 25°C in the dark for an additional seven days. For the pathogenicity assay, the forage corn variety TX448 (relative maturity 120, Takii Co., Ltd., Kyoto, Japan) was sown on 25 May 2011 in a field in Nasushiobara city. Ten female ears at the milk-ripe stage on 30 July were inoculated by piercing toothpicks cultured with the isolates (Fig.1B). Disease development was assessed on 7 September when the plants reached the yellow-ripe stage. Re-isolation was carried out using the method described above, and the isolated fungi were identified based on their morphology. Ears pierced with toothpicks not cultured with fungus were used as controls.

Three isolates (B4-1 as *F. graminearum*, No. 51 as *F. fujikuroi*, and No. 54 as *F. verticillioides*) obtained from corn stalk rot were also subjected to pathogenicity testing. Cultured toothpicks were prepared using the same method described above. Maize variety KD777new (relative maturity 127, Kaneko Seeds Co., Ltd., Gunma, Japan) was sown on 20 May 2019 and inoculated by piercing the ground edge of the stalk at the milk-ripe stage on 24 July. Disease development was evaluated on 3 September at the yellow-ripe stage, followed by re-isolation of fungi using the described method. Plants pierced with toothpicks that did not culture the isolates served as controls.

Results

The samples affected by corn ear rot exhibited a reddish to brownish discoloration of the kernels, from which a total of 111 isolates of *Fusarium* spp. including those from deteriorated corn silage grains were obtained. These isolates were categorized into six types (A-F) based on their distinct colonial characteristics and conidial morphologies. Among these isolates, two type A isolates were obtained from samples collected in Miyagi and Tochigi prefectures. They formed pale red to pale yellow colonies with abundant white aerial mycelia on PDA. Microconidia, oval to allantoid, 5.7-19.3 ×

1.9-4.9 μ m, were produced in small masses on mono- or polyphialides, and macroconidia were generally straight, slightly hooked at the base, measuring 39.7-64.2 \times 2.6-4.2 μ m, with 3-5 septa (Fig. 2A, B). These morphological traits are consistent with the original description of *F. concentricum* Nirenberg & O'Donnell (Nirenberg & O'Donnell 1998). Species identification as *F. concentricum* was also supported by the molecular phylogenetic tree (Fig. 3).

Twenty-seven type B isolates were obtained from samples collected in Hokkaido, Iwate, Yamagata, Miyagi, Fukushima, Tochigi, Chiba, and Kumamoto prefectures. These isolates formed pale purple to pale yellowish-brown colonies with abundant white aerial mycelia on PDA. They formed microconidia, oval to obovoid, 5.6- 12.3×2.4 - $3.9 \,\mu m$, mainly in small masses on mono- or polyphialides, and macroconidia were generally straight, slightly hooked at the base, measuring 40.1- 58.5×3.2 - $4.4 \,\mu m$, with 3- $5 \, \text{septa}$ (Fig. 2C, D). This morphology corresponds to the description of *F. fujikuroi* Nierenberg (Choi et al. 2018) and the molecular phylogenetic tree (Fig. 3), confirming these isolates as *F. fujikuroi*.

Additionally, three type C isolates were obtained from samples collected in Akita and Iwate prefectures. These isolates formed red to dark red colonies with abundant light red aerial mycelia on PDA. The macroconidia were falcate, straight to slightly curved, with distinct pedicel cells, measuring 41.2-64.2 \times 3.9-5.4 μ m, and 3-5 septate. No microconidia were produced in the colony. This morphology is consistent with the description of *F. graminearum* Schwabe (Crous et al. 2021) and is also supported by the molecular phylogenetic analysis (Fig. 3).

