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REVIEW

Fusarium diseases of maize associated with mycotoxin contamination of agricultural products intended to be used for food and feed

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Abstract Infections of maize with phytopathogenic and toxinogenic *Fusarium* spp. may occur throughout the cultivation period. This can cause different types of diseases in vegetative and generative organs of the plant. Along with these infections, mycotoxins are often produced and accumulated in affected tissues, which could pose a significant risk on human and animal health when entering the food and feed chain. Most important fungal species infecting European maize belong to the *Fusarium* sections Discolour and Liseola, the first being more prevalent in cooler and humid climate regions than the second predominating in warmer and dryer areas. Coexistence of several *Fusarium* spp. pathogens in growing maize under field conditions is the usual case and may lead to multi-contamination with mycotoxins like trichothecenes, zearalenone and fumonisins. The pathways how the fungi gain access to the target organs of the plant are extensively described in relation to specific symptoms of typical rot diseases regarding ears, kernels, rudimentary ears, roots, stem, leaves, seed and seedlings. Both *Gibberella* and *Fusarium* ear rots are of major importance in affecting the toxinogenic quality of grain or ear-based products as well as forage maize used for human or animal nutrition. Although rudimentary ears may contain high amounts of *Fusarium* toxins, the contribution to the contamination of forage maize is minor due to their small proportion on the whole plant dry matter yield. The impact of foliar diseases on forage maize contamination is regarded to be low, as *Fusarium* infections are restricted to some parts on the leaf sheaths and husks. Mycotoxins produced in rotted basal part of the stem may contribute to forage maize contamination, but usually remain in the stubbles after harvest. As the probability of a more severe disease progression is increasing with a prolonged cultivation period, maize should be harvested at the appropriate maturity stage to keep *Fusarium* toxin contamination as low as possible. Ongoing surveillance and research is needed to recognise changes in the spectrum of dominating *Fusarium* pathogens involved in mycotoxin contamination of maize to ensure safety in the food and feed chain.

Keywords *Gibberella* ear rot · *Fusarium* ear rot · Rudimentary ear rot · Stem rot · Root rot · Seed rot · Seedling blight · Foliar diseases · Infection pathways · Disease symptoms · Trichothecenes · Zearalenone · Fumonisins · Grain maize · Forage maize · Food and feed safety

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Introduction

Numerous species of the genus *Fusarium* have phytopathogenic and toxigenic properties affecting yield, nutritive value and hygienic quality of agricultural products from arable crops worldwide. Infection of maize (*Zea mays* L.) and small-grain cereals by *Fusarium* spp. is of special concern due to the major importance of these crops for food and feed production. Along with the course of infection, crops may become contaminated with *Fusarium*

mycotoxins, which can cause toxic effects on plants, animals and humans (Placinta et al. 1999; Bennett and Klich 2003; Richard 2007; Streit et al. 2012; Bryden 2012; Arunachalam and Doohan 2013; Abbas et al. 2013).

Fusarium pathogens are ubiquitous and may endanger plant development throughout the cultivation period. Infections of maize with *Fusarium* spp. can cause serious diseases such as seed rot, root and stem rot, ear and kernel rot and rudimentary ear rot (Kabeere et al. 1997; Cotton and Munkvold 1998; Logrieco et al. 2002; Munkvold and O'Mara 2002; Oldenburg and Ellner 2005; Meissle et al. 2010). Important *Fusarium* species infecting European maize are members of the sections Discolour, Roseum, Sporotrichella, Gibbosum and Liseola (Table 1). The most common mycotoxins produced by these fungi in affected maize are trichothecenes, zearalenone, fumonisins and moniliformin (Chelkowski 1989; Nelson et al. 1993; Nedelnik 2002; Schollenberger et al. 2005).

Maize has a significant agronomic impact in the European Union (EU). In 2015, maize was cultivated on about 15 million hectares (Mha) to produce raw materials required for food, feed, bioenergy and other industrial purposes. Grain maize was produced on about 8.9 Mha, with Romania (29%), France (17%) and Hungary (13%) being the leading countries. The forage maize (silage maize) cultivation area amounted to 6.1 Mha including 1.2 Mha for biogas production with Germany (34%) and France (24%) being the main producers (Newsletter CEPM No. 6, October–December 2015). The hygienic and toxinogenic quality of grain maize is endangered when the kernels are affected by *Fusarium* spp., whereas all infected and mycotoxin-contaminated parts of the aboveground whole plant may contribute to the quality in forage maize (Oldenburg and Höppner 2003; Oldenburg et al. 2005; Dorn et al. 2009; Eckard et al. 2011; Schollenberger et al. 2012; Basler 2016).

In this review, detailed investigations about the pathways of *Fusarium* spp. infecting different organs of the maize plant and contamination with mycotoxins are summarised to get a broad understanding about the complexity of *Fusarium* diseases of maize and their contribution to food and feed safety aspects.

Ear diseases caused by *Fusarium* spp.

Amongst *Fusarium* maize diseases, ear rots are of major importance in affecting quantity and quality of grain or ear-based products used for human and animal nutrition (Leslie et al. 1990; Munkvold 2003; Kleinschmidt et al. 2005; Morales-Rodríguez et al. 2007; Miller 2008; Van Asselt et al. 2012; Gromadzka et al. 2016).

Ear infections with *Fusarium* pathogens are closely related to the special flower formation of maize and the way of its pollination. Maize develops male inflorescences on a terminal tassel and several female inflorescences in the axils of leaves in the lower half to midsection of the plant (Bortiri and Hake 2007). The female inflorescence consisting of hundreds of spikelets occurring in rows on a thickened axis called rachis represents the ear (Fig. 1), which is enclosed by numerous

Table 1 Important *Fusarium* spp. and associated mycotoxins occurring in European maize

Section	*Fusarium* spp. (syn.)	Teleomorph	Mycotoxins	References
Discolour	*F. graminearum*	*Gibberella zeae*	DON, acDON, NIV, ZEN, FUS	Logrieco et al. (2002) and Basler (2016)
	F. culmorum		DON, acDON, NIV, ZEN, ZOH	Logrieco et al. (2002) and Mesterhazy et al. (2012)
	F. cerealis (*F. crockwellense*)		NIV, FUS, ZEN, ZOH	Logrieco et al. (2002) and Goertz et al. (2010)
Roseum	*F. avenaceum*	*Gibberella avenacea*	MON, BEA, ENNs	Bottalico (1998) and Jestoi (2008)
Sporotrichella	*F. poae*		DAS, NIV, FUS, T2, HT2, ENNs	Logrieco et al. (2002) and Jestoi (2008)
	F. sporotrichioides		T2, HT2, DAS, MAS, BEA	Logrieco et al. (2002) and Jestoi (2008)
Gibbosum	*F. equiseti* (*F. scirpi*)	*Gibberella intricans*	ZEN, DAS, ENNs	Logrieco et al. (2002) and Jestoi (2008)
Liseola	*F. verticillioides* (*F. moniliforme*)	*Gibberella moniliformis*	FB_1, FB_2, FB_3, FB_4, MON, BEA	Pascale et al. (1997) and Bakan et al. (2002)
	F. proliferatum		FB_1, FB_2, FUP, BEA	Ritieni et al. (1997) and Pascale et al. (2002)
	F. subglutinans	*Gibberella subglutinans*	FUP, BEA, MON	Lew et al. (1996) and Jestoi (2008)

