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REVIEW: PATHOGEN PROFILE

Fusarium basal rot: profile of an increasingly important disease in *Allium* spp.

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Abstract
Fusarium basal rot (FBR) is a soil-borne disease that affects *Allium* species worldwide. Although FBR has long been recognized as a major constraint to the production of economically important *Allium* species, information that could support disease management remains scattered. In this review, the current knowledge on the causal agents, symptomology and epidemiology, impact, and management strategies of FBR is synthesized. We highlight that FPR is associated with different complexes of several *Fusarium* species, of which *Fusarium oxysporum* and *F. proliferatum* are the most prevalent. These pathogenic complexes vary in composition and virulence, depending on sites and hosts, which can be challenging for disease management. Research to improve disease management using chemical pesticides, resistance cultivars, biocontrol agents, and cultural practices has achieved both promising results and limitations. Finally, research needs and future directions are proposed for the development of effective FBR management strategies.

Keywords *Fusarium oxysporum* · *Fusarium proliferatum* · Diversity · Phenology · Specialization of pathogens · Virulence variability

Introduction

Allium is a genus of monocotyledonous flowering plants that includes more than 600 species, of which onion (*Allium cepa* L.), leek (*A. ampeloprasum* var. *porrum* L.), shallot (*A. cepa* var. *ascalonicum* L., *A. cepa* var. *aggregatum* L.), garlic (*A. sativum* L.), and chive (*A. schoenoprasum* L.) are the most studied edible species (Maude 1998).

Although the majority of the common *Allium* species are originally native to Asia, they are now widely cultivated in different countries and climates, ranging from sub-tropical to temperate climates (Marrelli et al. 2018). In 2019, the global onion planted area is estimated to 5.192.651 ha, which represents a production of 99.968.016 t (FAO 2020). China, India, the USA, and Egypt are the main producing countries, with quantities mounting to 24,966,366, 22,819,000, 3,170,270, and 3,081,047 t for onions, respectively. The volume for garlic produced globally is 30,708,243 t substantial, whereas the production of fresh *Allium* (onions, shallots) and leeks (including other alliaceous vegetables) only reached 4,491,246 t and 2,192,467 t, respectively (FAO 2020). *Allium* species are used not only for culinary preparations (Swamy and Veere Gowda 2006) but are also popular for medicinal purposes because most of them are rich in many bioactive compounds such as vitamins, carotenes, minerals, antioxidants, and antibiotic metabolites (Havey 1993; Sharifi-Rad et al. 2016).

Allium species can be grown from dried sets, bulblets (cloves), or seeds (Kamenetsky and Rabinowitch 2017). Long-term vegetative propagation occurs commonly in *Allium* crops, promoting the selection and adaptation of pathogens to *Allium* cultivars of diverse climatic and geographic regions (Katis et al. 2012). Despite their broad geographical distribution, *Allium* species are generally very sensitive to climate and soil. *Allium* species that produce bulbs such as onions and garlic generally require high temperature and bountiful sunshine, especially in the period from bulb growth to harvest. They also grow well in a loamy soil with well irrigation and

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excellent drainage (Kamenetsky and Rabinowitch 2017; Choudhary 2018). Poorly drained soil not only affects flavor and bulb development but also leads to the growth of diseases, especially soil-borne diseases.

Allium species are susceptible to a variety of fungal pathogens such as *Fusarium* spp., *Colletotrichum* spp., *Alternaria* spp., *Peronospora* spp., *Botrytis* spp., and *Phoma* spp., among others (Sharifi-Rad et al. 2016). Especially, *Fusarium* basal rot (FBR) is a major limitation to *Allium* production worldwide. FBR is also known as *Fusarium* rot or *Fusarium* wilt or basal plate rot of *Allium* spp. (Bayraktar et al. 2010; Stankovic et al. 2007). It is sometimes referred to "damping-off" or "die-back" disease of the seedlings (Kintega et al. 2020).

Despite the widespread occurrence of FBR in *Allium* spp., information on the disease is fragmented. The current work delves into the disease in terms of causal agents, impacts, symptomatology and epidemiology, population variability, and management strategies, highlighting knowledge gaps and research perspectives.

Causal agents of FBR

Globally, FBR of *Allium* spp. has been reported in Asia, Europe, the Americas, and Africa (Dauda et al. 2018; Dugan et al. 2003; Fletcher et al. 2017; Gálvez 2017; Gunaratna et al. 2019; Koike et al. 2003; Quesada-Ocampo et al. 2014; Ravi et al. 2014; Le et al. 2020). The disease has been associated with different species of *Fusarium*, including *F. oxysporum*, *F. proliferatum*, *F. solani*, *F. acuminatum*, *F. redolens*, *F. verticillioides*, *F. equiseti*, *F. culmorum*, *F. falciforme* and *F. brachygibbosum*, of which *F. oxysporum* and *F. proliferatum* are the most prevalent (Table 1).

Although FBR could also be caused by single *Fusarium* species (Dugan et al. 2003; Stankovic et al. 2007; Tirado-Ramírez et al. 2018a), a complex of different *Fusarium* species has been frequently found to be responsible for basal rot in *Allium* (Delgado-Ortiz et al. 2016; Ghanbarzadeh et al. 2014), which complicates identification and disease management. In addition, a correct estimation of the importance of each species in the disease complex is not easy. Even more compounding, the composition of the FBR pathogenic complex appears to vary with geographic regions and plant hosts and is also dynamic within and between growing seasons. For example, a complex of *F. oxysporum*, *F. proliferatum*, and *F. redolens* was responsible for basal rot of onion in Finland (Haapalainen et al. 2016), while *F. oxysporum*, *F. proliferatum*, *F. verticillioides*, *F. solani*, and *F. acuminatum* were co-associated with basal rot of garlic in North Central Mexico (USA) (Delgado-Ortiz et al. 2016). Similarly, while most of the aforementioned species were found in onions, *F. acuminatum* and *F. verticillioides* were found only in garlic, and *F. culmorum* was found only in leek plants with similar symptoms (Table 1).

