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REVIEW

Seed-borne diseases in pasture grasses and legumes: state of the art and gaps in knowledge

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Abstract
Information on fungal seed-borne diseases on main pasture grasses and legumes from the literature was reviewed. These diseases reduce biomass production, quality of forage, and persistence due to progressive plant mortality. The main fungal pathogens associated with forage seeds belong to the orders Hypocreales, Pleosporales, and Helotiales in the phylum Ascomycota. Hypocreales includes the genus *Fusarium*, which reduces seedling establishment, and contaminates plant tissues with mycotoxins. Pleosporales includes many genera associated with seeds of legumes (*Leptosphaerulina* and *Ascochyta*), grasses (*Bipolaris, Pyrenophora, Curvularia, Drechslera, Alternaria, Exserohilum*, and *Phoma*), and both (*Stemphylium*). Some fungal genera within this order induce the accumulation of coumestans (leafspot-producing fungi) or produce secondary metabolites that contaminate tissues (*Alternaria*). Within Helotiales, the main genera are *Sclerotinia* (affecting mainly legumes), *Clarireedia* and *Gloeotinia* (affecting grasses). *Pyricularia* (order Magnaporthales), *Colletotrichum* (order Glomerellales), and *Cercospora* (order Mycosphaerellales) also include seed-borne fungi that provoke diseases on forage species as well as *Rhizoctonia* (order Cantharellales) and *Ustilago* (order Ustilaginales) which belong to the phylum Basidiomycota. These pathogens affect pastures by (i) compromising seedling establishment at early stages and (ii) constraining growth by reducing yield and seed quality at later stages. Future research should address (i) generation of reliable data on forage yield loss due to seed-borne diseases, (ii) assessment of the interaction between seed-borne pathogens and other biotic and/or abiotic stresses, (iii) delve into the study of the role of wild and/or cultivated forage species as inoculum reservoirs of pathogens, and (vi) shed light on the contamination issue due to mycotoxins generation.

Keywords Seed-borne fungi · Diseases · Pastures · Forage species · Legumes · Grasses

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Introduction

A critical factor that is often overlooked when establishing pastures is the quality of the seed lot. A high-quality seed lot can produce a uniform and rapid germination and homogeneous seedling emergence under a wide range of environmental conditions (AOSA 1983). The quality of a seed lot is largely determined by its health status, among other seed attributes like botanical purity, moisture content, viability, vigour, mechanical damage, size, weight, and uniformity (Hampton 2002). Seed health status refers to the presence or absence of disease-causing organisms in seeds and pests like insects (Mlay 2013, Kumar and Gupta 2020). In grain crop, a significant effort has been put to provide farmers with healthy seed lots to attain a timely and quick seedling establishment. In the case of forage species there are gaps in knowledge in very similar areas despite sharing many diseases agents with crops.

Livestock production was historically based on the use of natural grasslands and pastures, where fungal diseases were not considered a significant problem. Nowadays, the development of improved pastures of high productivity through breeding, using (mostly) introduced legume and grass species, increased the attention focused on plant diseases causing economic losses to pastures (Clarke and Ealing 1994). Among these diseases, the ones produced by pathogens carried by seeds may provoke important losses in pastures due to: (i) emergence failures and the death of emerged seedlings (reducing the initial pasture stand), (ii) reduced biomass production and poor forage quality, (iii) low persistence, and (iv) reduced overwintering capacity (Altier 1996, Mikaliūnienė et al. 2015, You et al. 2008; Paseka et al. 2020). In addition, some seed-borne pathogens may (v) severely compromise forage seed production leading to pastures that need to be reseeded (Barbetti et al. 2006) and (vi) contaminate the animal feed with toxins (Barbetti et al. 2007). However, the information on seed-borne diseases occurring in pasture species is scattered (e.g. Jones 2022). So, in this work, we have gathered the available information to provide an easy and focused way to approach this topic.

This review aims to (i) briefly discuss key differences between field crops and pastures which may explain their differential disease assessment, (ii) provide a detailed description of the current knowledge about the major seed-borne pathogens causing diseases to pastures, and (iii) outline some gaps in knowledge related to the impact of seed-borne diseases on pasture establishment, productivity, quality, and safety. For this review, we have based our definition of the term 'seed-borne pathogens' on that of Baker (1979), to mean pathogens that are associated with seeds (thus, may be carried by them).

Disease assessment in pastures

A 'field crop' generally refers to species with an annual growth cycle. These species normally establish quickly, produce seeds, and are harvested, all in less than one calendar year, so they must be re-sown every year. They are grown to provide food (soybean, maize, wheat), fuel (maize, rapeseed, sugarcane), oil (sunflower, maize, soybean), and/or clothing (cotton, flax). 'Pasture' generally refers to a community of herbaceous species which have the purpose of feeding animals and are harvested by grazing. It is characterized by the predominance of species of herbaceous plants, especially grasses and legumes, which may be found in pure stands or in mixes. Pastures can be classified into: *(i)* introduced or cultivated (i.e. composed by species from other regions of the world, e.g. *Megathyrsus maximus* and *Melilotus albus* in Argentina), or *(ii)* native or wild (i.e. composed by species that are original or native and so grows spontaneously, e.g. *Trichloris crinita* in Argentina). The species composing cultivated pastures can be split into *(i)* short-lived annual or biannual species (e.g. *Lolium multiflorum*, *Bromus catharticus, Melilotus* spp., *Trifolium subterraneum*, *T. michelianum*, among others) and *(ii)* long-lived or perennial species (e.g. *Urochloa* spp., *Festuca arundinacea*, *Panicum* spp., *Dactylis glomerata, Agropyron elongatum, Phalaris* spp., *Medicago sativa, Trifolium repens, T. pratense, Lotus* spp., among others).

Seed-borne pathogens might be introduced into the pasture fields by sowing infested and/or infected seeds and so may be responsible for the introduction of diseases in new regions (Macchi-Borrell et al. 2013). Importantly, even a small percentage of infested/infected seeds can result in significant diseases in the field (Melo et al. 2017, Gawande et al. 2020). For example, an incidence of 0.06% of Stemphylium in lotus seeds may represent more than five thousand pathogen foci per hectare Altier (1996). Sowing seeds with a poor health status may cause germination failures and/or seedling death with reduced plant stands, reduced biomass production, poor forage quality, and low persistence in the subsequent pasture (Paseka et al. 2020). Pathogens affecting forage species are also known to reduce the overwintering capacity of plants, as seen in Trifolium pratense (Mikaliūnienė et al. 2015). It is important to note that plants in pastures often have multiple infections which complicate disease identification and diagnosis (Altier 1996).

A literature search was conducted to assess the number of reports addressing the problem of the seed-borne diseases in forage species when compared to field crop ones. The number of articles about seed-borne diseases found for forage/pasture species represented 16–18% of the total informed for crops (33.300–38.300 vs. 208.000 articles). The main field crops where seed-borne diseases were reported are wheat (33%), rice (30%), maize (21%), and soybean (16%), while in forage species stand out *Medicago* spp. (40%), *Trifolium* spp. (16%), *Lolium* spp. (13%), *Festuca* spp. (10%), and *Panicum* spp. (9%), among few others. The differential attention that has been given to pathogens affecting field crop species compared to the ones affecting forage species may be explained based on general differences between intrinsic (at the species level) and extrinsic (at the productive system level) features characterizing field crops vs. pastures. Annual field crops are generally uniform and harvested all at once, so the sanitary aspect is usually possible to be assessed by regular monitoring and the impact of diseases on yielding and the quality of their products are visible in the short term. In contrast, pastures are subject to management decisions concerning grazing, resting, and/or cutting. Grazing or cutting usually does not allow visualizing the intensity of diseases that might be present in a field due to the continuous removal of diseased foliage (by the animal or machinery). According to Altier (1996), the removal of diseased material may result in a temporary decrease in inoculum (which stops the development of diseases), but the presence of pathogens in stubble or abscinded leaves and stems on the ground ensures the survival of pathogens leading to a gradual increase in the inoculum in the field over the years.