acDON monoacetyl-deoxynivalenols 3-acDON and 15-acDON; *BEA* beauvericin; *DAS* diacetoxyscirpenol; *DON* deoxynivalenol; *ENNs* enniatins; *FB_1, FB_2, FB_3 and FB_4* fumonisins B_1, B_2, B_3 and B_4; *FUP* fusaproliferin; *FUS* fusarenone-X; *HT2* HT2 toxin; *MAS* monoacetoxyscirpenol; *MON* moniliformin; *NIV* nivalenol; *T2* T2 toxin; *ZEN* zearalenone; *ZOH* zearalenols α and β isomers

Fig. 1 Female inflorescence of maize consisting of hundreds of spikelets situated on a thickened axis (rachis), showing emerged silks, enclosed with foliaceus bracts (husks)

foliaceous bracts, called husks. The styles called silks first develop from the middle of the ear, thereafter from the base and finally from the tip and become visible outside the husks when leaving the silk channel. The silks are hairy, especially at the top where the stigma is situated thus helping to catch the pollen, which migrates down the style to reach the ovules which after fertilisation mature into kernels. From all of the ears, usually the uppest one transformed into a harvestable ear (main ear). Depending on the variety, the climate and cultivation conditions two or more ears may gain maturity, however. Rest of the ears situated below the harvestable ear(s) is called rudimentary ears. They lag behind in growth due to disturbed or missing fertilisation, remain immature and stunted in between the stem and the leaf sheath (Fig. 2).

Undamaged husks covering the female inflorescence are an effective barrier against fungal attack (Warfield and Davis 1996), but they allow an entry from exposed silks through the silk channel to the ear tip. However, in case of physical injuries, fungi gain access to the ear or kernels wherever wounds were set (Duncan and Howard 2010). A direct penetration of the pathogens from outside of intact developing or mature kernels is relatively uncommon, probably due to the structure or biochemical ingredients of the pericarp, e.g. thickness, wax layer, cell wall phenolic acids and flavonoid pigments, which may reduce the risk of infection with *Fusarium* spp. (Hoenisch and Davis 1994; Bily et al. 2003; Sampietro et al. 2009; Venturini et al. 2016).

Gibberella ear rot

The predominant *Fusarium* spp. infecting maize ears in cooler and humid climate regions of Europe belong to the section Discolour. *Gibberella* ear rot or 'red ear rot' is mainly caused by *Fusarium graminearum*, but other pathogens may also be involved in the disease, amongst them *F. culmorum*, *F. avenaceum*, *F. cerealis*, *F. poae*, *F. equiseti* and *F. sporotrichioides* (Table 1).

Usually, *Gibberella* ear rot starts at the ear tip after entry of the pathogens via the silks at female flowering (Reid et al.

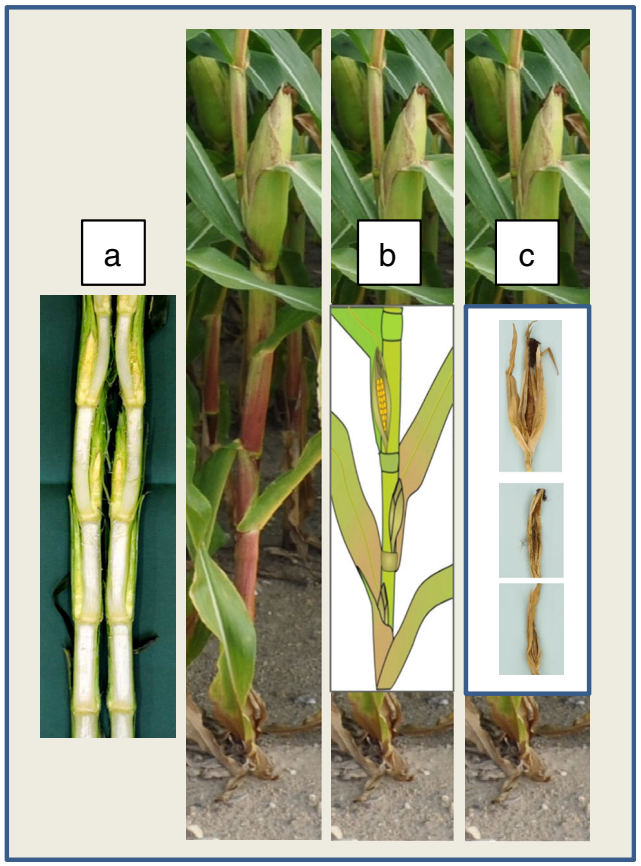

Fig. 2 Rudimentary ears situated below the main ear in leaf axils between the stem and leaf sheaths. **a** Developing female inflorescences (longitudinal cut of the lower stem). **b** Schematic diagram of rudimentary ears situated below the main ear. **c** Rotted rudimentary ears at harvest

1999; Duncan and Howard 2010). After spore germination on young emerged silks, the fungi grow through the silk channel and primarily infect the rachis tip and proceed through the piths towards the rachis base (Oldenburg and Ellner 2015). The infection progress is recognizable through a greyish-brownish to pink-reddish discolouration of the infected parts of the rachis. With some temporal delay, the developing kernels are subsequently infected from interior infected rachis top-down the ear (Oldenburg and Ellner 2015). This is first observable on tip kernels paling or showing beige brown marbled spots or white smears and later on white over pink and reddish coloured mould layers spreading downward in between the outer ear corpus and the husks (Fig. 3). It usually takes several weeks after the initial infection until typical disease symptoms outside the ear become visible and fungal development becomes measurable by polymerase chain reaction (Atanasova-Penichon et al. 2012; Oldenburg and Ellner 2015). In late season, symptoms of *Gibberella* ear rot may develop at the ear base (Fig. 4) when rainwater infiltrates in leaf axis leading to long-term humid conditions around the ear peduncle (Lauren and Di Menna 1999).