Impact

FBR results in yield and quality losses in *Allium* spp. both pre- and post-harvest in many parts of the world (Coşkuntuna and Özer 2008; Taylor et al. 2013). Disease incidence varies greatly (Köycü and Özer 1997), depending on the pathogenicity of *Fusarium* species, disease intensity, the susceptibility of varieties, and the plant's phenological stages (Cramer 2000).

Exact data on the impact of FBR on yield are scarce; however, 45% loss in yield and about 12–30% of bulb loss in storage have been reported in shallot (Sintayehu et al. 2011). Although onion can get infected by *Fusarium* spp. at any point in its developmental stage, losses due to FBR vary among growth stages and between regions (Cramer 2000). Among damping-off pathogens, *Fusarium* spp. can contribute to up to 70% of damage in nurseries (Mishra et al. 2014). *Fusarium* spp. also affect bulbs, causing losses up to 50% in the field and from 30 to 40% in storage, as was, for example, reported in Asia by Gupta and Gupta (2013) and Mishra et al. (2014). FBR was observed to affect 50% of seedlings in African fields (Dauda et al. 2018), whereas in southern New Mexico (USA), the disease incidence for fall-planted cultivars and spring-planted cultivars reached 40% and 29%, respectively (Cramer 2000). Even when cultivated in virgin soil, the presence of FBR is quite high as observed in Zambia, where 80–90% of the transplants were infected by *F. oxysporum* f. sp. *cepa*, resulting in enormous losses in post-transplanting seedlings (44%) and potential yield (69%) (Naik and Burden 1981). The level of losses is usually higher in organic farms than in conventional farms (Haapalainen et al. 2016).

The production of other *Allium* species is also influenced by FBR. In garlic, FBR has been associated with 60% loss of both bulbs and seed crops (Cramer 2000; Sankar and Babu 2011), and about 10–60% of clove losses in storage (Cramer 2000; Quesada-Ocampo et al. 2014). Similarly, the transplanting of infected seedlings resulted in an increase of more than 50% of the disease in greenhouse leek in coastal California, causing significant economic losses (Koike et al. 2003). FBR has also been reported to impact the conservation of *Allium* germplasms, with the destruction of 20% of bulbs of *A. giganteum* (an ornamental *Allium* species) at a germplasm resource center in Yunnan Province, China, in 2013 (Zhang et al. 2016). Previously, *F. oxysporum* f. sp. *cepae* and *F. proliferatum* were responsible for severe losses of seed and clonal garlic collections of the National Plant Germplasm System in Pullman, WA, in 2002–2003 and 2005–2006 (Dugan et al. 2007). As FBR infection is favored by high temperature, the losses were projected to increase in the future due to climate change (Cramer 2000).

Table 1 *Fusarium* spp. associating with basal rot disease of *Allium* spp

Species	Hosts	Symptoms	Countries	References
F. oxysporum	Onion	Basal rot	USA	Abawi and Lorbeer 1971
		Seedling death Basal rot	USA	Cramer 2000
		Basal rot	Zambia	Naik and Burden 1981
		Basal rot	Finland	Haapalainen et al. 2016
		Damping-off	Serbia	Stankovic et al. 2007
		Basal rot	Turkey	Bayraktar et al. 2010
		Damping-off Basal rot	Iran	Ghanbarzadeh et al. 2014
		Basal rot	India	Manimaran et al. 2011
		Basal rot, Damping-off	Israel	Kalman et al. 2020
	Onion	Damping-off Basal rot	Vietnam	Le et al. 2020
	Garlic	Blossom-end rot	Mexico	Delgado-Ortiz et al. 2016
		Clove rot	USA, China	Dugan et al. 2003
		Damping-off	Serbia	Stankovic et al. 2007
	Shallot	Basal rot	Hungary	Sintayehu et al. 2011
F. oxysporum	Welsh onion Leek	Basal rot Damping off Damping off	Vietnam	Le et al. 2020
F. proliferatum	Onion	Basal rot	USA	Dugan et al. 2003
		Basal rot Damping-off	Vietnam	Le et al. 2020
		Basal rot	Finland	Haapalainen et al. 2016
		Basal rot, Damping-off	Israel	Kalman et al. 2020
		Seedling rot	Serbia	Stankovic et al. 2007
		Damping-off Basal rot	Iran	Ghanbarzadeh et al. 2014
		Bulb rot (purple, reddish)	India	Ravi et al. 2014
		Salmon blotch	Israel	Fletcher et al. 2017
		Basal rot	Serbia	Klokocar-Smit et al. 2008
		Salmon blotch	USA	du Toit et al. 2003
		Chlorosis, dry leaf tips, bulb rot	Argentina	Salvalaggio and Ridao 2012
	Garlic	Chlorosis and dry leaf tips, bulb rot	Argentina	Salvalaggio and Ridao 2012
		Bulb rot, tan to salmon-pink	USA	Quesada-Ocampo et al. 2014
		Bulb rot	USA	Dugan et al. 2003
		Bulb rot, tan lesion	India	Sankar and Babu 2011.
		Blossom-end rot	Mexico	Delgado-Ortiz et al. 2016
		Seedling rot	Serbia	Stankovic et al. 2007
F. proliferatum	Garlic	–	Germany	Seefelder et al. 2002
	Garlic	Bulb rot	Hungary	Simey 1990
		Bulb rot	Spain	Gálvez et al. 2017
		Basal, clove rot	Italia	Tonti et al. 2017
F solani	Onion	Damping off	Serbia	Klokocar-Smit et al. 2008
		Basal rot	Sri Lanka	Gunaratna et al. 2019
			Iran	Ghanbarzadeh et al. 2014
		Damping off	Vietnam	Le et al. 2020
	Garlic	Blossom-end rot	Mexico	Delgado-Ortiz et al. 2016

