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Potato Fusarium Dry Rot in Tunisia: Current Status and Future Prospects

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ABSTRACT

Fusarium dry rot (FDR) is a postharvest disease of potato tubers of economic importance worldwide. In Tunisia, losses attributed to *Fusarium* spp. infections may be aggravated in the presence of other tuber rot pathogens. A review of published data indicates that five *Fusarium* species (*F. sambucinum*, *F. graminearum*, *F. culmorum*, *F. oxysporum* and *F. solani*) are involved in a disease complex in Tunisia. These species present a great range of inter- and intra-specific variability in growth, sporulation and aggressiveness. Their level of aggressiveness is variable, depending on storage conditions (mainly temperature) and potato cultivar. Although a large number of cultivars have been assessed, no cultivar was resistant to FDR although potato cultivars exhibited different levels of susceptibility to the disease. The ranking of cultivars with regard to their susceptibility to FDR changed depending on the *Fusarium* species involved in disease development and on the temperature used for tuber storage. Chemical-based treatments using old and new generations of fungicides tested against *Fusarium* species have successfully limited dry rot severity and revealed the appearance of benzimidazole-resistant isolates of *F. sambucinum*. Biological control studies undertaken based on various and complementary experiments *in vitro*, *in vivo* and under natural conditions permitted the selection of potentially important microbial agents (fungi and Gram-positive bacteria) for the control of potato FDR. Their mechanisms of action were also elucidated. Other alternatives of disease control which may be a part of an integrated management strategy are also cited. This review highlights the specificity of problems related to FDR in Tunisia, regarding mainly pathogen aggressiveness, genetic resistance and control alternatives and their limits which may be useful for the development of an integrated strategy for FDR management and for better guiding future research on the influence of the *Fusarium* species complex, potato cultivar, storage conditions and their interactions on the effectiveness of disease control.

Keywords: aggressiveness, control alternatives, cultivar susceptibility, disease severity, *Fusarium* species, *Solanum tuberosum* L.

CONTENTS

INTRODUCTION

Fusarium dry rot is caused by several species of the soil-borne fungus *Fusarium*. The most typical symptom of this disease is a dry rot of potato tubers which may become more evident after long-term storage. The first symptoms may develop within 1-3 weeks following infection depending on environmental conditions (humidity and temperature). Infected tubers exhibit, at points of infection, few small, brown to dark brown and sometimes sunken areas. These sunken spots may not enlarge and no further rot may be noticed until the whole tuber has rotten completely. However, when a large part of the tuber surface is affected, symptoms develop externally into typical wrinkling appearing in concentric rings, which can be covered with spores of different colours depending on *Fusarium* species involved in rot development. The internal tuber decay is expressed as brown streak of rotten tissue exhibiting hollows filled with fungal spore masses and mycelia. Heavily infected tubers will eventually shrivel and become mummified (Hooker 1981; Turkensteen 2005; Wale 2008).

FDR occurs on potatoes worldwide but its relative importance varies greatly from one country to another due to the variation of cultivars used, frequency and nature of *Fusarium* species involved in disease development, soil types, inherent environmental conditions and other factors

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Invited Review

(Tivoli and Jouan 1981). Thus, due to the specificity of the disease, this mini-review is focused on research studies, cited chronologically, undertaken in Tunisia from 1993 until now and dealing in whole or partially with potato FDR.

Economic importance

FDR is an important postharvest disease of potato tubers that causes significant losses in storage and transit of both seed tubers and those for table consumption. It is also a major cause of seed-piece decay after planting. It is of economic importance worldwide (Seppanen 1983; Davis *et al.* 1983; Cappellini *et al*. 1984; Thanassoulopoulos and Kitsos 1985; Bedin and Tivoli 1990; Carnegie *et al*. 1990; Theron and Holz 1991; Theron and Millard 1996; Cullen *et al*. 2005). In several African and non-African countries and from 1979 to 1986 surveys on bacterial and fungal diseases, Turkensteen (1987) had noted a tendency of increasing importance of *F. solani* among other fungal pathogens such as *Verticillium albo-atrum* and *Spongospora subterranea*.

In Tunisia, the incidence of tuber rots was assessed at the end of storage during 1993 and 1994 agricultural campaigns. This follow-up revealed that the percentage of rotten tubers ranged between 0.1 and 8.8% with an average of 2.2% in 1993 whereas in 1994, tuber rot incidence varied from 0 to 13% with an average of 1.7%. The diagnostic of symptoms and isolation of the causal agents revealed that 50% of the recorded damages were attributed to fungal agents causing tuber dry rot (Priou and El Mahjoub 1999). *F. sambucinum*, one of the *Fusarium* species complex involved in disease development, was commonly reported to be responsible for losses higher than 25%, especially under traditional storage, where environmental conditions are particularly conducive to dry rot development (Daami-Remadi and El Mahjoub 1996b). Furthermore, based on a more recent investigation (Chérif *et al*. 2000), losses caused by FDR exceeded 50% in some years even in refrigerated stores.