Correlating with the infection progress and development of *Gibberella* ear rot symptoms, mycotoxins are produced and mainly accumulate in visibly affected parts of the ears. The sooner ear tissues are infected, the higher mycotoxin concentrations are produced, which results in a top-down gradient from high to low toxin levels within the ear corpus. When infected via the silks, highest *Fusarium* toxin concentrations are usually found at the ear tip (Fig. 5), whereas the rachis is considerably higher contaminated compared to the attached kernels (Oldenburg and Ellner 2011). Oldenburg and Ellner (2015) found mean concentrations of DON about 3–5 and 17–129 mg kg^{-1} in harvest kernels situated at the tip segment of maize ears when inoculated with *F. culmorum* or *F. graminearum* at flowering, respectively, followed by lower levels of 3-acDON (0.4–8 mg kg^{-1}) and ZEN (maximum 0.15 mg kg^{-1}). Compared to the kernel fraction, rachis parts showed several times higher levels of DON, 3-acDON and ZEN. These results indicate that the kernels were internally infected via the connection to the rachis. Considerably higher DON and NIV concentrations in *Fusarium*-infected maize rachis compared to associated kernels were also observed by Lauren and Di Menna (1999). Czembor (2015) as well detected highly increased DON contamination of maize rachis compared to corresponding grain both under natural infection and inoculation with *F. graminearum*.

In maize grain infected with *Fusarium* spp. of the Discolour section, main mycotoxins produced are type-B trichothecenes, primarily DON, acDON and NIV, as well as ZEN (Table 1), which may accumulate to concentrations up to several mg kg^{-1} (Lew et al. 2001; Logrieco et al. 2002; Dorn et al. 2011). Type-A trichothecenes such as DAS, T2 and HT2 produced by members of the sections Sporotrichella and Gibbosum (Table 1) occur less frequently ranging at lower concentrations, usually below 1 mg kg^{-1} (Schollenberger et al. 2012; Ferrigo et al. 2016).

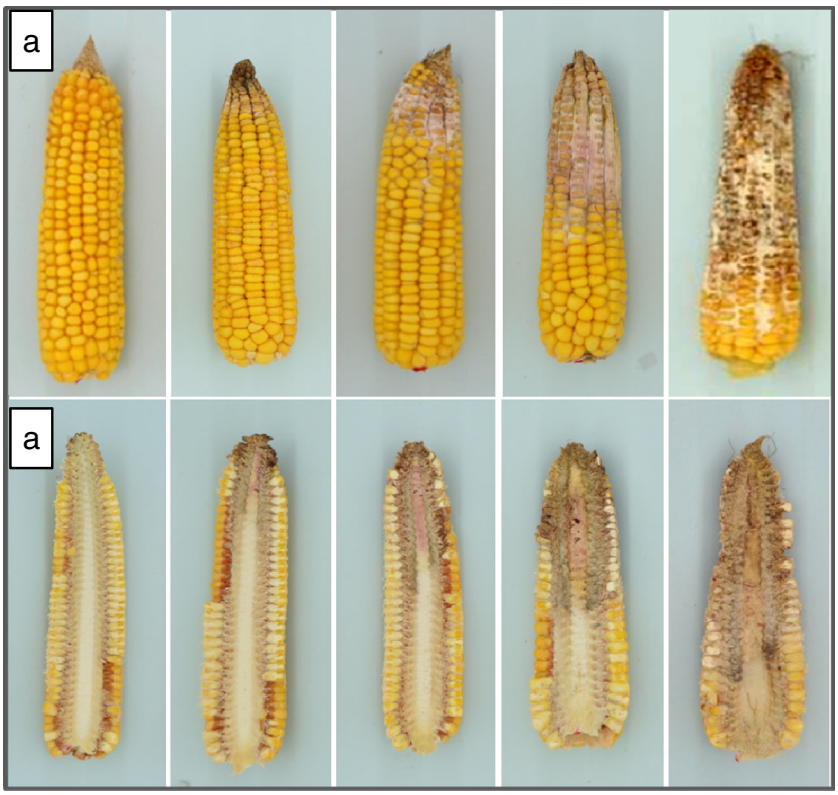

Fig. 3 External and internal symptoms of *Gibberella* ear rot. External symptoms: tip kernels pale or showing *brown* marble spots, *white* and *pink reddish* coloured mould layers spreading downward the ear; Internal symptoms: *greyish-brownish* to *pink-reddish* discolouration of rachis pith. **a** Healthy ear without disease symptoms

Fig. 4 *Gibberella* ear rot symptoms on ear and rachis originating from infected peduncle (symptoms on ear tips originating from silk infection)

Fusarium ear rot

In warmer and drier climate regions, *Fusarium* spp. of the section Liseola (Table 1) occur more frequently and cause *Fusarium* ear rot or 'pink ear rot' of maize (Srobarova et al. 2002; Doohan et al. 2003; Munkvold 2003; Folcher et al. 2009; Dorn et al. 2009; Shala-Mayrhofer et al. 2013). *F. temperatum*, a closely related species to *F. subglutinans*, was recently identified as a new pathogen causing ear rot in European maize (Scauflaire et al. 2011a; Czembor et al. 2014; Boutigny et al. 2017).

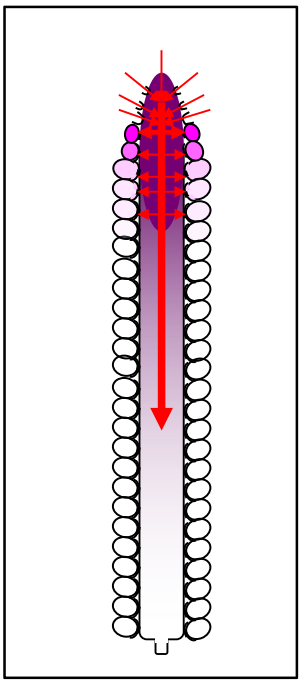

Fig. 5 Schematic diagram of infection progress (*red arrows*) and heaviness of mycotoxin contamination (intensity of *red colour*)

Main entry for these pathogens to gain access to the kernels is more common through wounds, e.g. set by insects such as European corn borer, thrips or corn earworms, by birds or hail than via the silks by growing down through the silk channel to the ear tip (Farrar and Davis 1991; Desjardins et al. 1998; Sobek and Munkvold 1999; Munkvold 2003; Bacon et al. 2008; Parsons and Munkvold 2010; Duncan and Howard 2010; Mesterházy et al. 2012; Scarpino et al. 2015). However, a direct penetration of the fungi through the intact pericarp was not observed, but a path for infection might be possible through the stylar canal to a developing kernel at the time of pollination (Bacon et al. 2008; Duncan and Howard 2010).

Typical symptoms of *Fusarium* ear rot caused by *F. verticillioides* (Fig. 6) are tan to brown discolouration or white or light pink mould on random kernels, limited ear areas or groups of kernels scattered over the ear (Bottalico 1998; Mesterházy et al. 2012; Al-Juboory and Juber 2013).

Symptomless kernel infection resulting from systemic growth of *Fusarium verticillioides* from infected seed, roots or stalks through ear peduncles was also observed, showing an endophyte-like behaviour of the fungus in association with maize (Nelson 1992; Kedera et al. 1994; Bacon et al. 2001; Munkvold 2003; Murillo-Williams and Munkvold 2008; Bacon et al. 2008). Under stress conditions, the endophytic state of the fungus may switch into a pathogenic state that may result in the development of macroscopic symptoms in the infected plant organs (Bacon and Hinton 1996; Bacon et al. 2008). However, the contribution of systemic kernel infection from infected seed or stem is considered to be less important than local kernel infection via the silks (Munkvold and Carlton 1997; Munkvold et al. 1997; Oren et al. 2003).