Although the quantitative impact of diseases on the yield of the main field crops has been extensively evaluated, little is known about the quantitative impact of diseases on forage production. Exception to this are pastures for seed production, where the development of diseases follows similar patterns to those of annual field crops (for grain production) and so the effects of pathogens are easily measured making quantitative assessments possible (Altier 1996). In the case of pastures for grazing, diseases affect the number of plants regenerating and the stand persistence after the first year (Barbetti et al. 2006), so the problem may not be evident until the stand of plants is compromised, the progressive plant mortality is irreversible and/or the regeneration of swards (and yield loss) is visualized in the next season (Altier 1996, Barbetti et al. 2006). In other words, the reduction of yield and quality and the death of plants in pastures due to diseases are gradual but recurrent and cumulative, so they may not be visibly until forage production, and thus animal production, is affected (Xia et al. 2018). In addition, while field crops are mostly monocultured, pastures may involve a mixture of species giving place to a significantly more complex ecosystem, which results in increasing difficulties when assessing the sanitary aspect.

Major seed-borne fungal pathogens causing diseases to the main forage species

Seeds of forage species are frequently contaminated with impurities, e.g. clod, pieces of plants, microorganisms, and insects (dos Santos et al. 2014). Among the microorganisms, the largest number of species associated with forage seeds are fungi, then followed by bacteria, viruses, and lastly nematodes (dos Santos et al. 2014). This section provides a description of the main seed-borne fungal pathogens of forage species used in pastures worldwide. The text is organized according to the phylum, order and then genus of the fungi (based on Mycobank Database, https://www.mycobank.org, and on Index Fungorum, http://www.indexfungorum.org). Also, summarizing tables with the important data are provided for ease of ID of the main seed-borne diseases, causal agents, symptoms (or other features), and affected forage species. The main pathogens which can be found associated with forage seeds belong to the orders Hypocreales (Table 1), Pleosporales (Table 2), and Helotiales (Table 3). Other fungi that may be often found associated with seeds of forages are classified within the orders Magnaporthales, Glomerellales, and Mycosphaerellales, which also belong to the phylum Ascomycota, and Cantharellales and Ustilaginales which belong to the phylum Basidiomycota (also summarized in Table 3).

Order hypocreales

The main genera of seed-borne fungi causing diseases to forage species within the order *Hypocreales* are *Fusarium* and *Claviceps* (Table 1). Species of the genus *Fusarium* generally provoke failures during germination and seedling establishment, thus compromising the stand of future plants in the field. Species of the genus *Claviceps* are floral pathogens that replace the seeds with sclerotia, therefore guarantying their selves their survival, perpetuation in the field, and dissemination to new areas (see references and details in Table 1). These genera include some species with the capability to produce mycotoxins, which may result in mycotoxicosis in animals feeding on contaminated plants.

Genus Fusarium

The genus *Fusarium* includes several pathogenic species associated with seed rot and drowning of seedlings during preemergence, and damping-off during postemergence on multiple pasture temperate and tropical species of grasses and legumes (Altier 1996, Zarza and González 2010; Wiewióra 2011). Seedlings are susceptible during a critical initial period of 5–10 days, after which all plant tissues (except for the root tips) become less susceptible due to the thickening of the secondary cell wall (Altier 1996). Some *Fusarium* species are mycotoxigenic and their toxins may produce mycotoxicosis if consumed by animals when feeding (Castañares et al. 2019, Ekwomadu et al. 2021).

Among the *Fusarium* species affecting legumes, Wakelin et al. (2016) reported the *F. incarnatum-equiseti* complex (FIESC) as the causal agent of the root rot of *Trifolium alexandrinum* (Egyptian clover or berseem clover) in New Zealand, a disease characterized by leaf drooping and tiller death. The *F. solani* species complex (FSSC) is cited by Gawande et al. (2020) as the causal agent of the root and crown rot and seedling blight, the most destructive disease of *Melilotus indicus* (sweet clover) and *Trifolium resupinatum* (Persian clover). This disease is known to severely affect young seedlings by wilting and blight. In adult plants, a generalized yellowing, withering, stunting, and wilting may be observed as the pathogen colonize and block the vascular tissues. The primary inoculum sources are infected seeds and infected residues in the field, and the development of the disease is favoured by certain edaphic conditions (e.g. high moisture, a high percentage of organic matter, and warm temperature) and nematode injuries. *F. avenaceum* is reported as the causal agent of the widespread root rot disease of *Trifolium subterraneum* (subterranean clover)

Table 1 Summary table showing the main seed-borne fungal pathogen of the order Hypocreales (phylum Ascomycota) provoking diseases to forage species, host species, symptoms, and a backup of the references in the international literature

Genus	Fungus species	Host species	Symptoms/involved organs/others[1]	References
Fusarium	*Fusarium* spp.	Forage legumes	Seed rot, drowning of seedlings (preemergence), damping-off (postemergence)	Altier (1996), Zarza and González (2010), Wiewióra (2011)
		Species of *Festuca* and *Lolium*	Postemergence damping-off, plant blight	Wiewióra (2011)
		Megathyrsus maximus, Urochloa brizantha	Seed death, reduced seed germination and seedling emergence percentage	Melo et al. (2017), Martins et al. (2017), da Silva et al. (2019)
		Urochloa brizantha, U. decumbens	–	Lasca et al. (2004)
	F. incarnatum-equiseti complex	*Trifolium alexandrinum*	Root rot, leaves drooping, tillers death	Wakelin et al. (2016)
	F. solani complex	*Melilotus indicus, Trifolium resupinatum*	Root and crown rot, seedling blight	Gawande et al. (2020)
	F. avenaceum	*Trifolium subterraneum, Medicago* spp.	Root rot	Nik and Parbery (1977)
	F. tricinctum complex, *F. avenaceum*, *F. incarnatum-equiseti* complex, *F. chlamydosporum* complex, *F. graminearum* complex	*Medicago* spp.	Poor germination, low seedling growth, toxins production	Lamprecht et al. (1990), Barbetti et al. (2006)
	F. fujikuroi complex	*Medicago sativa*	Root rot	Cong et al. (2016)
	F. oxysporum complex, *F. solani* complex	*Trifolium subterraneum, Lotus corniculatus*	Crown and root rot	Ayala (2001), O'Rourke et al. (2009)
	F. culmorum	*Lolium perenne, Festuca arundinacea*	Seed rot, seedling death	Clarke and Eagling (1994)
	F. oxysporum complex, *F. fujikuroi* complex, *F. pallidoroseum*	*Cenchrus ciliaris*	Plant dieback	Mlay (2013)
	F. avenaceum, *F. incarnatum-equiseti* complex	*Agrostis capillaris, Cynosorus cristatus*	Seed rot, seedling death	Varga et al. (2006)
	F. incarnatum-equiseti complex	*Paspalum guenoarum*	Foliar lesions	Gasparetto et al. (2017)
	F. avenaceum, *F. solani* complex	*Lolium perenne*	Postemergence damping-off, plant blight	Wiewióra (2012)
	F. sambucinum complex	Species of *Paspalum, Chloris, Eragrostis,* and other species of the family Poaceae	Asymptomatic plants contaminated with mycotoxins	Nichea et al. (2022)
	F. dactylidis	Wild and cultivated grasses, including *Dactylis glomerata*	Mycotoxin production	Aoki et al. (2015)
	F. fujikuroi complex, *F. incarnatum-equiseti* complex, and *F. chlamydosporum* complex	Wild and cultivated grasses	Asymptomatic seeds	Costa et al. (2021)
	F. chlamydosporum complex, *F. proliferatum, F. poae,* and *F. verticillioides*	Mono- and dicotyledonous wild species	Asymptomatic tissues	Martínez et al. (2021)

Table 1 (continued)

Genus	Fungus species	Host species	Symptoms/involved organs/others[1]	References
Claviceps	*Claviceps* spp.	Species of *Urochloa*, *Paspalum*, *Andropogon*, *Setaria*, *Pennisetum*, *Agrostis*, *Phalaris*, *Bromus*, *Dactylis*, *Lolium*, *Poa*, *Agropyron*	Ergot, seed loss (replacement of ovaries by sclerotia), toxins production	Seaman (1980), Alderman et al. (2004), Alderman (2006), Gawande et al. (2020), Liu et al. (2021)
		Cenchrus ciliaris	Ergot	Mlay (2013)
	C. purpurea	Forage grasses	Ergot	Alderman et al. (2004), Shoukouhi et al. (2019), Liu et al. (2020)
	C. fusiformis	*Pennisetum glaucum*	Ergot	Miedaner and Geiger (2015), Abraham et al. (2019), Gawande et al. (2020)
	C. purpurea, *C. paspali*	*Lolium perenne*, *Paspalum dilatatum*, *Lolium multiflorum*	Ergot	Skipp and Hampton (1996), Pérez et al. (2013)
	C. paspali	*Paspalum distichum*	Ergot	Píchová et al. (2018), Wyka and Broders (2022)
	C. cynodontis	*Cynodon dactylon*	Ergot	
	C. purpurea	*Bromus* spp.	Ergot	

