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CROP PROTECTION

LITERATURE REVIEW

Fusarium crown rot disease: biology, interactions, management and function as a possible sensor of global climate change

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Abstract

E.A. Moya-Elizondo. 2013. *Fusarium* crown rot disease: biology, interactions, management and function as a possible sensor of global climate change. Cien. Inv. Agr. 40(2):235-252. Wheat crops are commonly affected by the dryland root rot complex (DLRRC) under dry and semiarid conditions. This complex is associated with seedling blight, and rotting of roots, crowns and stems of wheat plants. Several pathogens are associated with this complex, but Fusarium crown rot disease (FCR) is the most common and is of worldwide importance. Increased drought frequency and changes in rainfall regimes associated with global climate change may increase the prevalence of this complex of diseases, especially of FCR, in wheat crop areas. This review discusses the characteristics of the pathogen species involved in DLRRC, the known interactions between the pathogens, and information regarding management strategies. We also discuss the possibility that the activity of FCR pathogens could act as a sensor of global climate change.

Key words: *Fusarium* crown rot, wheat, climatic change.

Introduction

The semiarid conditions associated with short or non-existent rotations, and the widespread use of no-till or conservation tillage system practices favor survival of pathogens that cause the dryland root rot complex (DLRRC) in wheat crops. If it is considered that about 32% of the 99 million hectares under wheat cultivation in developing countries experiences varying levels of drought stress (Rajaram *et al*., 1996), we can expect considerable yield losses caused by the pathogens associated with DLRRC in wheat crops worldwide. Semiarid conditions enhance the expression of the diseases associated with DLRRC because this complex of pathogens reduces the amount of functional root and crown tissue, which is critical under moisture-restricted conditions (Papendick and Cook, 1974; Cook, 1981; Bailey *et al*., 1989; Burguess *et al*., 2001; Paulitz *et al*., 2002). The measurable effects on yield are most apparent when the cereals are subjected to water stress later in the growing season and temperatures are high (Cook, 1981; Paulitz *et al*., 2002). Moreover, the damage is especially acute when drought occurs during the seedling and post-anthesis growth stages (Smiley *et al*., 2005a). However, infections by some *Fusarium* species, such as *F. pseudograminearum*, can occur

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in relatively moist soils (Burgess *et al*., 1981) and in irrigated systems (Paulitz *et al*., 2010).

Agricultural concerns related to global climate change are associated with the potential threat to the food supply derived from impacts such as changing patterns of rainfall, increasing incidence of extreme weather, and the changing distribution and incidence of diseases and their vectors (Tubiello *et al*., 2007; Soussana *et al*., 2010). Nevertheless, modeling studies indicate small beneficial effects on crop yields in temperate regions (resulting from local mean temperature increases of 1–3°C accompanied by CO_2 increases and rainfall changes). On the other hand, there is a general agreement among the scientific community that the consequences of global climate change will negatively affect all regions of the world (Soussana *et al*., 2010), especially subsistence or smallholder farmers, due to the increased likelihood of crop failure (Morton, 2007). Additionally, during the 20th century, the major drought index has increased over a number of regions (Bates *et al*., 2008), which is expected to increase the frequency of heat stress, droughts, and floods (IPCC, 2007; Beniston *et al*., 2007). Furthermore, extreme rainfall regimes are expected to increase the duration and severity of soil water stress in temperate areas as intervals between rainfall events increase (Knapp *et al*., 2008; Soussana *et al*., 2010). In this context, drought increases and extreme rainfall regime changes associated with climate change may lead to an increase of yield losses, and prevalence of the diseases and pathogens associated with the DLRRC. This provides a basis for further study in this field in order to deepen our knowledge of the biology, interactions and management of the pathogens associated with DLRRC.