Table 1 (continued)

Species	Hosts	Symptoms	Countries	References
	Welsh onion	Basal rot Damping off	Vietnam	Le et al. 2020
F. acuminatum	Garlic	Blossom-end rot	Mexico	Delgado-Ortiz et al. 2016
F. equiseti	Onion	Die-back	Nigeria	Dauda et al. 2018
F culmorum	Leeks	Basal rot	Spain California	Armengol et al. 2001 Koike et al. 2003
F. falciforme	Onion	Basal rot	Mexico	Tirado-Ramírez et al. 2018b
F. brachygibbosum	Onion	Bulb rot	Mexico	Tirado-Ramírez et al. 2018a
F. redolens	Onion	Bulb rot	Finland	Haapalainen et al. 2016
		Damping off Basal rot	Iran	Ghanbarzadeh et al. 2014
F. verticillioides	Garlic	Blossom-end rot	Mexico	Delgado-Ortiz et al. 2016
F. acutatum	Onion	Basal rot, Damping-off	Israel	Kalman et al. 2020
F. anthophilium	Onion	Basal rot, Damping-off	Israel	Kalman et al. 2020

Symptomatology and epidemiology

Primary inoculum causing FBR in *Allium* spp. often originates from soil and seeds (Ozer et al. 2004). Under favorable conditions, this inoculum can infect and colonize the host, resulting in disease symptoms. Infection and disease development are favored by moisture and high soil temperatures, with an optimum temperature of 28–32 °C (Abawi and Lorbeer 1972). Generally, FBR diseases can occur at all stages of *Allium* development (Taylor et al. 2019), but seedlings and dormant- or postharvest bulbs are the most susceptible (Cramer 2000).

Primary infection of *Fusarium* spp. occurs when the fungus penetrates directly into roots or through wounds on roots or on the basal parts of bulb scales (Bayraktar et al. 2010; Cramer 2000; Gutierrez et al. 2006). In early stages of germination, the infection results in a delay of seedling emergence (Gutierrez and Cramer 2005; Gutierrez et al. 2006) or damping-off of the seedlings (Fig. 1f) (Galeano et al. 2014; Kintega et al. 2020; Saxena and Cramer 2009). *Fusarium* pathogens also cause a loss of transplanted seedlings (Fig. 1a). Some infected seedlings can still survive but are poorly developed and stunted in growth. Occasionally, the pathogens infect plants in the seedling stage, but symptoms become more conspicuous during crop maturity or after harvest (Kintega et al. 2020). This was observed with several specific isolates of *Fusarium* spp., which were inoculated at the seedling stage (Kintega et al. 2020).

The first signs of mature plants being infected are the yellowing of leaves, followed by symptoms of withered and curly leaf. Subsequently these symptoms begin to spread downwards (Fig. 1b). Rotting of bulbs and the appearance of root abscission layer are noticeable symptoms of infection, leading to easily uprooting bulbs from roots (Fig. 1c). When the disease symptoms become severe, rotting of the entire bulb plates could occur and the development of white mycelium on the surface of bulbs or the basal areas of exterior bulb scales could be observed easily (Fig. 1d and e) (Cramer 2000; Lee et al. 2012). When infection occurs late in the season, symptoms may not be apparent at harvest but become advanced during storage (Cramer 2000; Retig et al. 1970).

Similar symptoms were observed on leek and other *Allium* spp. where affected roots appeared gray to pink, water soaked, or rotted. Infected roots and basal plates also form abscission layers separated easily from the rests of plant when uprooting. Seedlings, transplants, and mature plants could be all infected by the pathogen, causing a poor growth, chlorosis of old leaves, and collapse of plants (Fig. 1a) (Armengol et al. 2001; Koike et al. 2003).

FBR is a soil-borne disease (Cramer 2000; Köycü and özer 1997). The causal agents can survive either as chlamydospores in soil or as saprophytes in crop residues. Chlamydospores are particularly important, as they persist under adverse conditions with the absence of hosts for many years (Köycü and Özer 1997; Cramer 2000). Thus, the movement of infested soils plays a critical role in short distance spread of FBR. *Fusarium* spp. in *Allium* can produce micro- and macro-conidia, but their contribution to the transmission of FBR still remains unknown. The pathogen is also transmitted by latently infected planting materials (bulbs, transplants). A seed-borne mechanism has been revealed in certain cases such as *F. oxysporum* f. sp. *cepae* in onion (Köycü and Özer 1997), and *F. culmorum* in leek (Koike et al. 2003). Weeds can contribute to the survival, proliferation, and spread of this pathogen (Abawi and Lorbeer 1972;