[1]When symptoms are not available in the cited literature, nothing, or other available key features regarding the effects of fungal infection/contamination (e.g. mycotoxins production) is informed

and species of *Medicago* in southern Australia (Nik and Parbery 1977). Also, Lamprecht et al. (1990) and Barbetti et al. (2006) identified *F. avenaceum*, together with the *F. tricinctum* species complex (FTSC), the FIESC, the *F. chlamydosporum* species complex (FCSC), and the *F. graminearum* species complex (FGSC), among the seed-borne *Fusarium* species causing poor germination, low seedling growth and the contamination with toxins (e.g. deoxynivalenol) in *Medicago sativa* (alfalfa, lucerne, or purple medic) in South Africa and Australia. Cong et al. (2016), reported *F. fujikuroi* species complex (FFSC) provoking root rot on *M. sativa* in China, a disease characterized by red-brown discolouration (necrosis) of vascular tissues within the root zone below the crown (with white mycelium appearing on the root), leaf chlorosis and wilt. The *F. oxysporum* species complex (FOSC) was reported to cause the crown and root rot of *Lotus corniculatus* (common bird's foot trefoil) in Uruguay and Argentina, followed in importance by the FSSC (Ayala 2001). O'Rourke et al. (2009) reported the FOSC as the causal agent of root diseases of *T. subterraneum*, being its severity significantly increased by the presence of other fungal species (e.g. *Ascochyta medicaginicola*).

Concerning grasses, *Fusarium* spp., are commonly found associated with seeds of *Megathyrsus maximus* (Guinea grass), *Urochloa brizantha* (palisade grass), and *U. decumbens* (signal grass), causing seed death and reducing germination and seedling emergence (Laca et al. 2004, Melo et al. 2017, Martins et al. 2017, da Silva et al. 2019). *F. culmorum* was reported associated with *Lolium perenne* (perennial ryegrass) and *Festuca arundinacea* (tall fescue) seeds in Australia and North America, leading to ungerminated seeds and seedling death (Clarke and Eagling 1994). *Fusarium* is also mentioned as commonly associated with *Cenchrus ciliaris* (foxtail buffalo grass or bloubuffelgras) seeds, being the FOSC, FFSC, and *F. pallidoroseum* the most frequent species (Mlay 2013). Varga et al. (2006) found *F. avenaceum* and the FIESC associated with seeds of *Agrostis capillaris* (common bent) and *Cynosorus cristatus* (crested dogtail grass), leading to seed rot and seedling death. The FIESC was also found associated with *Paspalum guenoarum* (wintergreen paspalum) seeds coming from plants with lesions affecting more than 50% of the leaf area (Gasparetto et al. 2017). *F. avenaceum* and the FSSC were found associated with *L. perenne* seeds, producing postemergence damping-off and seedling blight (Wiewióra 2012).

The genus *Fusarium* is widely known to comprise potentially toxicogenic species whose toxins may contaminate not only the products of field crops but also the forage of pastures. In Argentina, asymptomatic plants of species of *Paspalum*, *Chloris*, *Eragrostis*, as well as other species of the family Poaceae, were found to be contaminated with mycotoxins (e.g. trichothecenes) produced by the *F. sambucinum* species complex (FSAMSC; Nichea et al. 2022).

Table 2 Summary table showing the main seed-borne fungal pathogen of the order Pleosporales (phylum Ascomycota) provoking diseases to forage species, host species, symptoms, and a backup of the references in the international literature

Genus	Fungus species	Forage host species	Symptoms/involved organs/others	References
Leptosphaerulina	*L. trifolii*	*Trifolium repens, Medicago* spp.	Leaf and stem spots	Skipp and Hampton (1996), Clarke (1999), Barbetti et al. (2006)
Stemphylium	*S. botryosum*	*Medicago sativa*	Leaf spots	Skipp and Hampton (1996), Clarke (1999)
		Agrostis capillaris, Cynosorus cristatus, Lolium perenne	–	Varga et al. (2006), Wiewióra (2012)
	S. loti	*Lotus corniculatus*	Leaf spots	Ayala (2001)
Ascochyta	*A. medicaginicola*	Species of *Medicago, Trifolium subterraneum, T. fragiferum*	Black stem, leaf spots, poor establishment, severe decline in the productivity	Skipp and Hampton (1996), You et al. (2000), Barbetti et al. (2006), Akamatsu et al. (2008), Barbetti et al. (2006), Barbetti and You 2014), Gawande et al. (2020)
Bipolaris	*Bipolaris* spp.	Forage grasses	Leaf spots, stem, crown, and root rots	Wiewióra (2011), Mehboob et al. (2015)
		Urochloa brizantha, Crotalaria juncea, Megathyrsus maximus	Poor germination, leaf spots in seedlings	dos Santos et al. (2014), da Silva et al. (2019)
		Cynodon dactylon	Foliar lesions and necrosis, rotting of stems, roots, and crowns	Pratt (2005), Read and Pratt (2012)
	B. sorokiniana	*Cenchrus ciliaris*	Leaf spots in seedlings	Mlay (2013)
		Lolium perenne, Festuca arundinacea, F. rubra, Agrostis capillaris, Cynosorus cristatus	Necrotic lesions on the leaf tissue, plant blight and death	Clarke and Eagling (1994), Zang et al. (2006), Varga et al. (2006), Wiewióra (2011, 2012), Xia et al. (2018), Li et al. (2020
	B. oryzae	*Andropogon* spp.	–	dos Santos et al. (2022)
Drechslera	*Drechslera* spp.	*Cynosorus cristatus*	Weak germination, abnormal seedling growth, seedling killing	Varga et al. (2006)
		Species of *Agropyron, Thinopyrum* and *Bromus*	Low germination	Wiewióra et al. (2015)
	D. siccans, D. catenaria, D. dictyoides and D. andersenii	Species of *Lolium* and *Festuca*	Leaf net blotch	Wilkins (1973), Cromey (1985), Lam (1985), Xue et al. (2020)
	D. dictyoides, D. teres, D. poae, D. lolii, D. biseptata, D. dematioidea, D. nobleae	*Lolium multiflorum*	Leaf net blotch	Alfieri et al. (1984), Pennycook (1989), Pratt (2006), Roane (2009), Crous et al. (2011)
Pyrenophora	*P. lolii*	*Lolium perenne, L. multiflorum* and *Dactylis glomerata*	Brown blight	Clarke and Eagling (1994), Skipp and Hampton (1996)
	P. chaetomioides	Species of *Phalaris*	Leaf spots	Cegiełko et al. (2011), Kaur and Sharma (2021)
	P. dictyoides, P. triseptata, P. lolii	*Festuca rubra, Lolium perenne*	Leaf spots	Wiewióra (2011, 2012)

Table 2 (continued)

Genus	Fungus species	Forage host species	Symptoms/involved organs/others	References
Curvularia	*Curvularia* spp.	*Urochloa brizantha* and *U. decumbens*	Decreased germination, low seedling emergence, spots on seedlings leaves, seedling death, leaf, and stem spots	Lasca et al. (2004)
	C. penniseti	*Pennisetum glaucum*	Leaf spots, seedling death	Gawande et al. (2020)
	C. lunata	*Setaria italicum, Cynodon dactylon, Lolium perenne, Cenchrus ciliaris,* species of *Andropogon*	Leaf spots, seedling death	Yago et al. (2011), dos Santos et al. (2018, 2022), Brecht et al. (2007), Mlay (2013), Wiewióra (2012)
	C. spicifera	*Cynodon dactylon* and *Festuca arundinacea*	Damping-off of seedlings	Chun et al. (2003)
	C. hawaiiensis and *C. lunata*	*Cynodon dactylon*	Leaf spot, leaf tip necrosis	Pratt (2003), Brecht (2005)
Alternaria	*Alternaria* spp.	*Megathyrsus maximus* and *Urochloa mutica*	–	Supritha et al. (2020)
		Trifolium repens	Leaf spots	Wang et al. (2020)
		Wild grasses	Contaminated with mycotoxins	Nichea et al. (2015)
		Mouldy grass silages	Contaminated with mycotoxins	Penagos-Tabares et al. (2022)
		Andropogon spp.	–	dos Santos et al. (2022)
		Cenchrus ciliaris	Leaf spots	Mlay (2013)
	A. alternata	*Lolium perenne*	Ungerminated seeds, abnormal seedlings	Wiewióra (2012)
		Forage-derived feed	Contaminated with mycotoxins	Yu et al. (1999)
	A. infectoria complex, *A. tenuissima* complex, *A. alternata*	Species of *Agropyron*, *Bromus, Festuca, Dactylis, Phalaris, Lolium*	–	Dugan and Lupien (2003), Zhou et al. (2015)
	A. tenuissima complex, *A. alternata*, and *Alternaria* spp.	Cultivated legume and grass forages	Contamination with mycotoxins	Kononenko et al. (2015)
Exserohilum	*Exserohilum* spp.	*Urochloa brizantha*	Leaf and stem spots	da Silva et al. (2019)
		Urochloa brizantha, U. decumbens	–	Lasca et al. (2004)
	E. rostratum	*Pennisetum glaucum*	Leaf blight	Gawande et al. (2020)
		Cenchrus ciliaris, Cynodon dactylon	–	Mlay (2013), Pratt (2003)
Phoma	*Phoma* spp.	*Megathyrsus maximus, Urochloa brizantha*	Low germination, seed death, reduction of seedling emergence percentage	Marchi et al. (2010), dos Santos et al. (2014), Melo et al. (2017), Martins et al. (2017), da Silva et al. (2019)
		Urochloa brizantha, U. decumbens	Low germination, spots on seedlings leaves, seedling death	Lasca et al. (2004)
		Cenchrus ciliaris	Low germination, seed death, reduction of seedling emergence percentage	Mlay (2013)