The DLRRC is known by a variety of names including dryland foot rot, Fusarium foot rot, crown rot, dryland root rot, and common root rot (Paulitz *et al*., 2002). The disease complex is dominated by different pathogens in different areas or even by different pathogens during successive growing seasons in individual fields (Paulitz *et al*., 2002). This article focuses on the diseases associated with pathogens of the genus *Fusarium*. Fusarium crown rot (FCR) is the generic name used to refer to the disease caused by different pathogen species of the genera *Fusarium*. FCR is primarily caused by *F. culmorum* (W. G. Sm.) Sacc., *F. pseudograminearum* (O'Donnell & T. Aoki; group I) (= *Gibberella coronicola*), and *F. graminearum* Schwabe (group II) (= *G. zeae* (Schwein.) Petch) (Paulitz *et al*., 2002; Cook, 2010). In some geographical regions, *F. avenaceum* (Fr.) Sacc., *F. acuminatum* Ellis & Everh., *F. equiseti* (Corda) Sacc., *Microdochium nivale* (Fr.) Samuels & Hallett (= *F. nivale* (Fr.) Sorauer), and several *Fusarium* spp. have also been included and reported in the crown rot disease complex in wheat, but these species are considered less virulent and more environmentally or geographically restricted than the first three species listed (Cook, 2010). Although many species are associated with the DLRRC, *F. pseudograminearum*, *F. culmorum,* and *Bipolaris sorokiniana* (anamorph of *Cochliobolus sativus* (S. Ito & Kurib.) Drechsler ex Dastur [1942]), the last pathogen associated with common root rot disease and the spot blotch disease, are considered to be the most virulent and economically important pathogens (Burguess *et al*., 2001; Paulitz *et al*., 2002; Smiley *et al*., 2005a). FCR causes symptoms such as grain yield loss, stand reductions, and rotting of seeds, seedlings, roots, crowns, subcrowns, and lower stem tissues, and is also associated with the white-head or premature death of wheat tillers (Paulitz *et al*., 2002). Additionally, some species of *Fusarium* are also able to infect the heads or spikes, causing Fusarium head blight, which is associated with mycotoxin production (Cook, 2010). *Fusarium* species cause a soilborne disease of seedlings similar to that caused by soilborne pathogens such as *B. sorokiniana*, *Gaeumannomyces graminis* var. *tritici*, the causal agent of take-all, and *Rhizoctonia* spp. (Paulitz *et al*., 2002).

FCR disease on wheat is a perennial problem in cereal agro-ecosystems and causes significant losses in different regions worldwide (Burgess *et*

al., 2001; Paulitz *et al*., 2002), such as the Pacific Northwest (Cook, 1968; Smiley and Patterson, 1996; Smiley *et al*., 2005a), the Texas Panhandle (Specht and Rush, 1988), Southeastern Idaho (Strausbaugh *et al*., 2004); the upper coastal plain area of the Mississippi (González and Trevathan, 2000), the wheat "Golden triangle" of Montana (Moya-Elizondo *et al*., 2011a), the Canadian Prairies (Bailey *et al*., 1995; Hall and Sutton, 1998; Fernández and Jefferson, 2004; Fernández *et al*., 2007a-b; Fernández *et al*., 2009), eastern Australia (Backhouse *et al*., 2004); South Australia (Fedel-Moen and Harris, 1987), Queensland Australia (Wildermuth, 1986; Wildermuth *et al*., 1997), the United Kingdom (Pettitt *et al*., 2003), Turkey (Tunali *et al*., 2008), northwest Iran (Saremi *et al*., 2007); Argentina (De Souza, INTA Parana, Entre Ríos, Argentina, personal communication) and Chile (Madariaga, INIA Quilamapu, Chillán, Chile, personal communication). Scherm (2004) suggests that there are continuing problems with the application of models for predicting the effects of climate change on disease, including the lack of data on the geographic distribution of disease, non-linear relationships and thresholds in the relationship between climatic variables and epidemiological responses, and the potential for adaptation by plants and pathogens, which is often ignored in models. Interestingly, recent publications about DLRRC surveys have associated pathogen distributions with georeferenced geographical distribution and environmental data (Tunali *et al*., 2008; Moya-Elizondo *et al*., 2011a), and it has been suggested that some environmental and ecological adaptations of some fusaria could be used in the future to assess changes associated with global warming (Moya-Elizondo *et al*., 2011a). These studies have shown the impact of agroecological zones on the distribution, incidence and prevalence of different *Fusarium* species, and have also highlighted the importance of conducting continuous surveys that associate pathogen incidence with their spatial distribution and environmental data. In fact, these surveys could be a useful tool to monitor the effects of global climate change.