These reported losses attributed to *Fusarium* spp. infections only may become more severe in presence other tuber rot pathogens such *Pythium* spp., *Pectobacterium* spp. (syn. *Erwinia* spp.), *Phytophthora erythroseptica* and other soil-borne pathogens (Priou and El Mahjoub 1994, 1999; Triki *et al*. 1996a, 1996b; Daami-Remadi 2001b; Triki *et al*. 2001b; Daami-Remadi *et al*. 2007).

PATHOGEN

Inventory of Fusarium dry rot agents

In Tunisia, the first results of isolation of fungi from potato rhizosphere and/or from local potato tubers exhibiting dry rot symptoms revealed the omnipresence of *F. solani* which induced similar dry rot signs when inoculated to healthy tubers and was thus, identified as *F. solani* var. *coeruleum* (Daami-Remadi and El Mahjoub 1994; Priou and El Mahjoub 1994). Moreover, the investigations of Daami-Remadi and El Mahjoub (1996b) revealed the involvement of *F. solani* which remained the most prevalent. *F. sambucinum* (syn. *F. roseum* var. *sambucinum*), *F. culmorum* (syn. *F. roseum* var. *culmorum*) and *F. graminearum* (syn. *F. roseum* var. *graminearum*) were also isolated from tubers with dry rot symptoms. Chérif *et al*. (2000) have also demonstrated that *F. sambucinum* is the dominant fungus found on potatoes during traditional and cold storage and the main reason for losses. In 2004, *F. oxysporum* f. sp. *tuberosi* was also detected from potato plants as a serious wilting and tuber rotting agent (Daami-remadi and El Mahjoub 2004). The ongoing works revealed that dry rot caused by *F. oxysporum* f. sp. *tuberosi* is still common in Tunisia and that *F. graminearum* re-emerged as an increasingly important occurring dry rot pathogen in traditional as well as cold storages.

Pathogen biology

The mycelial growth and sporulation of *Fusarium* species collected were studied depending on culture medium and temperature of incubation. The mycelial growth of *F. culmorum*, *F. graminearum* and *F. sambucinum* was optimum at 20-25°C whereas the highest sporulation occurred at temperatures situated between 25 and 30°C. However, for *F. solani* var. *coeruleum*, the optima of growth and sporulation were 25-30 and 20-25°C, respectively (Daami-Remadi 1996).

The effect of incubation temperature on the radial growth of *Fusarium* species was also studied with newly isolated dry rot agents. All *Fusarium* species tested did not develop at 40°C whereas at 5°C, only *F. solani* and *F. oxysporum* f. sp. *tuberosi* did not grow whilst slight growth was observed for *F. sambucinum* and *F. graminearum*, indicating possible growth even at lower temperatures and eventual dry rot induction in refrigerated stores. Moreover, it was also shown that at temperatures below 25°C, *F. graminearum* and *F. sambucinum* grow more rapidly than *F. solani* and *F. oxysporum* f. sp. *tuberosi* which exhibited optimal *in vitro* growth at 25-30°C (Daami-Remadi *et al*. 2006e). Among the various culture media tested, PDA and Tanaka (Tivoli 1988) allowed optimal growth of *Fusarium* species (Daami-Remadi 1996). Thus, a great range of variability in growth and sporulation was noted within and among dry rot agents which may influence their aggressiveness under natural or artificial inoculation conditions.

Pathogen aggressiveness

F. sambucinum was ranked as the most dominant and the most destructive fungus prevailing on stored potatoes worldwide (Boyd 1972; Schisler *et al.* 1997). In Tunisia, the *Fusarium* population associated with potato has been changed due to the occurrence of new species and the increase of frequency of some of them. Collected dry rot agents showed intraspecific and interspecific variations in their aggressiveness when inoculated to a given potato cultivar and incubated at a constant temperature (Daami-Remadi 1995, 2006).

The aggressiveness of *Fusarium* spp. was significantly influenced by storage temperature. *Fusarium* species possessed two thermal peaks of aggressiveness on potato cv. 'Spunta' tubers: the first one situated at 10-15°C and the second at higher temperatures (30-35°C). At temperatures below 25°C, *F. sambucinum* and *F. graminearum* induced the severest dry rot symptoms while *F. solani* was the most aggressive at temperatures above 30°C (Daami-Remadi *et al*. 2006e).

Dry rot severity also varied depending on the cultivar used. *F. graminearum* was highly aggressive on 7 out of 11 potato cultivars tested (**Table 1**), aggressive on 3 cultivars ('Latona', 'Mondial' and 'Timate') and moderately aggressive only toward 'Liseta'. *F. sambucinum*, *F. solani* and *F. oxysporum* f. sp. *tuberosi* showed an aggressiveness comparable to *F. graminearum* only in some cultivars i.e. 'Fabula', 'Latona', 'Mondial', 'Plantina' and 'Safrane' (Daami-Remadi *et al*. 2006a). Thus, the level of aggressiveness of dry agents was variable depending on storage conditions and plant material. Assessment of the aggressiveness of a mixed inoculum of *Fusarium* species may give additional information on disease severity observed under natural environments.