When symptoms are not available in the cited literature, nothing, or other available key features regarding the effects of fungal infection/contamination (e.g. mycotoxins production) is informed

Table 3 Summary table showing seed-borne fungal pathogens of the orders Helotiales, Magnaporthales, Glomerellales, Mycosphaerellales (phylum Ascomycota), and Cantharellales and Ustilaginales (phylum Basidiomycota), host species, symptoms, and a backup of the references in the international literature

Order/genus	Fungus species	Forage host species	Symptoms/involved organs/others	References
Helotiales *Sclerotinia*	*S. trifoliorum*	*Trifolium alexandrinum, T. pratense, T. repens, T. subterraneum, T. resupinatum, Medicago sativa, Lotus corniculatus*	Crown and root rot, plant wilt	Barbetti and You (2014), Gawande et al. (2020), Mikaliūnienė et al. (2015), Scott and Evans (1980), Skipp and Hampton (1996), Kanbe et al. (2002), Ayala (2001)
Helotiales *Clarireedia*	*C. homoeocarpa*	*Poa pratensis, Agrostis stolonifera, Festuca rubra, Cynodon dactylon, Paspalum vaginatum*	Leaf spots	Couch and Bloom (1960), Rioux et al. (2014), Espevig et al. (2015, 2017), Entwistle et al. (2018), Hu et al. (2019)
Helotiales *Gloeotinia*	*G. granigena, G. temulenta*	Species of *Lolium* and *Festuca*	Blind seed, poor germination	Skipp and Hampton (1996), Mebalds and Price (2008, 2009)
	G. temulenta	Species of *Agrostis, Lolium, Festuca, Bromus* and *Poa*	Low germination	Alderman (2001)
Magnaporthales *Pyricularia*	*Pyricularia* spp.	Species of *Cenchrus, Lolium, Pennisetum*	Leaf blast or blight	Rivera et al. (2015), Zhang et al. (2016)
	P. oryzae	Species of *Setaria* and *Eleusine*	Leaf blast	Zhang et al. (2016)
		Species of *Eragrostis, Setaria, Urochloa, Lolium, Festuca, Bromus*		Valent et al. (2019)
		Lolium multiflorum		Vincelli et al. (2008)
	P. grisea	*Digitaria sanguinalis*	Leaf blast	Zhang et al. (2016), Valent et al. (2019)
		Festuca arundinacea	Grey leaf spots	Tredway et al. (2005)
		Pennisetum glaucum	Leaf spots, leaf blast	Sharma et al. (2018), Singh et al. (2021)
		Cenchrus ciliaris	Leaf blight	Mlay (2013), Rivera et al. (2015)
		Urochloa brizantha, U. decumbens	–	Marchi et al. (2005), Martins et al. (2017)
	P. pennisetigena	*Pennisetum glaucum*	Leaf blast	Valent et al. (2019)
Glomerellales *Colletotrichum*	*Colletotrichum* sp.	*Urochloa brizantha*	–	Martins et al. (2017)
	C. acutatum	*Lotus corniculatus*	Flower blight	Altier (1996), Ayala (2001)
	C. trifolii, C. destructivum	*Medicago sativa*, *M. truncatula, T. pratense*	Dark localized lesions in leaves and stems, flower drooping (known as anthracnose)	Mould et al. (1991), O'Neil et al. (1996), Skip and Hampton (1996), Frate and Davis (2007), Torregrosa et al. (2004), Barbetti and You (2014), Gawande et al. (2020)
	C. graminicola	*Lolium perenne, L. multiflorum, Bromus willdenowii, Dactylis glomerata, Festuca arundinacea*	Leaf spots, leaf blight	Skipp and Hampton (1996)

Table 3 (continued)

Order/genus	Fungus species	Forage host species	Symptoms/involved organs/others	References
Mycosphaerellales *Cercospora*	*Cercospora* sp.	*Megathyrsus maximus*	–	Melo et al. (2017)
	Cercospora spp.	*Agrostis, Urochloa, Bromus, Cenchrus, Pennisetum, Cynodon, Festuca, Panicum, Paspalum, Setaria,* and *Lolium*	Leaf spots	Braun et al. (2015), Victoria-Arellano et al. (2021)
	C. zebrina	*Trifolium repens*, *T. pratense, T. subterraneum*	Leaf spots	Skipp and Hampton (1996)
	C. medicaginis	*Medicago* spp.		Barbetti et al. (2006)
Cantharellales *Rhizoctonia*	*R. solani*	*Melilotus indicus*	Plant blight, black stem	Gawande et al. (2020)
		Species of *Trifolium* and *Lotus*	Root and crown rot, damping-off	Alteri 1996), You et al. (2008), You and Barbetti 2014
		Pennisetum glaucum, P. typhoides	Seed rot, damping-off during pre and post seedling emergence, leaf and sheath blight, discolouring and death of roots	Wilson (2000), Gawande et al. 2020
		Festuca rubra and species of *Lolium*	Plant blight, brown patch	Stephens and Davoren (1997), Wiewióra (2011)
Ustilaginales *Ustilago*	*U. bullata*	Species of *Bromus, Lolium* and *Festuca*	Head smuts	Fischer (1953), Falloon and Hume (1988), Falloon and Rolston (1990), Iannone et al. (2017)
	U. striiformis complex	Species of *Agrostis, Agropyron, Dactylis, Poa, Setaria, Phalaris, Bromus, Festuca,* and *Lolium*	Leaf-stripe smuts	Smiley et al. (2005), Alderman et al. (2007), Vánky (2012), Savchenko et al. (2014), Kruse et al. (2018)

When symptoms are not available in the cited literature, nothing, or other available key features regarding the effects of fungal infection/contamination (e.g. mycotoxins production) is informed

F. dactylidis is cited by Aoki et al. (2015) as a fungal species affecting several wild and cultivated grasses, e.g. *Dactylis glomerata* (cock's foot or orchard grass) and producing mycotoxins (nivalenol *in planta* and zearalenone in vitro). Through pathogenicity tests, the authors found also that the fungus may induce mild head blight on wheat, suggesting the key role of this species as an inoculum source of the disease in wheat. In accordance, Costa et al. (2021) isolated many *Fusarium* species (mainly members of the FFSC, the FIESC, and the FCSC) from asymptomatic seeds of wild and cultivated grasses collected in Brazil and show that these species not only harbour a high diversity of already known *Fusarium* species which affect maize, sorghum, rice, and sugarcane but also novel species. In line with these discoveries, Martínez et al. (2021) isolated members of the FCSC, the FFSC, *F. proliferatum*, and *F. poae* from asymptomatic plant tissues (stems, leaves, and inflorescences) of different mono- and dicotyledonous wild species. The authors evaluated the pathogenicity of the fungal species for wheat and barley and concluded that weeds may act as reservoirs of *Fusarium* species, highlighting the importance of weed control within the integrated disease management of field crops.