Two type D isolates were obtained from samples collected in Yamagata and Fukushima prefectures, forming pale yellow to pale purple colonies with abundant white aerial mycelia on PDA. They produced microconidia of two kinds, (i) pyriform 6.1-11.2 × 4.4-8.6 µm and (ii) clavate to fusiform 5.8-12.6 × 2.1-4.4 µm, mainly in chains at the tips of mono- or polyphialides, and macroconidia were generally straight, slightly hooked at the base, 27.8-51.7 × 3.2-4.4 µm, and 3-5 septate (Fig. 2E, F). This morphology aligns with the original description of *F. miscanthi* W. Gams, Klamer & O'Donnell (Gams et al. 1999), and based on molecular phylogenetic analysis (Fig. 3), these isolates were identified as *F. miscanthi*.

Additionally, 36 type E isolates were obtained from samples collected in Hokkaido, Aomori, Akita, Iwate, Miyagi, Fukushima, Tochigi, and Chiba prefectures, forming pale purple to purple colonies with abundant white aerial mycelia on PDA. They produced microconidia, oval to elliptical, $6.1-14.8 \times 1.9-4.2 \, \mu m$,

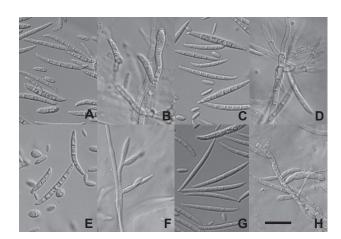


Fig. 2. Anamorphs of Fusarium spp. causing corn ear rot
Micro- and macroconidia and phialides of Fusarium
concentricum (A, B), F. fujikuroi (C, D), F. miscanthi
(E, F), and F. proliferatum (G, H). Bar: 20 µm

mainly in chains on mono- or polyphialides, and macroconidia were generally straight, slightly hooked at the base, $44.1\text{-}67.1 \times 3.5\text{-}4.7 \,\mu\text{m}$, and 3-5 septate (Fig. 2G, H). This morphology corresponds to the description of *F. proliferatum* (Matsushima) Nirenberg (Choi et al. 2018), and species identification as *F. proliferatum* was further supported by the molecular phylogenetic tree (Fig. 3).

Forty-one type F isolates were obtained from samples collected in Hokkaido, Aomori, Akita, Iwate, Yamagata, Miyagi, Fukushima, Tochigi, and Kumamoto prefectures, forming pale purple to dark purple colonies with abundant white aerial mycelia on PDA. They formed microconidia, oval to clavate, 5.4- 14.9×1.9 - $4.1 \, \mu m$, in long chains on mono- or polyphialides and were identified as *F. verticillioides* based on the molecular phylogenetic tree (Fig. 3).

The samples affected by corn stalk rot exhibited symptoms of female ears drooping at the yellow-ripe stage and the upper ground parts withering. The rootlets showed slight plexiform characteristics, decreased root volume, and a red surface. The inside of the stems at the ground edge became hollow and filled with a white to red mold (Fig. 1C), from which six isolates of *Fusarium* spp. were obtained from the internal stem tissue. The isolates collected in Hokkaido and Ibaraki prefectures were identified as *F. graminearum* (three isolates), *F. fujikuroi* (two isolates), and *F. verticillioides* (one isolate) based on molecular phylogenetic analysis (Fig. 3) and morphology, as described above.

Regarding toxin production by ear rot isolates, 83%-100% of the tested isolates of *F. fujikuroi*, *F. proliferatum*, and *F. verticillioides* were found to produce FUM, whereas *F. concentricum* and *F. miscanthi* did not

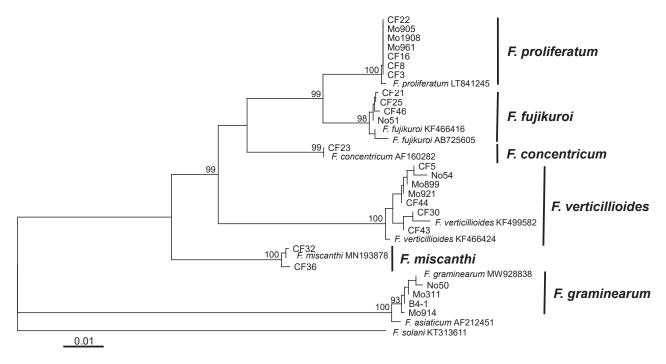


Fig. 3. A neighbor-joining tree inferred from the sequences of the *TEF* gene of *Fusarium* spp.