The most prevalent occurring mycotoxins produced by *F. verticillioides* and *F. proliferatum* in maize ears are the B series of fumonisins (FB_1 to FB_4), amongst which FB_1 is the most frequently investigated derivative (Marín et al. 2004; Griessler et al.

Fig. 6 External symptoms of *Fusarium* ear rot caused by *F. verticillioides* showing *tan* to *brown* discoloration or *white* to *light pink* mould at random kernels or groups of kernels scattered over the ear

2010; EFSA 2014; Santiago et al. 2015). This might be attributed to different chemotypes of fumonisin-producing strains of *F. verticillioides*, dominated by strains producing large amounts of $FB_1 > FB_2$, and considerably smaller amounts of $FB_3 > FB_4$ (Szécsi et al. 2010). Production of FB_1 by *F. verticillioides* in maize kernels was proven to be affected depending on their content of water, amylase and starch, which changes constantly from beginning of the ripening process until maturity (Waskiewicz et al. 2012). In that study, FB_1 biosynthesis was positively correlated with the increase of amylase and starch and the corresponding decrease of kernel moisture with kernel age, beginning from the third to fifth week and being highest during sixth and seventh week from inoculation at green silk stage. No accumulation of FB_1 in immature *F. verticillioides*-infected kernels lacking starch was also observed by Bluhm and Woloshuk (2005), who identified amylopectin as triggering substance to induce FB_1 production. The role of amylopectin as inducing factor for fumonisin production was confirmed both under field conditions, showing highest fumonisin productivity at the dent stage of maize kernels corresponding to high amylopectin content (Picot et al. 2011) and laboratory conditions culturing *F. verticillioides* and *F. proliferatum* on maize-based substrates (Lazzaro et al. 2013). A delayed increase of FB_1, FB_2 and FB_3 production starting from 4 to 8 weeks after silking was also observed in forage maize by Okabe et al. (2015).

In surveys focusing on the natural occurrence of fumonisins in European maize grain, higher concentrations of FB_1 up to several mg kg^{-1} or in some cases some hundreds of mg kg^{-1} were more frequently reported from southern than from central European countries (Doko et al. 1995; Logrieco et al. 2003; Pietry et al. 2004; Butrón et al. 2006; Covarelli et al. 2011; Levasseur-Garcia et al. 2015). High FB_1 levels are more frequently resulting from coinfections with both *F. verticillioides* and *F. proliferatum* (Logrieco et al. 2003), but FB_1 production of *F. verticillioides* is usually considerably higher compared to *F. proliferatum* (Lazzaro et al. 2013).

Visually asymptomatic kernels infected by *F. verticillioides* in endophytic state may contain toxins at rather low concentrations, but when the fungus is switching to the pathogenic state, higher amounts of fumonisins may be produced (Bacon et al. 2008). Mixed infections with other *Fusarium* pathogens, e.g. *F. subglutinans*, *F. avenaceum* or *F. equiseti* (Table 1), may lead to cocontaminations with MON, BEA, ENNs and/or FUP (Schütt et al. 1998; Bottalico and Logrieco 2001; Jestoi 2008).

Cooccurrence of ear rot pathogens

Due to the great impact of climatical/weather conditions on the infection process, both *Gibberella* and *Fusarium* ear rot pathogens may start on single-maize ears under supportive conditions within a growing season (Logrieco et al. 2007). Coexistence of different *Fusarium* spp. on growing maize under field conditions is the usual case and may lead to multi-contamination with *Fusarium* mycotoxins (Logrieco et al. 2007; Streit et al. 2012; Czembor et al. 2015; Leggieri et al. 2015; Ferrigo et al. 2016). In case of mixed infections, the pathogens compete with each other, thus influencing the production of mycotoxins in infected tissues (Munkvold 2003). However, contradictory reports concerning interactions between major toxinogenic pathogens in maize like *F. graminearum*, *F. verticilliodes* and *F. proliferatum* (Marín et al. 1998; Reid et al. 1999; Velluti et al. 2000, 2001; Picot et al. 2012) do not allow a clear prediction, which species will dominate in a mixed population under specific circumstances. This shows the complexity of interfering influences on infection processes relating to production of certain mycotoxins.

Rudimentary ear rot

The rudimentary ears are prone to *Fusarium* infection due to infiltration of rainwater loaded with fungal spores, dust and anther/pollen residues which build a dirt layer on the blade-sheath boundary of leaves after pollination (Fig. 7). The water cannot drain off because leaf sheaths tightly enclose the stem

Fig. 7 Anther/pollen/dust residues on blade-sheath boundary of a leaf

at the base, thus leading to permanent humid conditions around the rudimentary ears. As a consequence, the rudimentary ears become mushy and produce a foul odour (Fig. 8).

When the rudimentary ears are infected with *Fusarium* spp., trichothecenes may reach extraordinary high concentrations compared to other parts of the maize plant including ears, kernels, stems and leaves (Oldenburg et al. 2005; Schollenberger et al. 2012). Oldenburg et al. (2005) found that the rudimentary ear, positioned just below the main ear, contained the highest DON concentration compared to those positioned further downwards the stem (Fig. 9) and observed a close relation between the amount of *Fusarium* biomass found in infected rudimentary ears and the level of DON concentration. Schollenberger et al. (2012) as well detected the strongest trichothecene contamination in rudimentary ear fractions of maize cultivated under field conditions in southwest Germany compared with fractions of kernels, ears, husks, stalks and leaves. Both type-A and type-B trichothecenes were found in rudimentary ears, at the highest levels DON (maximum 89 mg kg^{-1}), 3-acDON (maximum 32 mg kg^{-1}), NIV (maximum 125 mg kg^{-1}), scirpentriol (maximum 45 mg kg^{-1}), 15-monoacetoxyscirpenol (maximum 3 mg kg^{-1}), T2 tetraol (maximum 33 mg kg^{-1}) and HT2 (maximum 8 mg kg^{-1}).

Foliar diseases caused by *Fusarium* spp.

Disease symptoms caused by *Fusarium* infections may occur on husks, leaf sheaths and around the blade-sheath boundary, whereas the leaf blades appear visually unaffected by *Fusarium* pathogens throughout the vegetation period.

In case of early and heavy ear infections with *Fusarium* spp., disease symptoms appear outside husks showing whitish mycelium and/or pink spore layers (Fig. 10a). In late season, reddish discoloured zones may occur on outer husks when remaining in close contact with *Fusarium*-infected leaf blade-sheath boundary (Fig. 10b), but infection usually does not proceed to the inner ear corpus (Fig. 10c). Brownish perithecia of *Gibberella* may also occur on mature husks in late growth stage of the plant (Logrieco et al. 2002). Leaf sheath and blade/sheath boundary infections by *Fusarium* spp., recognizable by reddish discoloration zones and necrotic lesions (Fig. 11), are mainly resulting from close contact to previously infected rudimentary ears.