Genus Claviceps

Species of this genus are floral pathogens that infect the ovaries which are then replaced by ergot bodies or sclerotia. The symptoms of the disease appear during the flowering stage when a secretion (full of conidia) may be observed flowing (as honey dew) from the infected inflorescence of the panicles (Gawande et al. 2020). The fungus overwinters as sclerotia, which then germinate producing stromata with ascospores (primary inoculum). Secondary infections occur through the production of conidia (macro and/or micro conidia, depending on the fungal species) in the infected tissues during the honey dew phase (Alderman et al. 2004). In contrast to some cereals, where the ergot bodies may reach up to two centimetres in length, in forage grasses, they usually remain small and slender (Seaman 1980). Sclerotia may fall from the head to the soil before or during the harvest or may be harvested together with the seeds (thus being mixed with them). Open-pollinating (outcrossing) grasses are more susceptible to the infection than the self-pollinating (self-fertilized) ones because they allow easy access to the fungus into the flower (Miedaner and Geiger 2015). Broadleaf species are not susceptible to the ergot (Seaman 1980). Sclerotia of many *Claviceps* species contain toxic alkaloids which can poison animals if present in feed (Alderman et al. 2004; Píchová et al. 2018, Abraham et al. 2019).

Species of *Claviceps* are cited as common fungi causing the ergot disease to important forage grasses worldwide, e.g. *Paspalum, Andropogon, Setaria, Urochloa, Pennisetum*, *Agrostis, Phalaris, Bromus, Dactylis, Lolium, Poa, Agropyron, and Cenchrus* (Seaman 1980, Alderman et al. 2004; Alderman 2006; Mlay 2013; Gawande et al. 2020; Liu et al. 2021). In North America, *C. purpurea* is the predominant species with a wide host range including cereal crops and forage grasses (Alderman et al. 2004; Shoukouhi et al. 2019; Liu et al. 2020). *C. fusiformis* was cited causing the ergot of *Pennisetum glaucum* (pearl millet) a disease considered one of the most important biotic constraints to pearl millet production in Asia, Africa, and North America as it may decrease yielding in a 70% under the favourable weather conditions (Miedaner and Geiger 2015, Abraham et al. 2019, Gawande et al. 2020). *C. purpurea* and *C. paspali* were reported to cause the ergot disease to *L. perenne* and *Paspalum dilatatum* (dallisgrass) in New Zealand (Skipp and Hampton 1996) and *Lolium multiflorum* (annual ryegrass or Italian ryegrass) in South America (Pérez et al. 2013). Píchová et al. (2018) and Wyka and Broders (2022) mention *C. paspali, C. cynodontis*, and *C. purpurea* affecting *Paspalum distichum* (knotgrass), *Cynodon dactylon* (Bermuda grass), and species of the genus *Bromus* (respectively) in South Africa. Grasses of the genus *Bromus* may act as the primary source of *Claviceps purpurea* inoculum in barley fields, which, as mentioned before, highlights the key role of grasses as secondary hosts of field crop diseases (Wyka and Broders 2022). Despite the importance of the disease, it is rare to find seed lots containing more than 1% ergot (by weight) because sclerotia can be detected in the field before harvest, and the harvest and cleaning processes often remove most of this contaminant (Skipp and Hampton 1996).

Order Pleosporales

Pleosporales includes the major number of genera that includes seed-borne pathogens of forage species (Table 2). Among them, *Leptosphaerulina* and *Ascochyta* include species that may be found associated with seeds of forage legumes, provoking foliage diseases. *Stemphylium* may be found affecting both, legumes, and grasses, producing reductions on germination and seedling emergence. The genera *Bipolaris, Pyrenophora, Curvularia, Drechslera, Alternaria*, *Exserohilum,* and *Phoma* affect mainly grasses causing leaf-spots, being some of them related to low seed germination and/or abnormal seedling development.

Genus Leptosphaerulina

The Leptosphaerulina leaf and stem spot (also known as Pepper spot) of forage legumes, provoked by species of this genus, is a disease characterized by small brown spots surrounded by a pale halo appearing on the leaflets, which may enlarge (acquiring a tan aspect with an irregular brown border) and kill the leaves (Clarke 1999). *L. trifolii* was reported as producing this disease on *T. repens* and species of *Medicago* in New Zealand, Australia, South Africa, and North America (Skipp and Hampton 1996, Clarke 1999; Barbetti et al. 2006). This fungus is known to induce the accumulation of oestrogenic coumestans (e.g. coumestrol) in plants, which negatively affects feeds nutritional quality and safety as these molecules may cause animal infertility (Skipp and Hampton 1996).

Genus Stemphylium

The Stemphylium leaf spot of *M. sativa* is provoked by the fungus *S. botryosum* (Skipp and Hampton 1996, Clarke 1999). It is a common disease characterized by oval or irregular, slightly sunken, dark brown leaf spots (often surrounded by a pale-yellow halo), which may be concentrically ringed (resembling a target) when older (Clarke 1999). It may provoke defoliation when severe. *S. botryosum* was found associated with seeds of the grasses *A. capillaris*, *C. cristatus,* and *L. perenne* in Europe (Varga et al. 2006, Wiewióra 2012). Another species, *S. loti*, was reported by Ayala (2001) causing leaf spots on *L. corniculatus* in Uruguay.

Genus Ascochyta

Ascochyta includes a species, *A. medicaginicola,* which causes the spring black stem and leaf spot of *M. sativa.* It has been reported in New Zealand (Skipp and Hampton 1996), Western Australia (Barbetti et al. 2006), and North America (Akamatsu et al. 2008). The initial symptoms of this disease are small, brown spots on leaves, petioles, and stems, which enlarge and coalesce as the disease progresses (Gawande et al. 2020). The pathogen may cause reductions in biomass production and seed yield of about 16% and 20% (respectively) if the pasture is grazed, whereas in non-grazed swards losses of biomass and seed yield may achieve 32 and 53%, respectively (Barbetti et al. 2006; Barbetti and You 2014). You et al. (2000) highlight the contamination of seeds with this pathogen as the main cause of the severe decline in the productivity of *Medicago*-based pastures in Western Australia, being also responsible for the poor establishment of pastures in this area. Ascochyta black stem disease is also cited as one of the most frequently occurring and important diseases on annual *Medicago* species in Europe, North America, and South Africa (Barbetti et al. 2006). *A. medicaginicola* also affects other legume species like *T. subterraneum* and *T. fragiferum* (strawberry clover) provoking the clover black stem and leaf spot, a very common disease among these clovers (Barbetti et al. 2007, Barbetti and You 2014).

Genus Bipolaris

Bipolaris includes seed- and soil-borne species which provokes leaf spots as well as stem, crown, root rots, stunting, and dieback (thinning) of stands of grasses, e.g. *U. brizantha*, *Crotalaria juncea* (sunn hemp or Indian hemp), *M. maximus*, *C. dactylon,* and *C. ciliaris* (Pratt 2005; Wiewióra 2011; Read and Pratt 2012; Mehboob et al. 2015). *Bipolaris* species in seeds lower germination and cause leaf spots to seedlings (dos Santos et al. 2014; Silva et al. 2019). *B. sorokiniana* is cited as the causal agent of the leaf spot disease of Poaceae species like *L. perenne, F. arundinacea*, *Festuca rubra* (red fescue), *A. capillaris*, and *C. cristatus* (Clarke and Eagling 1994, Zang et al. 2006, Varga et al. 2006, Wiewióra 2011, 2012, Xia et al. 2018, Li et al. 2020). *B. oryzae* is cited by dos Santos et al. (2022) as associated with seeds of grass species of the genus *Andropogon* in Brazil.

Genus Drechslera

Drechslera includes the seed-borne species which affect grasses provoking the net blotch, the Drechslera leaf spot or the brown leaf spot (Clarke and Eagling 1994, Skipp and Hampton 1996). Many species of *Drechslera* were found in association with seeds of *Cynosorus, Agropyron*, *Thinopyrum*, and *Bromus* leading to poor germination, abnormal seedling growth or even death (Varga et al. 2006; Wiewióra et al. 2015). *D. siccans*, *D. catenaria, D. dictyoides,* and *D. andersenii* were cited producing the net blotch disease of species of *Lolium* and *Festuca* (Wilkins 1973, Cromey 1985, Lam 1985, Xue et al. 2020). Particularly concerning *L. multiflorum*, several *Drechslera* species were reported from many places: *D. dictyoides, D. teres, D. poae,* and *D. lolii* in North America (Alfieri et al. 1984; Pratt 2006; Roane 2009), *D. biseptata* in Germany (Crous et al. 2011), and *D. dematioidea* and *D. nobleae* in New Zealand (Pennycook 1989).