GEOGRAPHICAL DISTRIBUTION

Fusarium spp. are common in most soils where potatoes are grown. In Tunisia, few studies were conducted on the geographical distribution and the relative importance of *Fusarium* inoculum responsible of potato dry rot in agro-ecological soils. However, in preliminary studies, Daami-Remadi and El Mahjoub (1994, 1996a) estimated the level of infectious potential of *Fusarium* spp. in rhizospheric soil removed

Table 1 Comparative aggressiveness of four *Fusarium* species toward 11 local potato cultivars recorded after 21 days of storage at 25-27°C.

Cultivar/ *Fusarium* species	**'Alaska'**	**'Asterix'**	**'Atlas'**	**'Fabula'**	**'Latona'**	**'Liseta'**	**'Mondial'**	**'Platina'**	**'Safrane'**	**'Spunta'**	**'Timate'**
F. graminearum	HA	HA	HA	HA	A	MA	A	HA	HA	HA	A
F. sambucinum	A	HA	HA	HA	A	A	MA	A	A	MA	HA
F. oxysporum	A	A	A	HA	A	MA	MA	A	A	MA	A
F. solani	A	HA	A	HA	A	HA	MA	A	A	A	A

Pathogen aggressiveness was estimated based on mean penetration according to the Lapwood *et al.* (1984) formula where P = [W/2 + (D-5)]/2 with (W, mm) and (D, mm) representing the maximum depth and width of the rot; MA: Moderately aggressive: mean penetration ≤ 10 mm; A: Aggressive: 10 mm < mean penetration < 15 mm; HA: Highly aggressive: mean penetration ≥ 15 mm; *F. oxysporum*: *F. oxysporum* f. sp. *tuberosi*.

Table 2 Comparative susceptibility of 16 local potato cultivars to four *Fusarium* species noted after 21 days of storage at 15°C.

***Fusarium* species/cultivar**	***F. culmorum***	***F. graminearum***	***F. sambucinum***	***F. solani***
'Ariane'	MS	MS	S	MS
'Atlas'	MS	MS	MS	MS
'Claustar'	MS	MS	S	MS
'Korrigane'	MS	MS	S	MS
'Yesmina'	MS	MS	MS	MS
'Ajax'	S	MS	MS	S
'Cardinal'	S	MS	MS	S
'Diamant'	HS	S	MS	S
'Famosa'	S	MS	MS	MS
'Kondor'	S	S	MS	S
'Maradona'	S	MS	MS	S
'Mondial'	MS	MS	MS	MS
'Baraka'	S	HS	MS	S
'Désirée'	HS	S	MS	S
'Nicola'	S	HS	HS	S
'Timate'	HS	HS	HS	HS

Ranking of cultivar susceptibility based on mean penetration according to the Lapwood *et al.* (1984) formula where P = [W/2 + (D-5)]/2 with (W, mm) and (D, mm) representing the maximum depth and width of the rot; MS: Moderately susceptible: mean penetration ≤ 10 mm; S: Susceptible: 10 mm < mean penetration < 15 mm; HS: Highly susceptible: mean penetration ≥ 15 mm; *F. solani: F. solani* var. *coeruleum.*

from different localities representing the main potato-producing areas, based on direct pathogen isolations on culture media and/or baiting on tuber slices and counting of pathogen colonies.

The degree of infection of fields varied depending on the production areas, the sampling period (at planting, during crop development or at harvest) and on potato cultivars used for baiting. This study also revealed the omnipresence of *F. solani* in potato soils and that for all prospected areas; the highest levels of inoculum were recorded in the areas with an intensive potato cropping history.

The level of infectious potential of the adhering soil from the tubers was also assessed depending on the cultivars used. Cultivars have a direct effect on pathogen development on the tuber surface within adhering soil even though no qualitative variation was recorded in pathogen inventory; *F. solani* remained the main species recovered. This study also indicated that the adhering soils to cv. 'Famosa' and to a lesser degree 'Diamant', 'Kennebec', 'Kondor', 'Mondial', 'Timate' and 'Vital' were those most infested with *F. solani*, suggesting the involvement of a *Fusarium* species-potato cultivar interaction on the infectious potential of cultivated soils (Daami-Remadi and El Mahjoub 1996a).

Further studies are needed to estimate the actual level of soil infestation with dry rot agents and to follow up on the eventual evolution of a *Fusarium* population associated with potato based on quantitative molecular diagnostic assays, baiting techniques and fungal isolations. The rhizospheric soil may be used as a potential source of biocontrol agents occupying the same ecological niche as dry rot agents.