Williams et al. (2007) observed that necrotic leaf lesions only on young maize seedlings emerged from seeds which were inoculated with fumonisin-producing strains of *F. verticillioides*, but not when seeds were treated with non-fumonisin-producing strains of the pathogen. Baldwin et al. (2014) detected FB_1 in maize seedling leaves, but without

Fig. 8 *Fusarium*-infected rudimentary ears showing immature and mushy female inflorescences

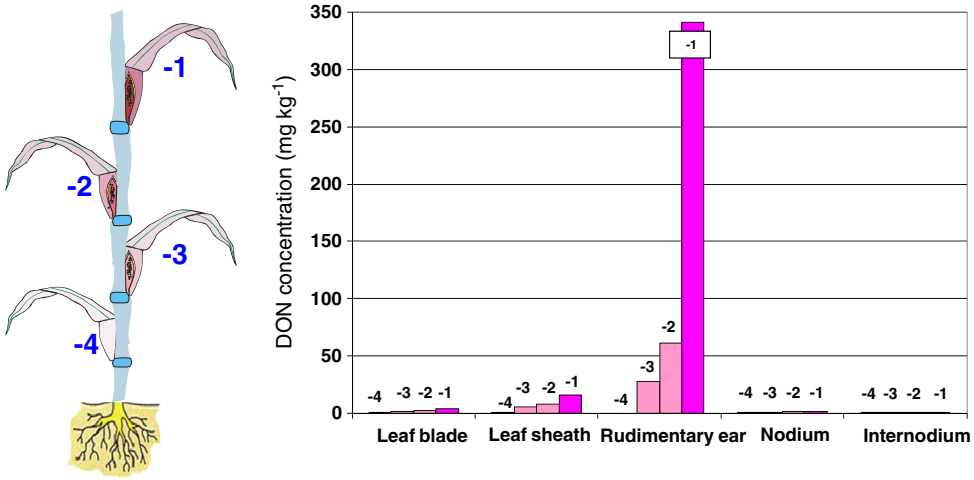

Fig. 9 Distribution of deoxynivalenol (DON) in maize organs at different leaf levels (−1, −2, −3, −4) below the main ear (intensity of *red* colour symbolizes heaviness of mycotoxin contamination)

colonisation of *F. verticilliodes* via aerial leaf tissues, and suggested that infection of a fumonisin-producing strain via the roots is necessary for accumulation of FB_1 in the leaves.

Results from trials with spore suspensions of *F. graminearum*, *F. verticillioides* and *F. proliferatum*, sprayed on leaves of maize seedlings cultivated under greenhouse conditions, showed that direct leaf infection via trichomes and stomata is possible (Nguyen et al. 2016a, b). However, disease symptoms such as yellow grey brown spots, necrotic lesion holes and streaks were only observed on young emerging leaves at rather low severity rates, but remained asymptotic on unfolded leaves (Nguyen 2014; Nguyen and Dehne 2015). It was furthermore observed that leaf infection occurred faster from *F. graminearum* than from *F. verticillioides* and *F. proliferatum* infection (Nguyen et al. 2016b).

Fusarium toxin contamination of maize leaves indicating infection with zearalenone- and trichothecene-producing pathogens was reported in several studies (Oldenburg 1993; Lew et al. 1997; Lauren and Di Menna 1999; Oldenburg et al. 2005; Schollenberger et al. 2012). Oldenburg (1993) found ZEN concentrations up to 290 μg kg^{-1} in leaves positioned at the bottom of the plant compared to those of the upper part, suggesting a correlation with natural leaf decay during plant ripening, thus probably decreasing the resistance of leaf tissues against fungal attack. Comparative analysis of leaf sheath and leaf blade contamination showed higher DON concentrations in leaf sheath than in leaf blades (Fig. 9; Oldenburg et al. 2005). These results indicate that *Fusarium* leaf infection may proceed from primarily infected leaf sheath into the leaf blades (Fig. 12). Lauren and Di Menna (1999) likewise found that *Fusarium* toxin contamination of maize leaves increases with ageing, showing highest levels of ZEN up to 16.6 mg kg^{-1} in leaf samples derived from lowest axils, without contamination in the corresponding blades.

In Austria, NIV was found in leaves of maize which were heavily infected by *F. poae* (Lew et al. 1997). Low amounts of

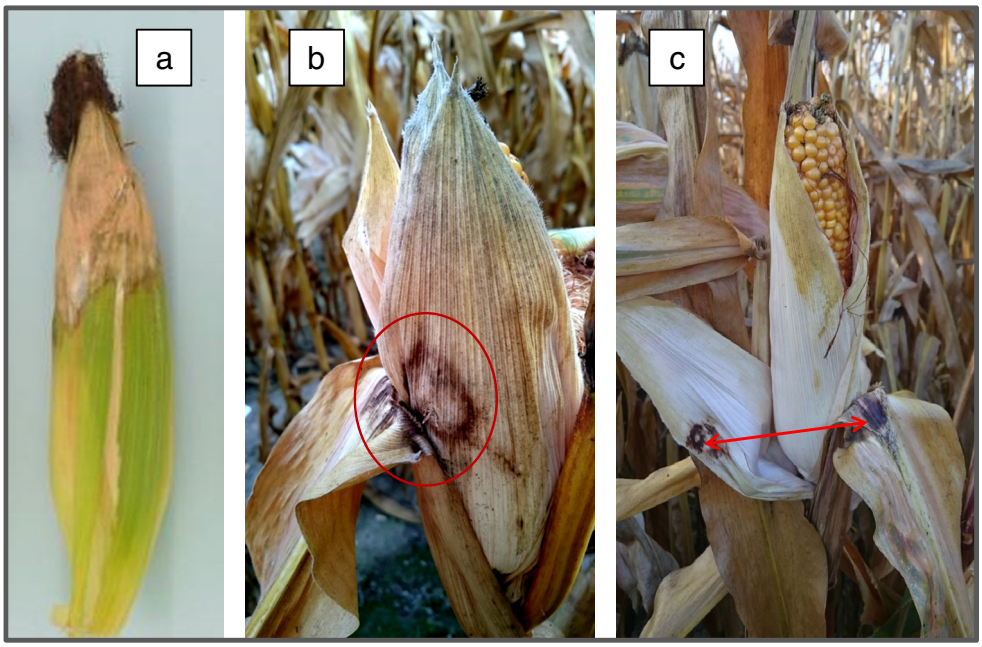

Fig. 10 *Fusarium* symptoms on husks. **a** *Pink* mould layer originating from infected ear tip. **b** Necrotic spot on husk showing a *reddish* border due to contact with a *Fusarium*-infected leaf sheath (**c**)