Genus Pyrenophora

Pyrenophora includes seed-borne species which provoke the brown blight disease of grasses. *P. lolii* is cited as the causal agent of this disease of *L. perenne, L. multiflorum,* and *D. glomerata* (Clarke and Eagling 1994, Skipp and Hampton 1996), while *P. chaetomioides* was reported producing leaf spots on grasses of the genus *Phalaris* in Europe, North and South America and Africa (Cegiełko et al. 2011; Kaur and Sharma 2021). Wiewióra (2011, 2012) mentioned the species *P. dictyoides, P. triseptate,* and *P. lolii*, which can be found associated with seeds and provoking leaf spots in *F. rubra* and *L. perenne*.

Genus Curvularia

Curvularia includes seed-borne species which provoke leaf-spots to grass species of *Urochloa* (Lasca et al. 2004), *Pennisetum* (Gawande et al. 2020), *Setaria* (Yago et al. 2011), *Andropogon* (dos Santos et al. 2018, 2022), *Cynodon* (Brecht et al. 2007), *Lolium* (Wiewióra 2012), and *Cenchrus* (Mlay 2013). The disease is characterized by typical small brown spots (surrounded by a yellow halo) in the leaves, which may grow and coalesce forming large lesions (Gawande et al. 2020; dos Santos et al. 2018, 2022). The pathogen is also known to cause low germination and seedling emergence, spots on seedling leaves and seedling death (Lasca et al. 2004). *C. penniseti* was reported to provoke the leaf spot disease and seedling death in *P. glaucum* (Gawande et al. 2020). *C. lunata* was observed causing seedling death of *Setaria italicum* (foxtail millet), and the spot disease of species of *Andropogon*. *C. lunata* is also the most frequent fungus found in association with seeds of *C. dactylon* in North America (Brecht et al. 2007), *L. perenne* in Europe (Wiewióra 2012), and *C. ciliaris* in Africa (Mlay 2013). *C. spicifera* was reported in Korea associated with *C. dactylon* and *F. arundinacea* seeds imported from North America and causing damping-off to seedlings (Chun et al. 2003). *C. lunata* and C. *hawaiiensis* were reported as the causal agents of the leaf spot and leaf tip necrosis disease in *C. dactylon* (Pratt 2003; Brecht 2005).

Genus Alternaria

Alternaria is considered a common genus when evaluating the health status of seeds of grasses as reported for *M. maximus* (Supritha et al. 2020)*, Urochloa mutica* (para grass or buffalo grass; Supritha et al. 2020), *C. ciliaris* (Mlay 2013), and species of *Andropogon* (dos Santos et al. 2022). *A. alternata* is commonly found associated with seeds of *L. perenne*, provoking ungerminated seeds and abnormal seedlings (Wiewióra 2012). *A. infectoria* complex*, A. tenuissima* complex*,* and *A. alternata* were reported in North America attached to seeds of *Agropyron, Bromus, Festuca, Dactylis, Phalaris,* and *Lolium* (Dugan and Lupien 2003, Zhou et al. 2015). The *A. tenuissima* complex and *A. alternata* were isolated from cultivated legume and grass forage species in Russia (Kononenko et al. 2015). Although many works mention *A. alternata* as associated with forage species, Andersen et al. (2015) suggest that this is a rare species and most of the strains originally identified as such belong to the *A. tenuissima* complex, the *A. arborescens* complex or other *Alternaria* complex. *Alternaria* species were also reported provoking the Alternaria leaf spot disease of legumes like *T. repens*, being found associated with seeds (Wang et al. 2020).

Many species within the genus *Alternaria* can produce a wide range of compounds (e.g. alternariol) with suspected toxic properties and harmful effects on animals, including genotoxicity, as well as mutagenic and teratogenic effects (Gallo et al. 2015; Nichea et al. 2015; Kononenko et al. 2015). Although secondary metabolites of *Alternaria* spp. have been studied as contaminants of the main field crop species (Chiotta et al. 2020), there are only a few reports on the natural occurrence of these compounds in forage species and their derived feeds. In this regard, Yu et al. (1999) found *A. alternata* metabolites (i.e. AAL toxins) in forage-derived hay and mouldy feeds. Similarly, Nichea et al. (2015) found a high prevalence of metabolites (e.g. alternariol monomethyl ether) in natural grasses intended for cattle grazing in Argentina. The authors highlight the difficulty to evaluate the risk of the presence of *Alternaria* toxins in feed due to the scarce database describing the occurrence of these mycotoxins in feedstuffs and the lack of knowledge regarding their effects on animal health. Kononenko et al. (2015) reported a high incidence of the *Alternaria* metabolite alternariol as regularly occurring in samples of legume and grass forages in Russia. In Austria, Penagos-Tabares et al. (2022) analysed mouldy grass silages and found toxins (e.g. tenuazonic acid and alternariol among other mycotoxins) commonly produced by *Alternaria* species and emphasize the role of mouldy grass silage as a substantial contributor of mycotoxins in cattle diets.

Genus Exserohilum

Seed-borne species of *Exserohilum* may be found associated with seeds of grass species as reported for *U. brizantha* and *U. decumbens* (Silva et al. 2019, Lasca et al. 2004), and species of *Pennisetum* (Gawande et al. 2020), *Cenchrus* (Mlay 2013), and *Cynodon* (Pratt 2003). The fungus can cause leaf and stem spots in seedlings and adult plants (Silva et al. 2019). *E. rostratum* is mentioned by Gawande et al. (2020) as the causal agent of the leaf blight disease of *P. glaucum,* characterized by dark brown spots appearing on leaves, which later turn to light brown and coalesce giving the leaves a blighted appearance. The same species was found associated with seeds of *C. ciliaris* in Africa (Mlay 2013) and *C. dactylon* in North America (Pratt 2003).

Genus Phoma

Phoma includes species which can be found associated with seeds of grasses like *M. maximus* and *U. brizantha* in Brazil (Marchi et al. 2010, dos Santos et al. 2014, Melo et al. 2017, Martins et al. 2017, Silva et al. 2019). Lasca et al. (2004) reported a species of *Phoma* associated with *U. brizantha* and *U. decumbens* seeds compromising seed germination and seedling emergence and survival and producing spots on leaf of seedlings prior to perish. Several species of this genus were reported as associated with seeds of *C. ciliaris* in Africa (Mlay 2013), provoking low germination, seed death and reduction of seedling emergence.

Order Helotiales

Helotiales includes three genera of fungi that may be found associated with seeds of forage species: *Sclerotinia*, which affects mainly legumes with the crown and root rot, *Clarireedia* which affect mainly grasses producing typical leaf spots, and *Gloeotinia* that affects grasses lowering seed germination (Table 3).

Genus Sclerotinia

Sclerotinia species are cited as the causal agent of the Sclerotinia crown and root rot or Sclerotinia wilt of forage legume species. The disease is characterized by a soft rot of the crown and roots which leads to plant wilt and death as the disease shows (under moist conditions) a white fungal mycelium with black sclerotia covering the dead tissues (Barbetti and You 2014). Sclerotia may survive in the soil for several years or arrive in the field during the sowing (mixed with seeds), thus functioning both seeds and soil as primary inoculum sources (Scott and Evans 1984).

Sclerotinia trifoliorum is considered the causal agent of the most destructive disease of forage clovers with a worldwide distribution (Skipp and Hamptom 1996). The species is cited as the aetiology agent of the root rot of *T. alexandrinum* (Gawande et al. 2020), *T. pratense* (red clover; Mikaliūnienė et al. 2015), *T. repens* (white clover; Scott and Evans 1980), *T. subterraneum* (Skipp and Hampton 1996), *T. resupinatum* (Gawande et al. 2020), *M. sativa* (Skipp and Hampton 1996, Kanbe et al. 2002), and *L. corniculatus* (Ayala 2001).

Genus Clarireedia

Clarireedia includes the causal agent of dollar spot disease which was found to affect grasses (Salgado-Salazar et al. 2018; Sapkota et al. 2022). The disease is characterized by light tan-coloured lesions on the leaves, bordered by a reddish-brown band, being common (especially in turfgrasses) to observe the presence of small (dollar size) spots of pale, bleached plants (Salgado-Salazar et al. 2018). The pathogen is known to overwinter mainly in the soil and plant debris. *C. homoeocarpa* was cited affecting *Poa pratensis* (Kentucky bluegrass or common meadow-grass), *Agrostis stolonifera* (creeping bentgrass), *F. rubra* and *C. dactylon* in North America and Europe (Couch and Bloom 1960, Espevig et al. 2015, 2017, Entwistle et al. 2018) and *Paspalum vaginatum* (seashore paspalum) in China (Hu et al. 2019). As it was found associated with commercial seeds of *A. stolonifera*, seeds appear to be a potential source of *C. homoeocarpa* inoculum (Rioux et al. 2014).