GENETIC RESISTANCE

It is well known worldwide that all commonly grown potato cultivars are susceptible to FDR and high levels of resistance in breeding stocks are not available (Schisler *et al.* 1997). However, due to variation of cultivars from one country to another and to differences in the recovered *Fusarium* species, site-specific studies should be undertaken to elucidate more host and dry rot agents interactions and consequently, rank cultivars based on their relative susceptibility to *Fusarium* spp. In fact, Daami-Remadi and El Mahjoub (1996b) tested 16 potato cultivars for their behaviour against four dry rot agents (*F. sambucinum*, *F. graminearum*, *F. culmorum* and *F. solani*). All cultivars exhibited dry rot symptoms after storage at 15°C for 21 days but disease severity varied depending on the *Fusarium* species used for inoculation. In fact, this assessment revealed that the cultivars 'Ariane', 'Atlas', 'Claustar', 'Korrigane' and 'Yesmina' were moderately susceptible to the majority of agents tested except for *F. sambucinum*; 'Nicola' and 'Timate' were ranked as susceptible to highly susceptible to the four *Fusarium* species (**Table 2**).

Comparative susceptibility of local potato cultivars to more recently (2003-2006) isolated dry rot agents (*F. graminearum*, *F. sambucinum*, *F. solani* and *F. oxysporum* f. sp. *tuberosi*) was also investigated. That study revealed that after 21 days of incubation at 25-27°C, all inoculated tubers of all cultivars exhibited dry rot symptoms but disease severity, estimated, based on rot parameters, varied depending on cultivars and agents used for inoculation. This finding of variable pathogen interaction with cultivars confirmed that a cultivar's resistance or behaviour was genetically distinct for the four *Fusarium* spp. tested. In fact, none of 11 cultivars tested were completely resistant. Eight cultivars ('Alsaka', 'Asterix', 'Atlas', 'Fabula', 'Latona', 'Platina', 'Safrane' and 'Timate') were found to be susceptible to highly susceptible to the four *Fusarium* species tested (**Table 3**). Only some cultivars ('Liseta', 'Mondial' and 'Spunta') were ranked as moderately susceptible to at least two to three dry rot agents. In fact, as summarized in **Table 3**, cvs. 'Mondial' and 'Spunta' behaved as moderately susceptible to *F. sambucinum* and *F. oxysporum* f. sp. *tuberosi* but as susceptible to highly susceptible to *F. graminearum* (Daami-Remadi *et al.* 2006a).

It should be also mentioned that among 14 potato culti-

Table 3 Comparative susceptibility of 11 local potato cultivars to four *Fusarium* species noted after 21 days of storage at 25-27°C.

Cultivar/ ***Fusarium* species**	'Alaska'	'Asterix'	'Atlas'	'Fabula'	'Latona'	'Liseta'	'Mondial'	'Platina'	'Safrane'	'Spunta'	'Timate'
F. graminearum	HS	HS	HS	HS	S	MS	S	HS	HS	HS	S
F. sambucinum	S	HS	HS	HS	S	S	MS	S	S	MS	HS
F. oxysporum	S	S	S	HS	S	MS	MS	S	S	MS	S
F. solani	S	HS	S	HS	S	HS	MS	S	S	S	S

Ranking of cultivar susceptibility was realized based on mean penetration according to Lapwood *et al.* (1984) formula where P = [W/2 + (D-5)]/2 with (W, mm) and (D, mm) representing the maximum depth and width of the rot; MS: Moderately susceptible: mean penetration ≤ 10 mm; S: Susceptible: 10 mm < mean penetration < 15 mm; HS: Highly susceptible: mean penetration ≥ 15 mm; *F. oxysporum*: *F. oxysporum* f. sp. *tuberosi*.

vars tested for their response to *F. oxysporum* f. sp. *tuberosi*, responsible for Fusarium wilt, cv. 'Platina', ranked as susceptible to this pathogen on potato tubers (**Table 3**), exhibited the severest wilt severity and was classed as the most susceptible whereas cvs. 'Asterix', 'Alaska', 'Safrane' and 'Timate' showed intermediate wilt severity (Ayed *et al.* 2006).

Furthermore, due to differences in response of potato cultivars, depending on *Fusarium* sp. used for inoculation (Hooker 1981), and depending on the effect of temperature of storage on the aggressiveness of dry rot agents, potato cultivars were recently re-ranked taking into account both these factors. In fact, the relative susceptibility of 11 potato cultivars towards *F. solani*, *F. oxysporum* f. sp. *tuberosi*, *F. sambucinum*, and *F. graminearum* was assessed under different storage temperatures. These species showed variable aggressiveness; *F. sambucinum* was the most aggressive among the cultivars tested. However, *F. graminearum* showed aggressiveness comparable to *F. sambucinum*, but only on some cultivars such as 'Mondial' and 'Atlas'. *F. oxysporum* f. sp. *tuberosi* and *F. solani* caused, in contrast, relatively less severe dry rot. None of the cultivars stored at 15, 20, 25 or 30°C was completely resistant to all *Fusarium* species and only some of them showed lesser susceptibility towards at most one species. 'Spunta', 'Mondial' and 'Nicola', the most commonly grown cultivars in Tunisia, tolerated at least one *Fusarium* species. This study also highlighted that the rank order of susceptibility levels to FDR varied depending on *Fusarium* species and storage temperature. Indeed, when tubers were inoculated with *F. sambucinum* (the most aggressive species), cultivars placed in the less susceptible group at 30°C moved to the highly susceptible group when stored at 15°C. However, cultivars inoculated with *F. oxysporum* f. sp. *tuberosi* (the least aggressive) that ranked in the less susceptible group exhibited stable reaction at all temperatures tested (Mejdoub-Trabelsi *et al.* 2012).