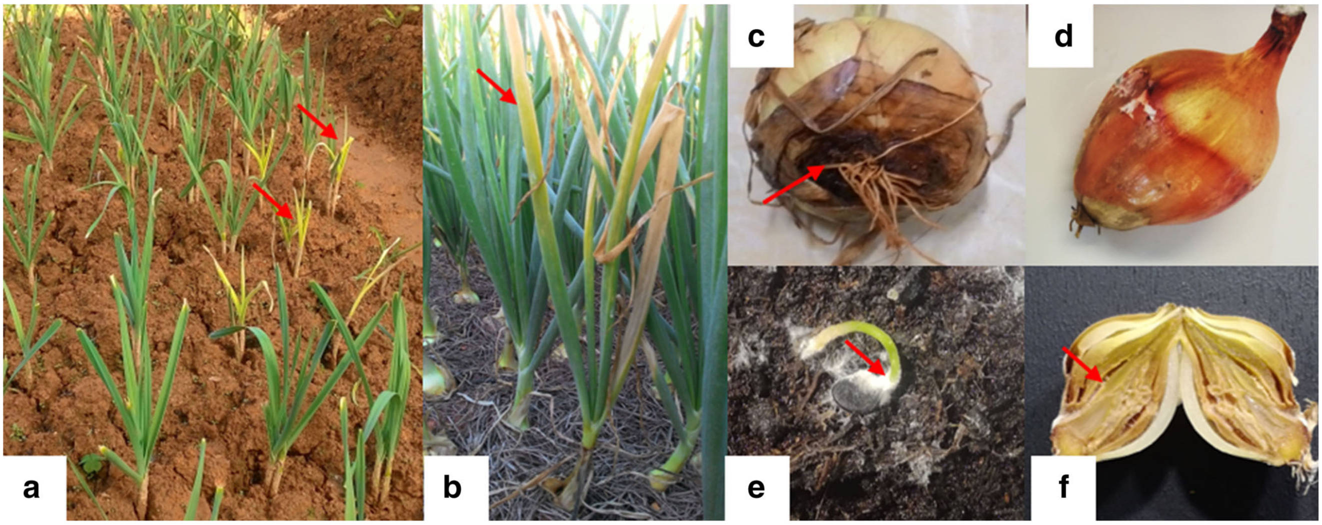

Fig. 1 Typical symptoms (red arrows) of *Fusarium* basal rot of *Allium* spp.: in transplanted leeks (**a**), in mature onion plants (**b**), in harvested bulb (**c**), in stored bulb (**d**), infected germinating seed (**e**), and inside of infected bulb (**f**)

Haapalainen et al. 2016). The widespread distribution of FBR can thus be attributed to their diverse spread mechanisms, in which spread through planting materials and latently infected bulbs are important factor in long distance dispersal of the pathogens. Haapalainen et al. (2016) have suggested that the increase of onion-pathogenic *Fusarium* species in Finland may be related to the import of planting materials.

So far, there is no evidence of secondary infection or spread of this disease in the field and even during storage. It appears therefore that *Fusarium* inoculum from soil or planting materials is critical for FBR occurrence in the field, while latently infected bulbs mainly contribute to postharvest basal rot of *Allium* spp. Therefore, a good FBR management strategy should focus on dealing with these inoculum sources. The development of FBR can thus be simulated as a monocycle disease (Fig. 2).

Furthermore, FBR creates favorable conditions for secondary pathogens to infect the bulb scales (Cramer 2000). Bacterial and *Phoma* bulb rots often occur in this fashion as secondary infections, although they are also known to be primarily problems on *Allium*. FBR can also associated with the feeding activity of insects like maggots, which are attracted by rotten tissues. However, the interaction between FBR and secondary parasites is not well understood. The occurrence of secondary pathogens can contribute to accelerate bulb decay, but assessing the contribution of each pathogen to the process is very challenging (Cramer 2000). Moreover, these mixed infections would present a difficulty in disease management, as diagnosis becomes a challenge.

Pathogenic variability and host susceptibility

Disease outcome is the result of a host–pathogen interaction under the influence of environmental conditions. The diversity of *Fusarium* and *Allium* species and the occurrence of mixed infections allow for a multiplicity of FBR disease outcomes (Dissanayake et al. 2009; Gei et al. 2014; Ozer et al. 2004).

The virulence of *Fusarium* spp. varies between *Allium* species (Galván et al. 2008). In general, *F. oxysporum* f. sp. *cepae* is more common and pathogenic in onions than other species, while *F. proliferatum* tends to be more virulent to other *Allium* species such as garlic and shallot (Palmero et al. 2012). However, in Finland, *F. proliferatum* was found in onions to be more dominant and aggressive than *F. oxysporum* f. sp. *cepae* (Haapalainen et al. 2016). In a similar report from Serbia, *F. proliferatum* isolates from garlic were even more pathogenic to onions than those from onions (Stankovic et al. 2007).

In situations of mixed infections by multiple *Fusarium* spp., one species may be more important than the others at particular stage of *Allium* phenology. Such is for instance the case in Vietnam, where co-infection by *F. solani*, *F. proliferatum*, and *F. oxysporum* was reported on onion, but while *F. solani* was only highly virulent on seedlings, *F. proliferatum* and *F. oxysporum* severely affected bulbs as well as seedlings (Le et al. 2020). Similarly, reports from Iran, Finland, and Burkina Faso suggest that *F. solani* and *F. redolens* typically results in lesions on seedlings while occurring in asymptomatic infections on bulbs (Ghanbarzadeh et al. 2014; Haapalainen et al. 2016; Kintega et al. 2020). Given that natural FBR epidemics are rarely found to be associated with a single species, identifying key species at a specific stage of host development can be useful in adjusting effective control strategies.