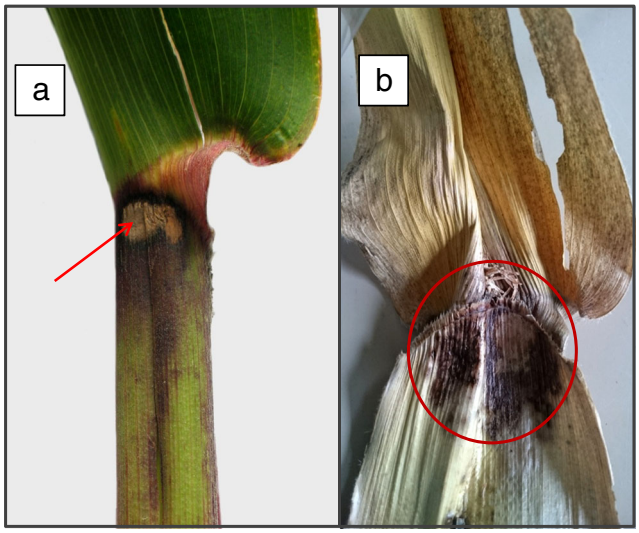

Fig. 11 *Fusarium* symptoms on leaf sheath showing a necrotic spot with reddish border (**a**) and a *reddish* discoloured blade-sheath boundary (**b**)

A- and B-type trichothecenes were more recently detected by Schollenberger et al. (2012) in some leaf samples of maize derived from German fields. Amongst them, DON (maximum 323 μg kg^{-1}) was followed by 15-acDON (maximum 72 μg kg^{-1}), 3-acDON (maximum 32 μg kg^{-1}), T2 (maximum 26 μg kg^{-1}) and HT2 (maximum 24 μg kg^{-1}), whereas in husks, higher contaminations with DON (maximum 1 mg kg^{-1}), NIV (maximum 10 mg kg^{-1}) and scirpentriol (maximum 1 mg kg^{-1}) were observed.

Stem and root rot caused by *Fusarium* spp.

Stem and root rot of maize may induce severe damage of the plant leading to premature senescence and lodging. Disease severity is depending on which species may get entry via different pathways at different growth stages of the plant and environmental factors, especially weather conditions during plant cultivation. As main causative pathogens, *F. graminearum*, *F. culmorum*, *F. verticillioides* and *F. proliferatum* were frequently identified to be involved in stem rot in Europe, but other species like *F. equiseti*, *F. avenaceum*, *F. cerealis*, *F. poae*, *F. subglutinans* and *F. temperatum* may also be involved in the disease (Kedera et al. 1994; Pronczuk et al. 1991; Lew et al. 1997; Bottalico 1998; Dorn et al. 2009; Scauflaire et al. 2011b; Pintos Varela et al. 2013; Shin et al. 2014a, b). *F. verticillioides* may have a special role in stem or root rot of maize because of its ability for either endophyte-like systemic growing (Bacon et al. 2008) or direct penetration of stem/roots or via wounds caused by insects and abiotic injuries, e.g. weather events like hail (Bottalico 1998).

Heavy infection with *Fusarium* spp. with typical stem rot symptoms, characterised by tan to pink or salmon discoloration and disintegration of the pith (Fig. 13), is often resulting from stress conditions weakening the plants, e.g. dryness or extreme wetness. Both are limiting the take-up of moisture and nutrients (Francis and Burgess 1975; Dodd 1980). Otherwise, pests like corn root worms, European corn borer or wireworms feeding on roots or tunnelling in maize stems can also cause stem or root rot (Chiang and Wilcoxson 1961; Gilbertson et al. 1986; Munkvold and Hellmich 2000; Gatch and Munkvold 2002). In later stages, white to light pink or salmon coloured fungal layers may be visible outside the

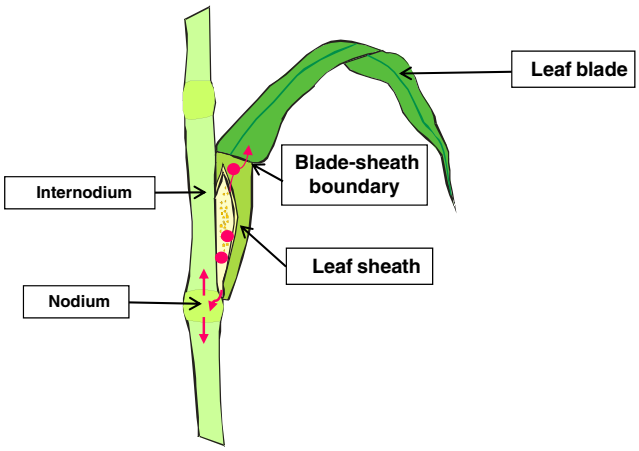

Fig. 12 Schematic diagram of *Fusarium* infection progress from infected rudimentary ear into adjacent tissues

Fig. 13 Symptoms of *Fusarium* stem and root rot. Symptoms of stem rot (**a**): disintegrated and *tan*, *pink* or *salmon* discoloured pith of the stem; Symptoms of root rot (**b**): *brownish-black* discolouration and stunted roots

nodes of infected stem parts (Fig. 14), which are prone to be broken especially at lower internodes in case of wind and storm. Root rot is leading to brownish/black discolouration and stunted roots resulting in the loss of its functionality (Fig. 13).

In diseased stem parts, diverse mycotoxins are produced by toxinogenic *Fusarium* species. Maize stalks from Italy and Austria, which were infected by *F. graminearum* or *F. culmorum* and *F. equiseti*, were contaminated with DON, 3-acDON, 15-acDON, ZEN and ZOH, respectively (Bottalico et al. 1985; Lew et al. 1997). *Fusarium*-infected stem parts, sampled from the lower half of maize plants below the main ear at the stage of silo maturity, showed low concentrations of DON (<1.5 mg kg^{-1}) both in node and internode sections, but node contamination started earlier and was related to DON contamination of the rudimentary ears (Oldenburg et al. 2005). These findings suggest that contamination of the stem resulted from *Fusarium* spp. progress via the node-attached peduncles of infected rudimentary ears. Schollenberger et al. (2012) detected rather low, but multi-contamination of both B- and A-type trichothecenes of some maize stalks from German fields ranging below 1 mg kg^{-1} (DON, 3-ac-DON, NIV, HT2, T2), except for 15-acDON reaching 1.5 mg kg^{-1}.

Seedling diseases caused by *Fusarium* spp.

Fusarium spp. are important pathogens causing seed rot, root rot or seedling blight of maize, leading to damping-off or weakened seedlings due to disturbances in germination and emergence (Dodd and White 1999). In particular, *F. verticillioides*, *F. proliferatum*, *F. subglutinans*, *F. graminearum*, *F. oxysporum* and *F. temperatum* are involved in seedling diseases (Kim et al. 1984; Kabeere et al. 1997; Munkvold and O'Mara 2002; Broders et al. 2007; Pintos Varela et al. 2013).