Numbers in front of the branches represent bootstrap values (1,000 replicates). The isolates used in this study are shown as isolate numbers (Table 1). The scale bar represents the genetic distance (0.01), showing the number of base changes.

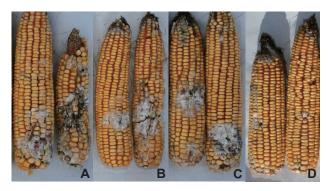


Fig. 4. Reproduced symptoms on corn ear by toothpick inoculation with *Fusarium* spp.

A: F. proliferatum, B: F. fujikuroi, C: F. concentricum, D: F. miscanthi

(Table 1). DON was exclusively produced by *F. graminearum*, with no other species exhibiting the toxin production. One *F. graminearum* strain isolated from stalk rot produced DON. No mycotoxins were detected in the control.

In the pathogenicity test, all isolates induced mold growth in the inoculated corn ears (Fig. 4), and the inoculated fungi were successfully reisolated from the ears. Specifically, *F. proliferatum*, *F. fujikuroi*, and *F. concentricum* displayed strong pathogenicity, following colonies > 5 cm in diameter at the inoculation site. The

colonies of all fungal species appeared generally white to grayish black with a slight pinkish tint; however, it was not possible to distinguish the inoculated *Fusarium* species based on colony appearance. In contrast, *F. miscanthi* formed small white to greyish-black colonies approximately 1 cm in diameter at the inoculation site. No mold symptoms were observed in the control. For stalk rot isolates, only *F. graminearum* induced dark red rot within the inoculated stems (Fig. 1D), and the inoculated fungus was successfully reisolated. *F. fujikuroi*, *F. verticillioides*, and the control showed no obvious signs of stalk rot disease.

Discussion

Fusarium fujikuroi, F. proliferatum, and F. verticillioides, members of the FFSC group producing FUM, have been isolated from corn silage in Japan (Uegaki et al. 2012). In the present study, F. fujikuroi and F. proliferatum were newly identified as ear rot pathogens affecting corn, confirming their pathogenicity to corn. These two Fusarium species have been reported globally for their FUM-producing capabilities (Bacon & Nelson 1994, Lee, S.-H. 2012, Leyva-Madrigal et al. 2014, Wang et al. 2014, Zhou et al. 2018, Qing et al. 2019). F. verticillioides, a previously confirmed pathogen in Japan (Okabe 2010), was also frequently isolated. These three

	Hokkaido	Northern Tohoku	Southern Tohoku	Kanto	Kyushu
F. concentricum			1	1	
F. fujikuroi	1	5	6	11	4
F. graminearum		3			
F. miscanthi			2		
F. proliferatum	8	21	2	5	
F. verticillioides	6	11	13	3	8
Total number	15	40	24	20	12

Table 2. Number of isolates of Fusarium spp. causing ear rot of corn in five regions of Japan

species accounted for 93.7% (104/111) of all the isolates. In vitro FUM production was confirmed for these three species, and their pathogenicity was validated through field inoculation tests for F. fujikuroi and F. proliferatum. This indicated that F. fujikuroi, F. proliferatum, and F. verticillioides are the major ear rot pathogens producing FUM in corn in Japan. F. concentricum, also belonging to FFSC, exhibited high pathogenicity but was isolated infrequently and did not produce FUM, indicating that it is a minor pathogen. However, F. concentricum is known to produce the mycotoxins beauvericin and fusaproliferin (Du et al. 2014), which pose a potential risk to corn production. On the other hand, F. miscanthi, a member of the F. nisikadoi species complex (FNSC), displayed weak pathogenicity, was isolated infrequently, and did not produce FUM. Therefore, it is considered a minor species in Japan, although its occurrence has been reported in China (Shang et al. 2021).