Due to the variability in the level of susceptibility to each *Fusarium* species demonstrated depending on storage temperature and the presence of these *Fusarium* spp. as mixed infections on potato tubers, ongoing studies are focused on the eventual variability of potato cultivars' response towards dry rot agents based on single or mixed inoculations with *Fusarium* species.

CONTROL METHODS

Chemical control

Benzimidazoles fungicides were largely used in the world for FDR control in storage (Hanson *et al.* 1996). In Tunisia, no fungicides were registered for Fusarium decay control. In an attempt to reduce disease incidence in storage, several works have tested fungicides commonly used for the control of other potato or *Fusarium* diseases against the complex of *Fusarium* species causing dry rot. In the work by Daami-Remadi (1995) and Daami-Remadi and El Mahjoub (1997), three benzimidazole (benomyl, thiabendazol and thiophanat-methyl) and one imidazol fungicides were tested *in vitro* and *in vivo* against *Fusarium* species (*F. culmorum*, *F. graminearum*, *F. sambucinum* and *F. solani*). The effectiveness of these fungicides varied depending on target pathogens and doses added to the culture medium. The greatest zone of inhibition of pathogen growth was achieved with 700 ppm of each fungicide tested. When used as a post-inoculation treatment, selected fungicides exhibited variable interaction with *Fusarium* species used for tuber (cv. 'Claustar') infection. Benomyl and thiabendazol failed to control the disease caused by *F. sambucinum* whereas thiophanat-methyl and prochloraz effectively limited dry rot development induced by this pathogen after 21 days of incubation at 10°C.

In the *in vitro* investigation by Triki *et al.* (1996a), 14 pesticides (systemic or contact), habitually used and registered for potato crop treatments, were screened for their inhibitory effect against bacterial, fungal and fungus-like pathogens involved in soft, dry or pink tuber rotting. They found that fungal and bacterial growth was inhibited with thiabendazol (minimum effective concentrations or MEC varying between 0.025 and 0.5% depending on the pathogen tested), mancozeb (MEC 0.08-0.5%), cymoxanil + mancozeb (MEC 0.1-0.5%), maneb (MEC 0.3-0.5%), metalaxyl + mancozeb (MEC 0.3-0.5%), copper (MEC 0.3-0.5%), folpel + ofurace (MEC 0.04-0.5%), and maneb + zineb + copper (MEC 0.1-0.5%). In the light of these findings *in vitro*, these authors (Triki *et al.* 1996b) selected four fungicides for evaluating their effectiveness in the control of dry rot caused by *F. sambucinum* associated or not with pink rot trying, thus, to mimic natural mixed infections. It was concluded from these laboratory experiments that the chemical treatments applied by dipping 'Spunta' potato tubers inoculated with *Phytophthora erythroseptica*, *F. sambucinum* or *P. erythroseptica* + *F. sambucinum* had reduced rot development by 75% compared to the untreated control. Fungicides composed of metalaxyl + mancozeb or maneb were the most effective in controlling these tuber diseases where rot extension was reduced by 50 and 91% on tubers inoculated with *F. sambucinum* and *P. erythroseptica* + *F. sambucinum*, respectively.

Taking into consideration these mixed infections of *Fusarium* species with tuber rotting causal agents, various combinations of chemical treatments were assessed for their potential in inhibiting the incidence of dry rot *in vivo* and *in situ* (open field traditional storage) as compared to individual treatments (Daami-Remadi *et al.* 2006c). *In vitro* screening revealed that *F. solani*, *F. graminearum* and *F. oxysporum* sp. *tuberosi* were inhibited by more than 90% compared to the untreated control whilst *F. sambucinum* interacted differently with fungicide mixtures tested in which pathogen growth was reduced by only 26 and 46% with benzimidazol-based treatments, namely benomyl and carbendazim, suggesting the probable development of lower sensitivity to this chemical family. The effectiveness of both these fungicides was enhanced, reaching 85-90% when supplemented with a fungicide mix (metalaxyl (10%) + mancozeb (48%), the dose used is 200 g/hl of Ridomil MZ 58^{TM}).

Chemical control of FDR was also achieved by using some fungicides belonging to a new generation called "low risk fungicides" because of their reduced risk of development of resistant population such as fludioxonil (chemical class of phenylpyrroles) and azoxystrobin (chemical class of strobilurins). They are also rated as "reduced risk" to the environment and humans by the United States Environmental Protection Agency (US EPA 1998; Förster *et al.* 2007; Duke *et al.* 2010) and registered for preharvest and postharvest use (Förster *et al.* 2007; Kanetis *et al.* 2007).