Seedling age and growth stage have been proposed as major determinants of FBR presence on *Allium* spp. (Cramer 2000; Galván et al. 2008; Galeano et al. 2014). FBR tends to be more aggressive when infection establishes at an early stage of seedling development and on mature bulbs in storage (dormant

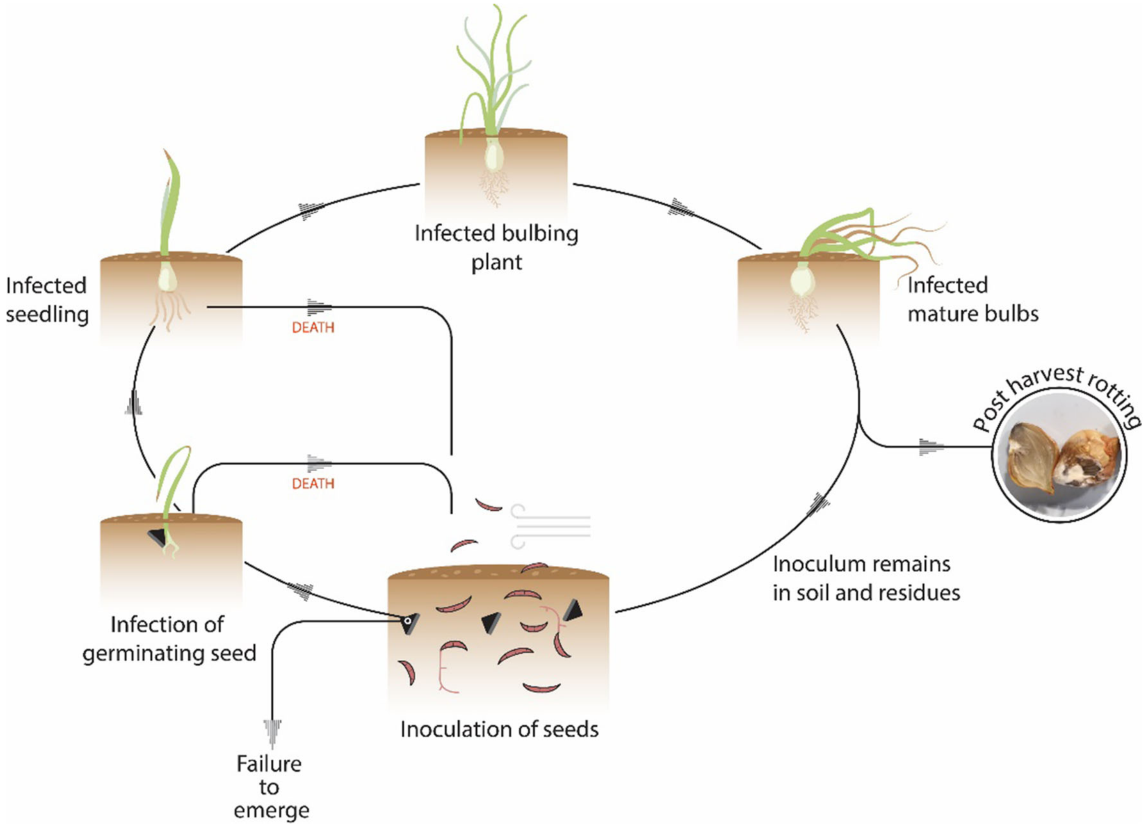

Fig. 2 Disease cycle of *Fusarium* basal rot in onion (*Allium cepa* L.). Notice that *Fusarium* spp. can infect at all developmental stages of onion. The figure does not include the infection of seedlings and mature plants

bulbs) (Retig et al. 1970; Stadnik and Dhingra 1997; Cramer 2000; Taylor et al. 2013; Galeano et al. 2014). Similarly, disease aggressiveness is also affected by the age of transplants, where older transplants might show no symptoms even though pathogenic fungi can still be recovered from them (Stadnik and Dhingra 1997). Age-related resistance is driven by diverse mechanisms in host plants (Develey-Riviere and Galiana 2007). Changes in the contents and biochemical activities of proteins, enzymes, and phenolics during developmental stages of host plants may determine the outcome of the interaction of plants with the pathogen. Galeano et al. (2014) have found that the enhanced activities of peroxidase and glucanase in onion seedlings after germination (at 7 days post-sowing) were significantly linked to the prompt decline in their susceptibility towards a *Fusarium* infection.

The susceptibility of a cultivar is a variable factor (Taylor et al. 2013). Indeed, the specialization of pathogens, which is influenced by host phenology, is likely to exist among *Fusarium* population, leading to some *Fusarium* isolates being only pathogenic in a certain set of *Allium* cultivars and even at specific growth stages of the host plants (Cramer 2000; Galván et al. 2008; Kintega et al. 2020). For example, some isolates of *F. oxysporum* f. sp. *cepae*, *F. proliferatum*, and *F. solani* cause severe disease symptoms on onion seedlings; however, others tend to be more virulent on mature bulbs (Kintega et al. 2020). This complex interaction may be related to changes in gene expression leading to biological changes, but the molecular mechanisms involved remains unknown. Furthermore, the aggressiveness of *Fusarium* isolates is also a variable (Taylor et al. 2013) that changes greatly among fields even within the same geographic region (Cramer 2000; Taylor et al. 2013; Gei et al. 2014). This could be a plausible explanation for inconsistent responses of tolerant cultivars under different conditions.

Fusarium basal rot management

Chemical control

Soil treatment or soil fumigation is among the most effective chemical control measures for FBR. Sodium salts like metam sodium and dazomet have shown their ability to effectively control FBR and improve plant growth (Nico and González Sánchez 2012). Sodium metabisulfite (at 0.4%) completely inhibited mycelial growth of *F. oxysporum* f. sp. *cepae* (Turkkan and Erper 2014). Compared to chemical treatments of planting materials, soil fumigation is more effective because it effectively reduces pathogenic propagules and it is especially suited for the control of soil-borne diseases (Sumner et al. 1997).

However, this measure involves mostly broad-spectrum fungicides that can kill beneficial microorganisms in soil.