The effect of DLRRC infections under drought stress can cause yield loss exceeding 50%, along with detrimental effects on grain quality such as light test weight (Tunali *et al*., 2008). In the Pacific Northwest (PNW), Paulitz *et al*. (2002) determined that 76% of the plants in winter wheat fields can be infested with FCR, with estimated losses of 18% in heavily infected fields and a negative impact of US$76 ha^{-1}. In a recent survey in the PNW, yield losses associated with DLRRC in commercial winter wheat fields were valued at US$219 ha^{-1} and US$51 ha^{-1}, considering field losses of 35% and 9.5%, respectively (Smiley *et al*., 2005b). In that survey, the greatest damage estimated for field yield losses caused by *F. pseudograminearum* was 13% (US$48 ha^{-1}), while plots inoculated with *F. pseudograminearum* showed a grain yield loss of 61%, which was valued at US$372 ha^{-1}. In Australia, FCR has been identified as the second most economically important disease in wheat. Present costs caused by this disease throughout Australia are AUS $ 56M per year (Brennan and Murray, 1998, cited by Wildermuth *et al*., 2001). Burgess *et al*. (1981) reported that *F. pseudograminearum* caused up to a 26% yield reduction in individual wheat fields in subtropical southern Queensland, Australia. In Montana, USA, Moya-Elizondo *et al*. (2011a) showed that in nine intensively sampled fields, populations of FCR pathogens expressed as DNA copy number of the trichothecene *TRI5* gene were associated with losses of 24.6% and 34.9% for the dryland fields, and 21% for the second year of wheat recrop in an irrigated field.

The pathogens involved in the DLRRC may occur singly, but they typically co-exist in the same field and even within individual plants. Dominant species in the complex at a specific location can vary from year to year, indicating a high level of adaptation as members of this pathogen complex respond to changes in temperature, seasonal moisture distribution, the amount of moisture, and edaphic factors (Smiley *et al*., 2005a-b; Moya-Elizondo *et al*., 2011a). In this context, it is important to understand the biol-

ogy involved in the establishment and disease infection of FCR.

Biology of Fusarium crown rot of wheat

Different fungal species of the genus *Fusarium* are associated with FCR. *F. culmorum*, *F pseudograminearum*, and *F. graminearum* are epidemiologically the most important species involved (Paulitz *et al*., 2002; Cook, 2010). *F. culmorum* is associated with cooler semiarid wheat growing regions, while *F. pseudograminearum* and *F. graminearum* are dominant in slightly warmer regions (Cook, 1981). It has been determined that the proportion of crops in which *F. pseudograminearum* infection occurs is positively correlated with maximum temperature during the summer months (Moya-Elizondo *et al*., 2011a). Increases in fungal biomass have been documented with elevated levels of CO_2 (Melloy *et al*., 2010), a condition also associated with climate global change. The importance of *F. pseudograminearum* is increasing to the extent that a 70% of incidence has been reported in a wheat crop field in Henan, China (Li *et al*., 2012). *F. pseudograminearum* has also been associated with barley kernels in Tres Arroyos, Buenos Aires, Argentina (Castañares *et al*., 2012).

Among the other species of fusaria, *F. avenaceum*, *F. acuminatum*, *F. oxysporum*, and *F. equiseti* are among the most common and widespread fungi isolated from underground tissues of wheat in Canada, but a low number of tillers are infected (Fernández and Jefferson, 2004). However, *F. avenaceum*, *F. acuminatum*, *F. equiseti*, *F. oxysporum*, and *M. nivale* are considered to be species of lesser importance in the FCR complex (Cook, 2010; Paulitz *et al*., 2002; Smiley and Patterson, 1996) because they are considered to be secondary colonizers rather than primary pathogens in semiarid regions (Burgess *et al*., 2001). *F. avenaceum*, *F. acuminatum* and *M. nivale* are more pathogenic in areas with wet and cold weather (Pettitt *et al*., 2003; Hall and Sutton, 1998) and their infection levels are very dependent on weather conditions (Hall and Sutton, 1998). A survey in progress between the Araucania and Los Lagos Regions in the South of Chile has identified primarily *F. avenaceum* over *F. culmorum* and *F. pseudograminearum* in these rainy and cold areas (E. Moya-Elizondo, unpublished data). Almost all species of FCR can cause *Fusarium* head blight (FHB). However, *F. graminearum* is the most common cause of head blight and seedling blight in wheat in the USA (Bai and Shaner, 2004; Cook, 2010), while *F. culmorum* is more common in Europe (Wagacha and Muthomi, 2007). FHB infections occur under wet or humid conditions at anthesis or shortly thereafter (Burrows *et al*., 2008), while FCR is favored by water stress late in the growth season (Paulitz *et al*., 2002). All members of the FCR complex produce, under dryland conditions, a chocolate brown discoloration in the first to the third internodes up the stem, which can be observed when the leaf sheaths are stripped back in the base of the tiller. When those culm internodes are open, a pink mycelium is observed inside and its presence can be considered as a diagnostic symptom of FCR (Cook, 1981, 2010).