The comparative efficacy of azoxystrobin, fludioxonil, chlorothalonil and hydroxyquinoline sulphate was assessed based on *in vitro* and *in vivo* experiments against isolates of four *Fusarium* species involved in tuber dry rot disease. All the tested fungicides significantly inhibited mycelial growth, observed after incubation at 25°C for 4 days, of all *Fusarium* isolates including those of *F. sambucinum* already reported to be resistant to benzimidazoles (Daami-Remadi and El Mahjoub 2006). After immersing 'Spunta' tubers for 10 min into different fungicide suspensions prior to their inoculation, the tested fungicides exhibited variable efficacy depending on the *Fusarium* species used for infection. In fact, azoxystrobin, fludioxonil and chlorothalonil significantly reduced the dry rot severity by more than 50% compared to the untreated controls, recorded after 21 days of storage at 25-27°C. Azoxystrobin and fludioxonil were found to be an effective chemical alternative for the control of dry rot induced by benzimidazole-resistant *F. sambucinum* isolates (Daami-Remadi *et al*. 2006f).

Fungicide resistance

Resistance of *F. sambucinum* to benzimidazole fungicides – mainly thiabendazol – was largely documented and reported in many potato-producing countries such as France (Tivoli *et al*. 1986), many Canadian localities such as Alberta, Nova Scotia and Saskatchewan (Kawchuck *et al*. 1994; Holley and Kawchuk 1996; Platt 1997; Thomson and Waterer 1999; Peters *et al*. 2001), many American states such as Idaho, Michigan, North Dakota, Oregon and Washington (Desjardins *et al*. 1993; Hanson *et al*. 1996; González *et al*. 2002; Ocamb *et al*. 2007), and UK (Hide *et al*. 1992; Peters *et al*. 2008).

In Tunisia, due to the lack of effectiveness of benzimidazoles in controlling *F. sambucinum* isolates reported in our previous studies (Daami-Remadi and El Mahjoub 1997; Daami-Remadi *et al*. 2006c), the response of Tunisian isolates of *Fusarium* spp. to three fungicides (benomyl, carbendazim and thiophanate-methyl) of this chemical class was investigated. A total of 55 isolates were tested. *F. solani* (12 isolates), *F. oxysporum* f. sp. *tuberosi* (23 isolates) and *F. graminearum* (10 isolates) were sensitive to carbendazim and benomyl at 5 mg/l. Tunisian isolates of *F. sambucinum* collected during the 2002-2004 period were resistant and exhibited, thus, a cross-resistance to these benzimidazoles. Moreover, *F. sambucinum* isolates grown on PDA supplemented or not with carbendazim (100 mg/l) induced comparable dry rot severity when inoculated on healthy 'Spunta' tubers. We concluded that these resistant isolates might have been introduced to Tunisia from Europe through seed tubers as no benzimidazole was registered for potato tuber or plant treatment. Thus, as resistant isolates may exhibit a higher growth rate and more severe disease than sensitive *Fusarium* spp. isolates (Ocamb *et al*. 2007), research studies are presently concentrated on biological control as an alternative to reduce the incidence of FDR attributed to benzimidazole-resistant or -sensitive isolates.

Biological control

Due to the absence of resistant potato cultivars to all *Fusarium* species involved in dry rot disease and to the risks of fungicides on the environment and human health, research interests were more focused on alternative control methods. Among alternatives being explored, microbial agents (fungi and Gram-positive bacteria) have shown significant potential.

1. Bacillus spp.

A total of 83 spore-forming bacteria belonging to the genus *Bacillus*, isolated from Tunisian salty soils, and five strains of *B. thuringiensis* exhibiting insecticidal activity, were tested *in vitro* and *in vivo* against *F. sambucinum*. Results of the *in vitro* dual culture screening revealed that more than 50% of *Bacillus* spp. inhibited pathogen radial growth whereas all five *B. thuringiensis* strains did not. When applied to wounded potato tubers, the reduction in dry rot ranged from 66 to 89% and the most effective isolates were *B. cereus* (X9, X16 and G7), *B. lentimorbus* (X7) and *B. licheniformis* (I32). *B. thuringiensis* strains, although ineffective *in vitro*, decreased disease severity by 41 to 52% (Sadfi *et al*. 2001). *Bacillus* isolates were more effective when applied as 24 h-old cultures (Sadfi *et al*. 2002b) whilst *B. thuringiensis* strains best inhibited pathogen growth when used as 48 to 72 h-old cultures (Sadfi *et al*. 2001).

B. cereus, *B. lentimorbus* and *B. licheniformis* were also assessed for their antagonistic effects against *F. sambucinum* under greenhouse and field conditions. Greenhouse trials undertaken in pots demonstrated that bacterial antagonists enhanced the emergence of potato tubers. Isolate I32 of *B. licheniformis* and X16 of *B. cereus* most effectively reduced disease severity. Field experiments also revealed that *B. cereus* X16 exhibited most effectively controlled FDR on seed tubers and increased growth parameters (plant height and vegetative mass) and consequently, the final tuber yield. Under traditional and cold storage conditions (6 and 8 months, respectively), the incidence of dry rot was significantly lower in potato boxes treated with each antagonist applied alone or as a mixture with other biological treatments compared to untreated boxes and those treated with carbendazim (Sadfi *et al*. 2002a).