Carbendazim, benomyl, and prochloraz are mostly used, alone or in combination with other fungicides to control FBR *via* a soil treatment (Abd-Elrazik et al. 1990; Naik and Burden 1981; Özer and Köycü 1998; Sintayehu et al. 2011). Seed treatments with benomyl and thiram resulted in a limited seed contamination of *F. oxysporum*, improved seedling emergence, and reduced damping-off, whereas seed coating with prochloraz provided remarkable protection in infested soil (Özer and Köycü 1998). Shallot basal rot can be managed effectively by bulb dressing or dip treatment in prochloraz or a mixture of carbendazim and imidacloprid (Sintayehu et al. 2011). Pre-planting dipping of onion bulbs with benomyl (100 $\mu g.mL^{-1}$ for 15 min.) reduced basal rot by 65% and enhanced yield with 54% (Naik and Burden 1981). Similar results were obtained when combined with vinclozolin (Özer and Ömeroğlu 1995) or mancozeb (Naik and Burden 1981).

The efficacy of chemicals in controlling FBR in greenhouse or at small scale under controlled conditions is undeniable. However, their field efficacy greatly varies and even it does not provide sufficient control of the disease (Ozer et al. 2002). In Finland, the incidence of bulbs infected with *Fusarium* spp. is up to 20% despite the application of chemical treatments (Haapalainen et al. 2016). This is probably due to a great variation of *Fusarium* populations and environmental uncontrolled factors under field conditions. Hence, field validation should be done to address not only the short-term disease response but also the impacts on the microbiological community of soils and plants (rhizosphere) (Dita et al. 2018) including the recolonization of soil.

Furthermore, the repeated application of fungicides not only causes environmental and ecological problems but also enhances the development of fungicide resistance in pathogens (Dekker 1976; Mishra et al. 2014). Although there has been no confirmed resistance in the *Fusarium* population in *Allium*, the occurrence of resistance to most fungicides such as benomyl, carbendazole, prochloraz, thiophanate-methyl, thiabendazole, and fludioxonil has been reported in the *Fusarium* populations pathogenic to lily, tomato, potato, wheat, chili, and sugarcane (Chen et al. 2007; Chen and Zhou 2009b; Chen and Zhou 2009a; Chung et al. 2009; Lugosch et al. 2011; Petkar et al. 2017; Xu et al. 2019). For instance, within *F. sulphureum* population, more than 90% of isolates from the seed potatoes from a storage in New Bundeslaender (Germany) were resistant to carbendazim, and data from isolates coming from ware potatoes indicated 60–74% resistance (Stachewicz et al. 1992). Increasing concerns in the development of fungicide resistance in *Fusarium* species in *Allium* are validated by recent findings that have shown a decrease in the effectiveness of carbendazole in controlling FBR on the field (El-Mougy and Abdel-Kader 2019).

Crop rotation

Inoculum build-up in soil is a key feature of soil-borne pathogens, and crop rotation is expected to be an effective solution. Successive cultivation of susceptible *Allium* species and varieties in fields with an infection history leads to uncontrolled damage (Abawi and Lorbeer 1972). Furthermore, the susceptibility of *Allium* species such as onions, garlics, leeks, chives, and scallions to *F. proliferatum* and *F. oxysporum* f. sp. *cepae* isolates coming from garlic and onion has been observed (Palmero et al. 2012), suggesting a rotation with crops from other families. A minimum of 4 years of rotation with such crops is recommended to reduce soil infection and bulbs losses (Cramer 2000; Wright et al. 2015). In the past, a sequence of crops has been found to be included in a rotation system for the purpose of reducing the pathogen inoculum and limiting onion FBR (Leoni et al. 2013).

However, crop rotation is likely not totally effective because pathogen can survive for a long time either in the soil or in/on the roots of symptomless alternative hosts (Abawi and Lorbeer 1972). Recently, some isolates of *F. oxysporum* f. sp. *asparagus*, *F. proliferatum*, and *F. solani* isolated from asparagus have also shown their capability to attack onion and garlic (Molinero-Ruiz et al. 2011), and even crops from completely distant families such as maize, wheat, potato, and sunflower are also suggested as reservoirs of these pathogens (Molinero-Ruiz et al. 2011). This shows the complexity of the *Fusarium* population related to diseases in *Allium* species. In fact, it is not clear whether *Fusarium* inoculum accumulates from previous crops in the crop rotation system or whether this might lead to an increased diversity of *Fusarium* pathogens on *Allium* species. If so, there would be a relation between crop species susceptible to *Fusarium* species in the historical crop rotation system of a field and the diversity of the *Fusarium* population in onion; *e.g.*, the more susceptible crops rotated the greater the population diversity. This would probably be a plausible explanation for differences in the *Fusarium* complex that were found among onion production regions around the world. Thus, in the complex of *Fusarium* species associated to basal rot disease in onions, it is likely that only one or two species are actually responsible for the disease, and the others are likely to exist only on the onion as its intermediate or alternative host.