Seed rot is mainly resulting from damaged or infected low-quality seeds making them susceptible for soil- or seed-borne pathogen damage prior to germination. Symptoms of seedling blight may occur before or after emergence, showing brown discolouration of the seedlings already died off or light-yellowish discoloured and stunted seedlings (Fig. 15). When the root system is affected, symptoms may vary from brown zones on the roots and the coleoptile leading to reduced seedling vigour or to black discolouration indicating total root rot. Originating from low to moderate root infection, the fungi may reach the base of the maize plants, where rotting processes may proceed in the crown or stalk at later growth stages (Kim et al. 1984).

There might be a contribution of seed infection on ear infection by fumonisin-producing *F. verticillioides* growing systemically from seed to the ear (Bacon and Hinton 1996; Bacon et al. 2001). However, a study comparing the aggressiveness of fumonisin-producing and non-producing strains of *F. verticillioides* showed successful systemic infection of maize seedlings from the roots to the basal internodes, regardless of fumonisin production capacity of the fungal strains (Dastjerdi and Karlovsky 2015).

Impact of mycotoxin contamination of maize products on food and feed safety

Many factors, such as climate/weather conditions, plant cultivation/protection measures and stress conditions, affect in a complex manner the potential risk for infection of maize with *Fusarium* pathogens and mycotoxin contamination,

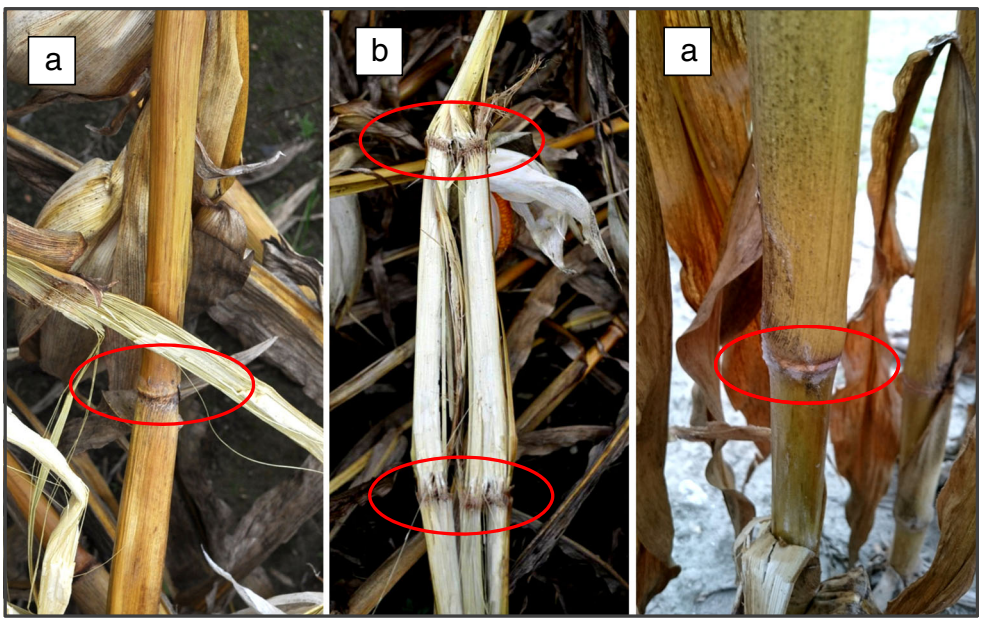

Fig. 14 *Fusarium* symptoms outside on nodes and inside the stem in late season at maize senescence. **a** *White* to *light pink* or salmon-coloured fungal layers on node. **b** Disintegrated and *reddish* discoloured node tissue

Fig. 15 Maize seedlings infected with *Fusarium graminearum*. **a** Discoloured and stunted seedlings, partly died-off. **b** *Brownish* discoloured coleoptiles

which was recently reviewed in detail by Ferrigo et al. (2016). Agricultural practises allowing an effective management to reduce mycotoxin accumulation risk are soil tillage ensuring a rapid decomposition of *Fusarium*-infected and contaminated plant debris, selection of low susceptible varieties, an extended crop rotation, a balanced fertilisation and insecticide treatment alone or in combination with fungicides where appropriate (Cotton and Munkvold 1998; Oldenburg and Höppner 2003; Blandino and Reyneri 2008; Blandino et al. 2008; Folcher et al. 2009; De Curtis et al. 2011; Dall'Asta et al. 2012; Balconi et al. 2014; Scarpino et al. 2015).

In general, the probability to gain highly mycotoxin-contaminated products of maize is increasing with prolonged growing time of the plants due to danger of a more severe disease progression (Reid and Sinha 1998; Reid et al. 2002). Depending on its usability for food or feed, maize is harvested at different maturity stages being best suitable for its nutritional value, successive conservation or subsequent technical processing. As grain maize used for crimping or drying is ready for harvest at 'fully ripe' stage and senescence (kernel dry matter 65–85%) in late season, the cultivation period of the plants is several weeks longer compared to forage maize used for ensiling, which is harvested earlier at 'dough' stage (whole crop dry matter about 32–35%, ear dry matter about 50%). Corn-cob mix is harvested in between at ear dry matter content of about 55%. Furthermore, distribution of mycotoxins within the maize plant is not homogeneous, but restricted to the different organs/zones that have been infected by the pathogens (Fig. 16). Therefore, mycotoxin contamination risk is regarded to be different for specific maize products intended to be used for food and feed.

The share of the harvestable ear in the total aboveground dry matter yield at maturity is ideally at least 50% (range 45–60%). Therefore, the ears are mostly responsible for quantity and quality of food and feed products. *Gibberella* and *Fusarium* ear rots are of major importance in affecting both quantity and quality of maize grain used for human and grain/ear products used for animal nutrition (Leslie et al. 1990; Munkvold 2003; Kleinschmidt et al. 2005; Morales-Rodríguez et al. 2007; Miller 2008; Van Asselt et al. 2012).

To ensure a high level of consumer protection, maximum levels for certain *Fusarium* mycotoxins (DON, ZEN, FB_1 + FB_2) in EU (EC 2007) were set in unprocessed maize, maize for direct human consumption and in processed maize-based foods, including special maize-based baby foods for infants and children. For the sum of T2 and HT2 toxins in maize grain and maize milling products intended for human consumption, indicative levels were defined (EC 2013).

For feeding purposes, guidance values for DON, ZEN, FB_1 + FB_2 in maize, maize products and by-products as well as for complementary and complete feedstuffs were specified according to the sensitivity of animal species (EC 2006, 2016). Due to a longer vegetation period, grain maize or corn-cob-mix production carries a higher contamination risk than forage maize. All measures to narrow down the danger of *Gibberella* and *Fusarium* ear rots should be exploited to fall below specified maximum and guidance values.