The *in vitro* interactions of *B. cereus* X16 and *B. thuringiensis* 55T with *F. sambucinum* were investigated based on light and transmission electron microscopy. Confrontation with *B. cereus* X16 on nutrient agar generally showed apparently intact fungal cells with densely stained protoplasm whilst, when cultured with *B. thuringiensis*, fungal cells appeared markedly damaged, with partial to complete cell wall disintegration and disorganization and generally complete loss of protoplasm. Interactions in liquid medium led to a total inhibition of the germination of pathogen macroconidia (Chérif *et al*. 2002). At the cytological and ultrastructural levels, tubers bacterized by *B. thuringiensis* 55T did not show structural host reactions whereas those treated with *B. cereus* X16 and challenged with the pathogen exhibited increased resistance to *F. sambucinum*, with decreased pathogen growth and viability, and the formation of physical barriers and a marked accumulation of new apparently fungitoxic products in the host (Chérif *et al*. 2003). Thus, several mechanisms of action may be deployed by *Bacillus* spp. isolates during their antagonism *in vitro* and *in vivo* toward *F. sambucinum*.

As tuber dry rot disease is caused by four *Fusarium* species (Daami-Remadi *et al*. 2006a), the use of *Bacillus* isolates was extended to the biocontrol of *F. solani*, *F. oxysporum* f. sp. *tuberosi*, *F. graminearum* and *F. sambucinum*. Light microscopic studies of *Bacillus* sp. × *Fusarium* spp. *in vitro* interactions showed several hyphal anomalies expressed mainly by decreased mycelium density, strong hyphae lysis, reduced or absent sporulation, formation of mycelial cords and premature induction of chlamydospores. This damage, caused on *Fusarium* spp. hyphae, contributes to a significant reduction in dry rot severity, on 'Spunta' tubers treated by *Bacillus* sp. 24 h prior to inoculation, compared to the untreated controls. Dry rot was 60 and 46% less severe on tubers treated with *Bacillus* sp. isolates and challenged with *F. graminearum* and *F. solani*, respectively (Daami-Remadi *et al*. 2006b).

2. Trichoderma spp.

Four strains of *Trichoderma* sp. (non-identified species) isolated from Tunisian soils were screened *in vitro* for their antagonistic effects against *F. solani* and *F. sambucinum* associated with potato tubers in traditional and refrigerated stores, respectively. The *in vitro* interaction of these microorganisms indicated a strong antagonism exerted by *Trichoderma* spp. against *Fusarium* spp. (Triki *et al*. 1996a). The effectiveness of these antagonistic agents was also evaluated *in vivo* against *F. sambucinum* together with other rot pathogens based on single or mixed tuber inoculations. Results demonstrated that tubers inoculated and dipped for 10 min in *Trichoderma* sp. condial suspensions (10^7 conidia/ml) exhibited rot symptoms after three days. Disease severity was reduced by 47 or 53% for treated tubers inoculated with *F. sambucnium* only or *F. sambucinum* + *P. erythroseptica*, respectively compared to the untreated controls (Triki *et al.* 1996b).

An indigenous isolate of *T. harzianum* was used against three dry rot agents. The *in vitro* tests revealed an important antagonistic effect of this agent toward *F. solani*, *F. sambucinum* and *F. graminearum*. Dry rot severity was significantly reduced by *T. harzianum*, applied on inoculated tubers as water-based conidial suspensions of kaolin powder formulations, compared to controls. The recorded effectiveness of this agent was significantly similar as a thiabendazol-based treatment (Daami-Remadi 2001a).

The effectiveness of *T. harzianum* in controlling dry rot disease was compared with *T. viride* isolates. Both antagonistic agents exhibited a strong antifungal activity toward *F. oxysporum* f. sp. *tuberosi*, *F. solani*, *F. graminearum* and *F. sambucinum*. Moreover, light microscopic observations of antagonist × *Fusarium* spp. *in vitro* interactions revealed several changes in the morphology of dry rot agents. In fact, the treated pathogen colonies showed reduced mycelium density and pathogen sporulation, severe lysis, formation of mycelial cords and premature induction of resting structures (chlamydospores) compared to untreated controls. These malformations caused by antagonistic fungi on *Fusarium* spp. hyphae may disturb and decrease pathogen infectivity and consequently, dry rot severity. These *Trichoderma* species, applied as tuber ('Spunta') treatment at inoculation sites (100 µl of conidial suspensions adjusted at 10^8 conidia/ml), 24 h prior to challenge inoculation with *Fusarium* species, showed reduced dry rot severity compared to the untreated controls (Daami-Remadi *et al*. 2006d).