Resistant cultivars

The use of resistant cultivars to control FBR has become highly significant due to undesirable impacts from fungicides (Cramer 2000; Galván et al. 2008; Lacy and Roberts 1982). Several *Allium* species such as *A. fistulosum*, *A. schoenoprasum*, and *A. galanthum* have been found to be consistently resistant to FBR (Abawi and Lorbeer 1971; Galván et al. 2008), but they are not popular cultivated species. Also, *A. pskemense*, *A. roylei*, and *A. galanthum* exhibited intermediate resistance to FBR

(Galván et al. 2008). Gene resources of such species were exploited for the development of resistance in onion against *Fusarium* spp. (Galván et al. 2008; Palmero et al. 2012; Taylor et al. 2013) because of no complete resistance found in onion selections (Retig et al. 1970; Lacy and Roberts 1982; Cramer 2000; Lopez and Cramer 2004; Gutierrez and Cramer 2005; Galván et al. 2008; Taylor et al. 2013). Among short-day onion cultivars, "NuMex Luna" and "NMSU 00-32" had the highest resistance potential at the seedling stage, whereas "NMSU 00-13-1" showed the best resistance level in the mature stage (Lopez and Cramer 2004). "NMSU 99-32", "NuMex Aurthur" and "NuMex Jose Fernandez" were among winter-sown onion cultivars found highly resistant to *F. oxysporum* f. sp. *cepae* (Cramer 2000; Gutierrez et al. 2006). In a similar study, Galván et al. (2008) found that onion cultivar 'Rossa Savonese' was intermediately resistant to FBR. Recently, cvs "Ailsa Craig Prizewinner" and "White Lisbon" showed the highest levels of resistance to *F. oxysporum* f. sp. *cepae* from UK and Netherlands of all commercial onion cultivars in UK (Taylor et al. 2013).

Once the infection is established in the field, the use of resistant cultivars is essential and the most effective method to control the disease. Despite recent efforts in the development of FBR-resistant cultivars (Abawi and Lorbeer 1971; Cramer 2000; Galván et al. 2008; Gutierrez and Cramer 2005; Gutierrez et al. 2006; Lacy and Roberts 1982; Retig et al. 1970; Saxena and Cramer 2009), the research on and application of resistant cultivars under the field circumstances are still facing a major challenge due to the large variability in the virulence of the *Fusarium* spp. responsible for FBR. The response of *Allium* species to the infection varies depending on their development stages (Galeano et al. 2014), pathogen virulence and cultivar properties (Dissanayake et al. 2009; Gei et al. 2014). The resistance mechanism of the cultivar and disease profile are completely unknown (Gei et al. 2014). Regardless of whether or not the interactions exist between isolates and specific cultivars resulting in disease expression, it is likely that the response of a selection to the infection of *Fusarium* does not depend largely on the characteristics of the cultivars, but the virulence of *Fusarium* species or its isolates occurs under specific conditions. Recent studies have expressed an increasing skepticism about the effectiveness of resistant cultivars. In fact, resistance selection is usually done locally and thus effective against a local, particular set of *Fusarium* spp. (Gei et al. 2014). Resistant cultivars under one condition may appear to be susceptible under another condition (Galván et al. 2008; Saxena and Cramer 2009; Taylor et al. 2013) or under disease pressure from other isolates (Gei et al. 2014). This has been demonstrated in Argentina where resistant onion lines from overseas had been defeated by other pathogenic isolates of *F. oxysporum* f. sp. *cepae* isolated in the country (Gei et al. 2014). These reviews seem to support the hypothesis that *Fusarium*-resistant varieties may be able to control a limit specific isolates within a certain range when the changes in the population of *Fusarium* spp. have not taken place yet. Therefore, the application of resistant cultivars for disease control under practical conditions seems to bring very limited effectiveness. Selection of FBR-resistant cultivars is still ongoing, and our suggestion is that screenings in the future should be done with a larger set of *Fusarium* isolates from many regions and carried out over the growth stages of *Allium* hosts.

Biological control

Biocontrol agents

Trichoderma spp. are the most widely applied biocontrol agents against many pathogens (Asad et al. 2014; Bae et al. 2016; Kifle et al. 2017; Muthukumar et al. 2011; Sid Ahmed et al. 1999). Inhibition of *F. oxysporum* f. sp. *cepae* by *Trichoderma viride* has been already shown *in vitro* (Ilhe et al. 2013; Rajendran and Ranganathan 1996). Combined seed treatment of *T. viride and Pseudomonas fluorescens* reduced onion basal rot incidence both in pot and in field conditions (Rajendran and Ranganathan 1996). A similar trial was conducted in India where FBR could be managed significantly (85%) by a mixture of *T. harzianum* (TH3) and *Pseudomonas* sp. (Pf12+ Pf27) isolated from the rhizospherical soil in naturally infected onion fields (Malathi 2015). *T. harzianum* KUEN 1585 (commercial product, Sim®Derma) has been shown to be effective in prevention and control of FBR in onion both *in vitro* and in pot experiments. This strain was particularly effective in stimulating the formation of antifungal compounds in onion and partly contributed to improve bulb size at harvest (Coşkuntuna and Özer 2008). Another strain of *T. harzianum*, T100 (at the rate of 1 × 10^6 cfu.g^{-1}), was shown to control FBR of onion caused by *F. proliferatum* in the presence of *Glomus mosseae* (3 g soil containing 80 chlamydospores.mL^{-1})—an arbuscular mycorrhizae (AM) being capable of effectively stimulating onion growth, although the presence of *Trichoderma* resulted in a partial inhibition of AM root colonization in onion (Ghanbarzadeh et al. 2016). *T. asperellum* and *T. virens* inhibit *F. solani* growth, a causal agent of damping off of onion seedlings in Sri Lanka (Gunaratna et al. 2019).

In addition, members of the genus *Bacillus* are well-known antibiotic producers exploited for biocontrol of FBR. *Bacillus subtilis* has exhibited its potential in controlling the disease both *in vitro* and in pot experiments (Manimaran et al. 2011).

From another perspective, several biocontrol agents might make certain contributions to improve onion growth through activating host key metabolite pathways. *T. longibrachiatum* isolated from desert soil triggers key metabolites resulting in the improvement of onion growth and its resistance to *F. oxysporum* f. sp. *cepae* (Abdelrahman et al. 2016). Furthermore, the volatile compounds produced by *Bacillus* species provided antifungal activity to inhibit mycelial growth of *F. oxysporum* which causes wilt of onion (Sharifi Tehrani and Ramezani 2003).