Description of causal organisms

The *Fusarium* species described above are most commonly associated with FCR disease and considered "unspecialized" pathogens because they can attack any plant tissue if conditions at the tissue surface are favorable for infection (Paulitz *et al*., 2002). In general, the anamorph of the different *Fusarium* species may or may not produce macroconidia, microconidia, chlamydospores, and conidia borne on mono or polyphyalides. The typical color of the mycelium on potato dextrose agar (PDA) plus the morphological structures mentioned above can be used to identify individual species throughout different synoptic keys (Nelson *et al*., 1983). Identification to the species level requires both practice and experience. Recently, specific primers have been developed to identify several of the *Fusarium* species (Scott *et*

al., 2003; Aoki and O'Donnell, 1999; Nicholson *et al*., 1998; Wildermuth *et al*., 1997), and they can be useful to confirm the pathogen identified with synoptic keys.

The teleomorph *Gibberella* spp. of the complex develop perithecia in clusters on the surface of plant tissues. Perithecia are globose, 125-265 µm in diameter, rough-walled, and vary from bluff to dark blue in color (Cook, 2010). Perithecia produce clavate asci of 4-10 µm in width x 50-80 µm in length with six to eight spores. Ascospores are hyaline, ellipsoidal, 3.3-6.5 x 13-17 µm, and one- to three-septate (Cook, 2010). The contrasting biology of the most important members of the FCR complex is described in Table 1.

Pathogenic variation among isolates is recognized for species associated with the crown rot complex (Smiley *et al*., 2005a-b). A comparison of pathogenicity of the FCR complex pathogens on hard red spring and durum wheat conducted in Montana showed that *F. culmorum* caused the greatest seedling blight, while *F. pseudograminearum* and *F. graminearum* caused greater crown rot (Dyer *et al*., 2009).

Disease cycle of Fusarium crown rot

Both seed-borne and soil-borne inoculums are important to the epidemiology of FCR (Cook, 1981). Chlamydospores, macroconidia, and mycelium are common survival structures in the soil and in crop residues (Paulitz, 2006; Cook, 1981). *F. culmorum* survives adverse conditions and generally remains as viable chlamydospores, while *F. pseudograminearum* and *F. avenaceum* most commonly survive as mycelium inside non-decayed plant residues. This is the major reason why the adoption of conservation tillage practices has resulted in an increase of FCR caused by *F. pseudograminearum* (Sitton and Cook, 1981; Paulitz *et al*., 2002).

Crown infection initially occurs 2-3 cm below the soil surface, either through openings around emerging secondary roots or by infection of newly emerging crown roots (Cook, 1981; Wiese, 1991). Coleoptile infection also occurs through stomata and between epidermal cells (Malalasekera *et al*., 1973). Infection of the seedling occurs through epidermal cell layers of the coleoptile and then expands into the parenchyma (Pisi and Innocenti, 2001). During pathogenesis, FCR pathogens produce an array of enzymes to overcome plant defense responses. Both induction of active laccases (Kwon and Anderson, 2002) and enhancement of catalase activity (Ponts *et al*., 2009) caused by FCR pathogens have been reported. These enzymes have been associated with reducing or inactivating active oxygen species (AOS) produced by the plant in response to necrotroph infection (Mayer *et al*., 2001). It is also important to note that trichothecene mycotoxin deoxynivalenol (DON), which is a toxin produced during infection by *F. graminearum* and *F. pseudograminearum* in the wheat stem base (Mudge *et al*., 2006), could play an important role in colonization of the wheat stem because DON is an inhibitor of protein synthesis. Thus, DON could suppress the production of host defense enzymes and other compounds, as has been suggested by Mudge *et al.* (2006). DON also elicits hydrogen peroxide production,

Table 1. Contrasting biological features among the most important members of the *Fusarium* crown rot complex.