Maize ears with kernels showing symptoms of *Gibberella* ear rot usually contain considerably lower amounts of *Fusarium* mycotoxins than the connected rachis, which represents about 8–12% of the ear dry matter. Therefore, corn-cob mix is regarded as a more risky maize product compared to grain in animal feeding. Corn-cob mix is the most prone component to exceed the *Fusarium* toxin guidance values for complementary and complete feedstuffs set for pigs and certain pet animals, which are low due to their high sensitivity against *Fusarium* toxins (Tiemann and Dänicke 2007).

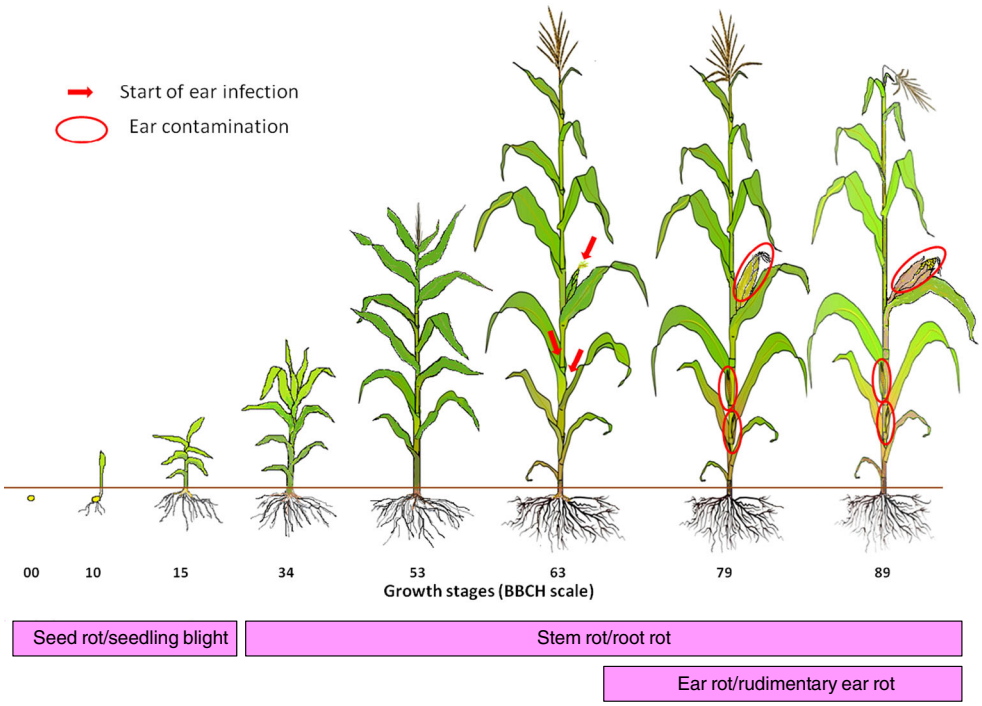

Fig. 16 *Fusarium* diseases of maize developing in the course of cultivation

For forage maize production, aboveground whole plant biomass except basal stem (stubble) is cut for ensiling, which includes all potentially *Fusarium*-infected and mycotoxin-containing vegetative and generative organs of the developed plants.

The rudimentary ears are the most probable heavy infected and contaminated structures at silage stage maturity, whilst the main ear usually is low to moderate affected by *Fusarium* spp. until this point in time. However, the rudimentary ears only stand for about 1% of the whole plant dry matter yield, so if even heavily contaminated with *Fusarium* toxins, it would not reach guidance levels specified for feed of ruminants, which is the predominant livestock fed with forage maize.

Leaf sheaths and husks of maize appear to be the main leaf parts being prone to *Fusarium* spp. infection, whereas the leaf blades representing about 22–30% of the plant dry matter yield usually remain either unaffected or just latently affected by *Fusarium* pathogens until senescence. As leaf sheaths and husk account for roughly 5% of the total dry matter yield and usually contain low *Fusarium* toxin concentrations, contamination of these organs is regarded to be of minor importance for forage maize safety.

Stem and root rot are predominantly leading to yield losses, especially when the disease is occurring during premature growth stages, resulting in disturbances in the plant nutrient/water supply, dry out and lodging. The associated *Fusarium* toxin accumulation in the stem, representing about 18–25% of the plant dry matter yield, may be involved in forage maize contamination, when cutting height is so low that infected basal parts get entry into the harvest material, which can be minimized by optimizing cutting height (Oldenburg and Höppner 2003).

Fusarium toxin contamination of nodes or internodes situated at higher position of the stem originating from preinfected rudimentary ears usually does not appear until senescence of the plants, when maturity stage of the plants is unsuitable for ensiling. However, in case of pest attack setting wounds into the stem, especially when caused by the European corn borer larvae, risk for *Fusarium* infection and toxin contamination increases endangering the quality of forage maize.

Fusarium seedling diseases of maize are of relevance for harvest yield in maize when of low or moderate severity, allowing plant development to reach the appropriate maturity stages. However, infection usually does not proceed throughout the whole plant, but remains restricted to the basal parts of the crop. A contribution to toxin contamination of harvest materials is therefore not likely, except in case of infection by *F. verticilliodes* which may develop an endophyte-like systemic growth within the maize plants.

Conclusion

Infection of maize with phytopathogenic and toxinogenic *Fusarium* spp. may occur throughout the vegetation period. This can cause different types of diseases in the affected vegetative or generative tissues of the plant (Fig. 16). Due to the major importance of ear diseases on quantity and quality of harvest products, growth stages from female flowering until grain maturity (BBCH codes 63–89; Meier 1997) are the most prone associated with *Fusarium* toxin contamination of maize intended to be used for food and feed.

Although heavy infections leading to high levels of *Fusarium* mycotoxin contamination can be prevented in maize production by applying effective agricultural management practises (Ferrigo et al. 2016), a total control of the pathogens is not achievable under natural conditions (Bryden 2012). This is mainly due to the great impact of climate/weather conditions influencing the complex and competitive biological interactions between the microbial and faunal members of the soil and the environmental conditions determining plant's growth and health in the field.

Therefore, infections with *Fusarium* spp. are and will remain an important risk endangering the quantity and quality of maize products, which in case of mycotoxin contamination may cause significant adverse effects on the health of humans and animals.

The surveillance of probable changes in the spectrum of pathogens, pests and mycotoxins affecting the plant's susceptibility against biotic attacks and the safety of feed and foodstuffs is recommended (Bryden 2012). A higher probability for changing risks with respect to mycotoxins due to predicted global warming is more expected for temperate regions of Europe (Paterson and Lima 2010). This applies especially fumonisin-producing *Fusarium* species, being more evident in southern countries so far (Bryla et al. 2013).

It is concluded that ongoing research is needed to recognize future risk which may alter or increase mycotoxin contamination of maize, but also to reinforce the development of suitable agricultural strategies to ensure safety in the maize-based food and feed chain.

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Compliance with ethical standards

Conflicts of interest None.

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