In general, the research and application of biological agents to control FBR is still limited: mainly studies focused on *Trichoderma* spp. tested *in vitro* and in pot experiments; their effectiveness is highly variable in relation to experimental conditions, making it difficult to successfully apply in the field.

Plant extracts

Extracts or essential oils from some plant species such as *Brassica* crops, *Fabaceae* crops, neem trees, and allelopathic grasses have antifungal potential against soil-borne diseases (Bowers and Locke 2000; Javaid and Rauf 2015; Moutassem et al. 2019). In an *in vitro* test, extracts of Ethiopian mustard (*Brassica carinata*) and rape seed (*B. napus*) showed high inhibition on the growth of shallot *F. oxysporum* f. sp. *cepae* pathogen (Sintayehu et al. 2014). Previously, extracts from allelopathic grasses (*Cenchrus pennisetiformis*, *Imperata cylindrica*, and *Dichanthium annulatum*) were also effective *in vitro* to control *F. solani* (Shafique et al. 2004). Among the oil cake extracts of neem, mahua, groundnut, mustard, pungam, castor, and gingelly investigated, neem and mustard extract exhibited an effective inhibition of the growth of *F oxysporum* f. sp. *cepae* in India (Saravanakumari et al. 2019; Yadav et al. 2014). Some botanical extracts and oils also partially stimulate plant defense mechanisms to some extent as suggested by Moutassem et al. (2019).

Soil amendments based on natural organic matters

Biodegradable materials such as crop residues, fresh plant extracts, and dry botanical biomass can be used as biofumigants, or a supplemental resource of microbial antagonists (Hoitink and Boehm 1999), to improve soil properties for biological agents (Ozer et al. 2002) as well as stimulating resistance in plants (Bonanomi et al. 2007; Yogev et al. 2010; Zhang et al. 1996).

The incidence of onion bulb rot was reduced in soil amended with stalks of sunflower (*Helianthus annuus* L.), alfalfa (*Medicago sativa* L.), or Hungarian vetch (*Vicia pannonica* Crantz) (Ozer et al. 2002). Sintayehu et al. (2014) found that rapeseed crops (*B. napus*) and Ethiopian mustard (*B. carinata*) have highly potential to reduce incidence and severity of FBR with 20–30% in shallot crops. Likewise, dry biomass of pigweed (*Chenopodium album*), swinecress (*Coronopus didymus*), and chinaberry (*Melia azedarach*) have shown a significant potential for controlling FBR on onion (Javaid and Rauf 2015). In general, the enrichment of organic matter with biocontrol agents to produce the so-called organic fertilizers obtained promising results in disease management. Dry leaf biomass of solanaceous weed (*Withania somnifera*) mixed with *T. harzianum* to control FBR in onion in Pakistan (Akhtar and Javaid 2018).

The use of organic amendments with municipality food waste compost to control FBR of onion was evaluated in combination with soil solarization. However, the efficacy of soil solarization reduced significantly from 68.7 to 16.3% (2010) and from 76.9 to 4.6% (2011) when soil was solarized after applying the organic amendments (Carrieri et al. 2013), indicating an adverse impact of organic amendments on the results of solarization.

To summarize, although many studies have shown a great potential of compost amendments and organic matter, the effectiveness of this technique on field level is inconsistent and unpredictable (Bonanomi et al. 2007; Carrieri et al. 2013). It may sometimes even be counterproductive and hamper the control of pathogens (Carrieri et al. 2013; Hoitink and Boehm 1999).

Other measures

A number of other measures have also been studied and applied effectively, making important contributions to the management strategies of *Fusarium* diseases in *Allium* spp. Bulb submerging in hot water (at 45–50 °C) for 30 min was effective in controlling FBR of shallot without negative effects on seed sprouting and seedling growth (Wibowo et al. 2016). Initially, hot water treatment and fungicides effectively controlled basal rot of narcissi (*F. oxysporum* f. sp. *narcissi*) in the field and during the storage (Hanks 1996). Soil solarization has been used to decrease the inoculum level in soil resulting in a partial reduction of FBR (Satour et al. 1991). Also, heating the soil layers on a seedbed by burning plant residues such as straw and thresh can provide an effective control measure to FBR in seedling production (Awuah et al. 2009). Furthermore, the maintenance of field hygiene and a regular treatment of equipment and machinery are also important measures to prevent infection sources of FBR disease.

Conclusions and perspectives

Fusarium basal rot (FBR) caused by a complex set of *Fusarium* species is an important disease of *Allium* crops pre- as well as post-harvest. The complexity of this disease is caused by different *Fusarium* species with a divergence in virulence and host susceptibility. Despite the fact that many control measures have been undertaken, the disease remains a major problem for *Allium* producers worldwide. It emerged in this review that each measure has a certain limitation in controlling FBR. Integrated pest management (IPM) is probably the ultimate option to explore in the context of agricultural ecosystem management. For a soil-borne disease such as

FBR, the management of soil and planting materials is an important dimension of this strategy. This review suggests the integrated use of environmentally friendly methods to proactively prevent infection and limit damage, with an emphasis on resistant cultivars and biological control using disease-free planting material and regularly maintaining field sanitation. Furthermore, the underlying aspects in *Allium-Fusarium* interaction need to be interpreted in order to provide the critical insights for the development of effective resistant varieties in the future. Finally, biological control is a promising method that needs to be explored more intensively before it can be implied in nurseries or in production fields.

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Data availability Data sharing is not applicable to this article as no datasets was generated or analyzed during the current study.

Declarations

Conflict of interest The authors declare no competing interests.

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