F. graminearum (teleomorph = *Giberella zeae*)	*F. culmorum* (teleomorph unknown)	*F. pseudograminearum* (teleomorph = *Giberella coronicola*)
Lighter macroconidia and less durable chlamydospore. Produces a sexual stage (perithecia and ascospores) that permits longer distance spread. DON mycotoxin producer	Heavier macroconidia and more durable chlamydospore. Produces asexual conidia (macroconidia) and has the least efficient dispersal method, but produces a more stable population once established. DON mycotoxin producer	Lighter macroconidia and less durable chlamydospore. Lighter than *F. graminearum*. Produces asexual conidia (macroconidia) and lacks a durable survival structure. DON mycotoxin producer

programmed cell death and defense responses in wheat (Desmond, 2008b). Additionally, defense responses of the plant during *Fusarium* colonization could be depleted by ammonization and pH modulation of apoplastic fluids by *F. culmorum* infection. Ammonization and pH modulation have shown to modulate the activity of the cell-wall-degrading enzymes polygalacturonase and pectin lyase (Aleandri *et al*., 2007). When FCR pathogens are inside the plant, colonization of the pith cavity is not restricted by the barrier of the lumen at each node (Clement and Parry, 1998). The lumen appears to provide a pathway for vertical growth, while the surrounding parenchyma cells provide a potential nutrient source and a humid environment (Mudge *et al*., 2006). Similarly, Stephens *et al*. (2008), working with histological and real-time quantitative polymerase chain reaction (qPCR) analyses, showed that when *F. graminearum* causes crown rot, three distinct phases of infection can be identified: i) initial spore germination with formation of a superficial hyphal mat at the inoculation point, ii) colonization of the adaxial epidermis of the outer leaf sheath and mycelial growth from the inoculation point to the crown, concomitant with a drop in fungal biomass, and iii) extensive colonization of the internal crown tissue. This study also examined gene expression during each phase using Affymetrix GeneChips. In total, 1,839 *F. graminearum* genes were significantly up-regulated, including some known FHB virulence genes associated with mycotoxin production (*e.g*., *TRI5* and *TRI14*), and 2,649 genes were significantly down-regulated *in planta* compared with axenically cultured mycelia. Plants infected by FCR rarely show obvious symptoms until after heading (Cook, 1981). However, if wheat plants are under drought conditions, plant defenses weaken and the pathogen infection expands in the vascular tissue, disrupts water movement and prevents the recovery of infected plants from water stress (Cook and Christen, 1976; Hare and Parry, 1996).

Antagonistic responses or interactions between fusaria and other pathogens have been studied. The negative relationship between pathogen populations in a field is likely to be regulated by dynamics of competition for colonizing the different wheat tissues or/and displacement between each pathogen, depending on environmental conditions that favor one pathogen or the other. For example, Tinline (1977) reported that prepossession of the internode by *B. sorokiniana* infection does not prevent subsequent invasion by *F. culmorum* and *F. acuminatum*, but that prepossession by fusaria pathogens greatly reduces subsequent infection by *B. sorokiniana* in studies of single or combined inoculation of wheat. In the same way, Moya-Elizondo *et al*. (2011b) assessed pathogen populations in the first internode at heading, milk, and harvest stage of wheat development using qPCR. They reported that high and low levels of *F. pseudograminearum* inoculum colonized lower internodes earlier and reduced *B. sorokiniana* populations in field trials, but *B. sorokiniana* inoculations did not affect *F. pseudograminearum* populations. However, neither of the pathogens prevented infection by the other in the first internode of wheat stems.

Management of Fusarium crown rot

The probable increase of FCR infestation in wheat crops under dryland field conditions, which could be associated with global climate change and adoption of no-till practices worldwide, will force growers and agricultural extensionists to deepen their knowledge of management strategies for this disease complex. Cook (2010) has recommended different control practices, such as the use of clean and chemically disinfected seed, management of seeding dates, proper fertilization, the use of tillage, crop rotations avoiding other cereals, and the use of cultivars with resistance or tolerance and/or with resistance to water stress. No single management strategy has proven effective in eliminating root and crown rots. However, combined practices have proved helpful, even though they do not provide high levels of control.

Chemical disinfection of seed. Fungicide seed treatments are recommended for the management of FCR and other soilborne diseases, combined with healthy seeds. In fact, their capability of reducing seedling blight has been widely observed (Cook, 2010). For example, emergence of winter wheat in fields was superior for seed treated with difenoconazole (Dividend®) alone or mixed with metalaxyl (Apron®) (Smiley and Patterson, 1995). Extension plant pathologists at Montana State University recommend using seed treatment fungicides such as Vitavax Extra (carboxin + imazalil + thiabendazole), Dividend XL or RT (difenoconazole + mefenoxam), Raxil XT or MD (tebuconazole + metalaxyl), Raxil MD Extra (tebuconazole + metalaxyl + imazalil), Baytan (tridimenol), and RR, Flo-pro, NuZone (imazalil) to promote healthy seedling growth (Dyer *et al*., 2007). However, as fungicides do not maintain their efficiency beyond 2-4 weeks (Balmas *et al*., 2006), chemical control is limited to the early stages of wheat growth, and later infections can be observed, especially in winter wheat.