F. graminearum, a member of the FGSC group, was isolated from the northern Tohoku region and confirmed to produce DON. This fungus is widely recognized in Japan, particularly in Hokkaido (Minato 2009); however, it was not isolated from Hokkaido in this study. It was not found in southern Tohoku or further south in Kyushu (Sasaya et al. 2015), indicating that its distribution extends northward from northern Tohoku. F. asiaticum, another species reported within the FGSC in western Japan (Kawakami et al. 2015), was not isolated in this study.

F. fujikuroi, F. proliferatum, and F. verticillioides are members of the FFSC and the major corn ear rot pathogens producing FUM in Japan. They were frequently isolated in the five regions where they were collected (Table 2; Fig. 5). Only F. proliferatum was not isolated in the Kyushu region, in southern Japan. However, Sasaya et al. (2015) isolated F. fujikuroi, F. proliferatum, and F. verticillioides in the Kyushu region, and there is no evidence that F. proliferatum is predominantly distributed in northern Japan. F.

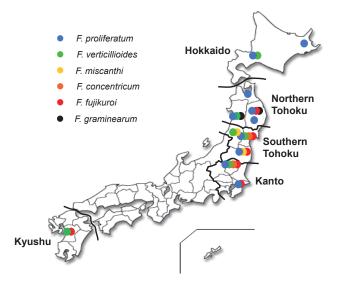


Fig. 5. Geographical distribution of *Fusarium* spp. causing corn ear rot in Japan

concentricum and F. miscanthi were isolated from the southern Tohoku and Kanto regions, but their frequencies were low, and their distribution patterns remain unclear.

Corn stalk rot is a globally recognized disease (Munkvold & White 2016); however, its occurrence in Japan has not been previously reported, so this paper marks the first description of the disease in the country. F. graminearum was isolated from stalk rot symptoms in Hokkaido and Ibaraki prefecture (the Kanto region), and the pathogenicity of the Hokkaido isolate was confirmed by field inoculation. The isolate was reisolated, confirming F. graminearum as the pathogen. Given that this isolate produces DON, this disease also represents a potential source of DON contamination during corn silage production. F. fujikuroi and F. verticillioides, commonly reported as pathogens in Southeast Asia (Darnetty & Salleh 2013), were isolated from the disease in this study. Their pathogenicity could not be confirmed through field inoculation. Therefore, the two species were assumed to be associated with stalk rot symptoms.

In the present study, toothpick piecing inoculation was used to confirm the pathogenicity of *Fusarium* spp. that cause corn ear rot, which produced distinct colonies in strongly pathogenic corn kernels. This inoculation method was used for Pythium root and stem rot of corn (Mitsuhashi et al. 2015) and was also useful as an inoculation method for Fusarium ear rot. This method reproduced stalk rot symptoms in inoculated corn and was effective in confirming the pathogenicity, as previously reported (Darko et al. 2024).

The occurrence of Fusarium ear rot in Japan is influenced by the practice of leaving forage corn in the field longer to allow kernels to fully ripen, leading to an increased incidence of ear rot. Historically, ear rot caused by FUM-producing fungi was primarily reported south of the Kanto region (Uegaki et al. 2012, Sasaya et al. 2015); however, this study revealed its occurrence extending into the Tohoku region, north of Kanto. Mycotoxin contamination of silage and corn kernels of forage corn has been a persistent issue in Japan, and the accumulation of mycotoxins has been shown to escalate rapidly during the yellow-ripe stage of corn (Okabe et al. 2015). This paper clarifies the species composition of FUM-producing fungi, including some species reported for the first time in Japan. Further investigation is needed to understand each Fusarium species' proliferation and toxin production dynamics in relation to corn growth stages to mitigate mycotoxin production.

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