3. Compost fungi

Compost teas were firstly used in Tunisia as potential sources of antagonistic agents for potato dry rot biocontrol. *T. harzianum*, *Penicillium* sp., *Aspergillus niger*, *A. flavus*, *A. nidulans* and *A. terreus* were screened for their antifungal activity against four dry agents based on *in vitro* (dual culture with *Fusarium* spp.) and *in vivo* (treatment prior to tuber inoculation) experiments. The mycelial growth of *F. graminearum*, *F. sambucinum*, *F. solani* and *F. oxysporum* f. sp. *tuberosi* was significantly inhibited and light microscopic studies revealed similar morphological changes as those noted with *Trichoderma* species (detailed above). Among the mechanisms of action first recorded in this study with compost fungal isolates was the mycoparasitism exerted by *A. niger* and *A. flavus* toward *Fusarium* spp. Applied as a preventive tuber ('Spunta') treatment, 24 h before their inoculation, these compost fungi significantly reduced dry rot incidence and severity compared to the untreated controls (Daami-Remadi *et al*. 2006g).

Abiotic agents

As part of the FDR control strategy undertaken in Tunisia, five abiotic agents i.e. chitin, chitosan, β-aminobutyric acid (BABA), salicylic acid and bion (benzothiadiazol) were evaluated for their inhibitory effects against *F. sambucinum*. Mejdoub-Trabelsi and Chérif (2009) found that the ability of these abiotic agents to control this tuber disease was variable depending on the concentration used. Chitin and chitosan, applied at 400 µg/ml, and BABA, used at 30 µg/ml, effectively limited disease severity on potato tubers whereas bion and salicylic acid failed to inhibit the pathogen growth.

Solarization

Triki *et al.* (2001a) used solarization for controlling some potato soil-borne pathogens, mainly *F. solani* and *P. aphanidermatum*, involved in tuber rots in storage as well as in delayed plant growth and/or wilting associated with root rotting in the field. The follow up of *F. solani* before and after soil solarization revealed that field mulching with polyethylene for 60 days during summer in Tunisia allowed an effective reduction in the soil infectious potential estimated at 30 cm depth where the inoculum level decreased from 3000 to 450 CFU/g of dry soil. After a subsequent autumn potato crop, soil infestation with *F. solani* increased by 40% in non-solarized soils but remained unchanged in solarized soils. It should be also mentioned that potato plant growth and yields were also improved in solarized plots. Thus, this physical control method could be involved in an integrated pest management of potato FDR as reduction of pathogen inoculum in the rhizosphere may decrease chances of successful infection.

CONCLUSION AND PERSPECTIVES

FDR is a postharvest disease of potato tubers of economic importance worldwide. *F. sambucinum*, *F. culmorum*, *F. solani*, *F. graminearum* and *F. oxysporum* were isolated from tubers exhibiting dry rot symptoms. These *Fusarium* species presented a great range of variability in growth and sporulation on culture media. Their ability to grow and to induce dry rot symptoms were assessed at different temperatures. Their optimum growth *in vitro* was determined and disease severity, as expression of pathogen aggressiveness, was estimated in function of temperature of storage and *Fusarium* species involved in disease development.

The susceptibility ranking of cultivars varied depending on *Fusarium* species used for inoculation suggesting distinct response or behaviour of local plant material. This phenomenon may complicate breeding programs as a cultivar tolerating one or two *Fusarium* species may be highly susceptible to the others especially in presence of mixed infections which were common in Tunisian potato producing fields. The susceptibility ranking of local potato cultivars to *Fusarium* species was significantly affected by the temperature of storage suggesting eventual breakdown of tolerance due to variations in this abiotic factor. Thus, studies should be focused on cultivar response taking into account these both factors (inoculum type and temperature).

Chemical based-treatments using old (mainly Benzimidazoles) and new (Phenylpyrroles and Strobilurins) generations of fungicides tested against *Fusarium* species have successfully limited pathogen growth *in vitro* and reduced dry rot severity on inoculated potato tubers. *F. graminearum*, *F. solani* and *F. oxysporum* f. sp. *tuberosi* were sensitive to benzimidazole fungicides whereas isolates of *F. sambucinum* exhibited resistance to this chemical class.

Biological control of FDR was achieved by exploring different microbial agents (fungi and Gram-positive bacteria) isolated from different sources (soil, rhizosphere, compost teas). These studies were undertaken based on various and complementary *in vitro*, *in vivo* and under natural conditions experiments which were corroborated by the selection of potentially important biocontrol agents.

Other alternatives of disease control including abiotic agents, tested *in vitro* on pathogen growth and used *in vivo* as tuber treatment, were found to be effective in reducing dry rot severity. Soil solarization has also contributed to the decrease of *F. solani* and *P. aphanidermatum* inoculum in the soil. All of these control alternatives proposed in this review may be apart of an integrated management strategy against potato FDR.

This review highlighted the specificity of problems related to FDR in Tunisia, regarding mainly pathogen aggressiveness variability, genetic resistance and control limits for better guiding future research. More attention should be paid to the mixed infections with dry rot agents during disease incidence qualification and control. Assessment of pathogen aggressiveness and cultivar responses should be undertaken in the future based on single or combined inoculations with *Fusarium* species for mimicking natural field conditions.

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