Genus Gloeotinia

Gloeotinia includes two species, *G. granigena* and *G. temulenta*, known to provoke the blind seed disease of grasses (Skipp and Hampton 1996, Mebalds and Price 2008, 2009). Many grass species are susceptible to *G. temulenta* around the world, including important forage species and turfgrasses of the genera *Agrostis, Lolium, Festuca, Bromus,* and *Poa* (Skipp and Hampton 1996, Alderman 2001; Mebalds and Price 2008, 2009). The disease is known to affect only the seed and lower the germination percentage to less than 10% in severely infected seed lots; thus, it is considered the most important cause of seed germination failures in grasses (Alderman 2001). Infected seeds are shrivelled, rough on the surface, and show rusty brown or pinkish, being hard to differentiate infected seeds from the healthy ones unless the lemma and palea are removed (Alderman 2001; Mebalds and Price 2008, 2009). Conidia can be seen on the seed surface as a waxy pale pink spore secretion or slime (Alderman 2001).

Other seed-borne fungal pathogens affecting forage species

Other orders within the Ascomycota phylum that include species commonly found in association with seeds of forage species are Magnaporthales (genus *Pyricularia*), Glomerellales (genus *Colletotrichum*), and Mycosphaerellales (genus *Cercospora*; Table 3). The phylum Basidiomycota also have many pathogens within the orders Cantharellales (genus *Rhizoctonia*) and Ustilaginales (genus *Ustilago*; Table 3).

Genus Pyricularia

Pyricularia species has been reported associated with seeds of grass species of *Cenchrus, Lolium*, *Setaria, Eleusine*, and *Pennisetum,* provoking the leaf blast disease of adult plants (Rivera et al. 2015; Zhang et al. 2016). This disease is characterized by water-soaked foliar lesions that enlarge and become necrotic, eventually resulting in extensive chlorosis, and drying of young leaves (Vincelli et al. 2008; Rivera et al. 2015; Zhang et al. 2016, Valent et al. 2019). *P. oryzae* was reported associated with seeds of *Setaria* and *Eleusine* (Zhang et al. 2016) and provoking the blast disease to species of *Eragrostis, Setaria, Urochloa, Lolium, Festuca, Bromus* (Vincelli et al. 2008, Valent et al. 2019). *P. griseae* is mentioned by many authors producing leaf blight and leaf spots to *Digitaria sanguinalis* (hairy crabgrass; Zhang et al. 2016, Valent et al. 2019), *F. arundinacea* (Tredway et al.

2005), *P. glaucum* (Sharma et al. 2018, Singh et al. 2021), *C. ciliaris* (Mlay 2013; Rivera et al. 2015), *U. brizantha,* and *U. decumbens* (Marchi et al. 2005; Martins et al. 2017). This species is considered one of the most important seed-borne pathogens of grasses, as it can severely affect forage production and quality as well as seed production (Mlay 2013; Rivera et al. 2015; Zhang et al. 2016). *P. pennisetigena* was cited as the causal agent of the leaf blast disease of *P. glaucum* (Valent et al. 2019). Gladieux et al. (2018) and Valent et al. (2019) considered *P. oryzae* as a single species with major crop-adapted lineages (*Eragrostis, Lolium, Triticum, Urochloa, Oryza,* and *Setaria* linages, among others), completely separated from *P. grisea* (which affects *D. sanguinalis*) and *P. pennisetigena* (which affects *P. glaucum*). Castroagudín et al. (2017) highlight the importance of grass species within the life cycle of the genus *Pyricularia* as these hosts may function as inoculum sources of the wheat blast disease, providing a temporal and spatial bridge connecting crop fields across the countries.

Genus Colletotrichum

Colletotrichum includes seed-borne fungi known to provoke the anthracnose disease of legumes species like *Urochloa brizantha* (Martins et al. 2017). The symptoms of this disease are leaflets and flower drooping, dark localized lesions in leaves and stems (stems turn brownish and bend, especially the tender ones), and crown rot (Gawande et al. 2020). It is spread by the seed, which is usually contaminated with spores during the threshing process, and the pathogen may also survive from season to season in infested residues (Barbetti and You 2014). *C. acutatum* was reported to produce the flower blight disease of *L. corniculatus* in Uruguay (Altier 1996, Ayala 2001), a disease of particular concern in pastures for seed production. *C. trifolii* and *C. destructivum* are mentioned as the causal agents of the anthracnose of *M. sativa* (Mould et al. 1991, O'Neil et al. 1996, Skip and Hampton 1996, Barbetti et al. 2006; Frate and Davis 2007), *M. truncatula* (barrel medic; Torregrosa et al. 2004), and the most susceptible one, *T. pratense* (Barbetti and You 2014). Although legumes are the main target of *Colletotrichum* species, *C. graminicola*, was cited provoking foliage diseases of grasses like *L. perenne*, *L. multiflorum*, *Bromus catharticus* (prairie grass), *D. glomerata,* and *F. arundinacea* (Skipp and Hampton 1996).

Genus Cercospora

Cercospora genus includes species of pathogens of many legumes and grasses, provoking leaf spots diseases that can seriously threaten the performance, productivity and/or yields of forages by reducing the leaf photosynthetic area (Chand et al. 1954). *C. zebrina* was cited causing the Cercospora leaf spot of *T. repens*, *T. pratense* and *T. subterraneum* (Skipp and Hampton 1996), while *C. medicaginis* was reported as the causal agent of this disease of species of *Medicago* in Australia and North America (Barbetti et al. 2006). Regarding grasses, a species of *Cercospora* was found associated with *M. maximus* seeds, and its high presence was suggested to depend on the cleaning machinery (employed to improve the quality of seeds before commercialization), which accumulates fungal structures and provokes damages on seeds, both resulting in increased fungal incidence (Melo et al. 2017). Also, *Cercospora* species were reported as the causal agent of leaf spot diseases of species of *Agrostis*, *Urochloa*, *Bromus*, *Cenchrus*, *Pennisetum*, *Cynodon*, *Festuca*, *Panicum*, *Paspalum*, *Lolium,* and *Setaria* (Braun et al. 2015, Victoria-Arellano et al. 2021).

Genus Rhizoctonia

Rhizoctonia comprises a species, *R. solani,* which provokes the root and crown rot of legumes species of the genera *Melilotus, Trifolium, Lotus, and Medicago* (Alteri 1996, You et al. 2008; You and Barbetti 2017; Gawande et al. 2020). The blight or black stem disease caused by *R. solani*, a common disease of *M. indicus* and species of *Trifolium* and *Lotus,* is characterized by greyish to small brown patches which initially appear on stems and then coalesce provoking severe blight and defoliation (Alteri 1996, Gawande et al. 2020). The fungus is also mentioned provoking damping-off at postemergence and root rot to *Trifolium* species (You et al. 2008; You and Barbetti 2017), and the root, stem, and crown rot of *M. sativa* (Samac et al. 2013) and *M. truncatula* (Batnini et al. 2021).

Regarding grasses, *R. solani* is the causal agent of the leaf and sheath blight disease of *P. glaucum* (Wilson 2000; Gawande et al. 2020) and *P. typhoides* (Khairnar 2015, Sher et al. 2019). The infection develops during seed germination and seedling growth, and it is characterized by seed rot, lesions in the collar zone of young seedlings and damping-off during pre- and postemergence, which compromise the pasture's establishment (Gawande et al. 2020). In adult plants, usual symptoms include spots, accelerated leaf senescence, and root discolouration and death. *R. solani* was found associated with seeds of *F. rubra* and species of *Lolium*, being the causal agent of the brown patch or the blight disease, which affect these species (Stephens and Davoren 1997, Wiewióra 2011).

Genus Ustilago

Ustilago includes species known to provoke head or leaf smuts to forage grasses. These fungi may overwinter in plant debris as dormant mycelium or as teliospores in the soil and seeds (Vánky 2012). One of the most common head smuts of grasses is caused by *U. bullata* which has been reported to have several cultivated and wild grasses as hosts, being species of *Bromus, Lolium,* and *Festuca* among them (Fischer 1953). This systemic fungus infects the host from the seed soon after the emergence of the coleoptile, it asymptomatically colonizes the meristem and grows inside the host, so the disease becomes visible at the anthesis when the ovaries of the infected plants are destroyed and replaced by a black mass of sori with teliospores (Iannone et al. 2017). The disease may provoke reduction of seedling establishment, scarce biomass production, and poor persistence (Falloon and Hume 1988, Falloon and Rolston 1990). *U. striiformis* species complex produces the leaf-stripe smut of species of *Agrostis, Agropyron, Dactylis, Poa, Setaria, Phalaris, Bromus, Festuca,* and *Lolium* (Smiley et al. 2005; Alderman et al. 2007; Vánky 2012; Savchenko et al. 2014; Kruse et al. 2018). This disease is characterized by long brown parallel striae running over the leaf blades from where black spore masses are released after the spores have matured beneath the epidermis of the leaves (Kruse et al. 2018). Leaf blades may curl down, turn brown, shred, and die, and, in severe infections, growth may be delayed, and inflorescence development inhibited (Vánky 2012). The severity of this disease may reach 10% of the infected plants and provoke significant economic losses (Savchenko et al. 2014).

Main problems caused by seed-borne fungal diseases in cultivated pastures and gaps in knowledge

Seed-borne fungal diseases in pastures originate problems from the sowing (immediate effects) to the productivity of pastures (down-stream effects) (Fig. 1). The problems caused by these pathogens include (i) reduced seed germination, (ii) uneven seedling emergence, (iii) weak and uncompetitive

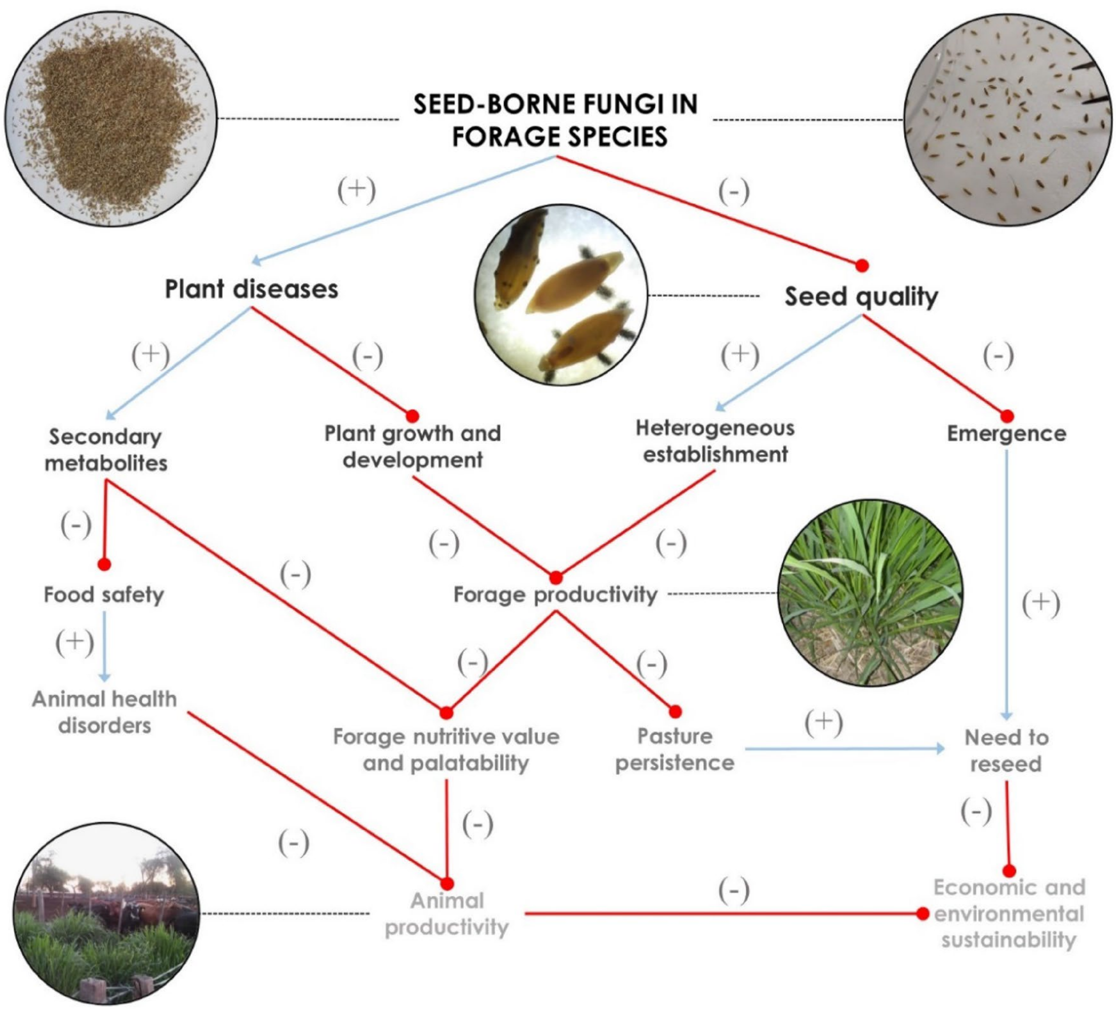

Fig. 1 Scheme of the main variables and processes affected by seed-borne fungi in forage species. Blue arrows indicate promotion or increase (also indicated with "+"), while red arrows indicate decline or reduction (also indicated with "– ") of these variables

seedlings, and sometimes (iv) necessity to reseed (Skipp and Hampton 1996, Mlay 2013; Leath 2019; Gawande et al. 2020). Later, other problems may appear in pastures planted to infected seeds that include (i) restricted plant growth, (ii) heterogeneous stand development (both in monocultures and mixtures of species), (iii) reduced seed production to below the levels needed to maintain the desired species dominance, (iv) increased senescence and death of plants leading to low stand persistence, and (v) low yield and poor quality of seeds for the natural reseeding in annual species (Barbetti et al. 2006; O'Rourke et al. 2009). An additional difficulty arising from seed fungal infection is the increase in the concentration of secondary metabolites (e.g. phytoestrogens, tannins, phenols, and mycotoxins), which can potentially affect the safety of feed and may lead to health disorders in cattle or even avoidance of feed (Barbetti and You 2014). This problem, together with decreases in the forage nutritional value (due to less protein and/or soluble carbohydrates content, lower dry matter digestibility) and palatability (Pottinger et al. 1993; Barbetti et al. 2006) reduce the quality of the forage so that impact negatively on grazing (Altier 1996).

Some fungal species may provoke diseases to both forage and crop species (Ellis et al. 2004; Martínez et al. 2021; Wyka and Broders 2022, Nichea et al. 2022), being important to highlight the role of wild and/or cultivated forage species as inoculum reservoirs of fungal pathogens affecting crops. The increased cost and side effects of control measures and the decreased earnings because of seed loss or lower pricing related to poor seed quality should also be considered among the impacts of fungal diseases (Barbetti et al. 2006; Mlay 2013).

Despite the efforts made towards understanding some important seed-borne diseases, there are several critical gaps in knowledge that should be guide future research on this area: (i) the information available about seed-borne pathogens is scattered, (ii) quantitative data is limited, (iii) the interaction between seed-borne pathogens and/or other diseases and abiotic stresses (drought, flooding, nitrogen deficiency, etc.), often co-occurring at field conditions, has rarely been investigated (but see Kirkpatrick et al. 2006; Sinha et al. 2019), (iv) effects over pasture persistence has not been evaluated, which might involve anticipated resowing and increased costs over time, and (v) the economic impact, in general, is mainly unknown.

Conclusions

Information on seed-borne diseases on pastures is limited and scattered when compared to large-acreage annual crops. The main pathogens found associated with forage seeds belong to the orders Hypocreales, Pleosporales, and Helotiales within the Ascomycota Phylum. These pathogens may affect pastures (i) at early stages by compromising germination and seedling establishment and (ii) at later stages by constraining growth, reducing yield and the nutritional value of the forage, and decreasing seed quality. Additionally, some fungal infections may increase the concentration of secondary metabolites reducing the safety of feeds. Future research should be directed towards the: (i) generation of reliable data on forage yield loss due to seed-borne diseases, (ii) assessment of the interaction between seed-borne pathogens and other biotic and/or abiotic stresses, (iii) delve into the study of the role of wild and/or cultivated forage species as inoculum reservoirs of pathogens, and (vi) shed light on the contamination issue due to mycotoxins generation.

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Declarations

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