Management of planting date. The use of cultivars with high yield potential and following the recommended date of planting in a geographic area can be simple actions that reduce the incidence of DLRRC disease. In general, early planting promotes disease in winter wheat (Cook, 2010). In the PNW, assessment of planting dates showed that FCR was more prevalent in early-planted winter wheat and generally reduced or absent in plantings made later in the fall (Smiley, 2009). Late-autumn seeding of winter wheat also reduces seedling exposure to warm soil and limits the amount of vegetative growth that can lead to premature reduction of soil water and water stress that promotes damage by pathogens (Cook, 2010). Despite the effectiveness of this practice, management of planting date depends on the amount of hectares managed by each farmer and weather conditions associated with each area of production.

Crop rotation with non-cereals. Crop rotation is the most effective method to control soilborne pathogens. Crop rotation also allows growers to limit alternative hosts and to control the more ephemeral *Fusarium* species (Wiese, 1991), which significantly reduces the pathogenic fitness level of *F. graminearum* and *F. pseudograminearum* on wheat (Akinsanmi *et al*., 2007). However, about half of the inoculum of *Fusarium* spp. present after harvest is functional a year later, and approximately 10% can survive for nearly two years (Wiese, 1991). Rotation with a broadleaf crop, such as peas or soybeans has proven beneficial to limit damage from both FHB and FCR caused by *F. graminearum*. In fact, a crop rotation with at least a two-year break from cereal is the most effective way to reduce damage from FCR caused by *F. pseudograminearum* (Burgess *et al*., 2001; Cook, 2010). The longevity of chlamydospore inoculum of *F. culmorum* makes the use of rotation more challenging, as evidenced by experiments that showed that a two-year break did not provide effective control of this species (Cook 1981, 2010). Fernández *et al*. (2007b) reported that summer-fallow was associated with increased infection by *B. sorokiniana*, whereas it appeared that relative levels of *Fusarium* spp., except for *F. acuminatum* and *F. equiseti*, consistently decreased when there was summer-fallow in the previous year, or in one of the previous 2 years. *Fusarium* species have a large host range, which includes numerous grass species; therefore, crop options for the rotations are limited. Additionally, crop rotation options are limited in some areas because low rainfall limits commercial economic alternatives (Strausbaugh *et al*., 2005).

Cultivar resistance or tolerance. Use of resistant cultivars would be the most effective and efficient measure to reduce the impact of FCR disease. Nevertheless, resistance to FCR pathogens in commercial cultivars is only partial (Cook, 2010) and disease outbreaks are common and can also be severe when climatic conditions are favorable for the pathogens on these partially resistant cultivars (Burgess *et al*., 2001; Strausbaugh *et al*., 2005).

Resistance to *Fusarium* pathogens is associated with FHB resistance (Bai and Shaner, 2004) or direct resistance to crown root rot disease

(Smiley *et al*., 2003). The two most important types of resistance to FHB in wheat have been described as resistance to initial infection (referred as type I) and resistance to spread of FHB symptoms within a spike (referred to as type II). Type II resistance has been found in a number of wheat cultivars and appears to be more stable and less affected by non-genetic factors than type I resistance (Bai and Shaner, 2004). However, while high resistance to FHB has been described (Bai and Shaner, 2004), work performed by Xie *et al*. (2006) and Li *et al*. (2010) suggested that FHB resistant germplasm did not offer any resistance to FCR. The idea of resistance inversion has been proposed for the observed phenomenon of differential resistance to FCR and FHB in wheat, where one plant genotype displays a resistant phenotype at one development stage but a susceptible reaction to the same pathogen at another stage (Li *et al*., 2010). Nevertheless, work conducted by Moya-Elizondo and Jacobsen (unpublished data) have shown dual resistance to FCR and FHB in cv. Volt, and their results contradict the idea of resistance inversion proposed by Li *et al*. (2010). Cultivar Volt is also considered to have good tolerance to FHB, but this resistance did not originate in the 1B chromosome from the Chinese Sumai 3 cultivar, which gives resistance to FHB. On the other hand, its performance against FCR is similar or worse than other cultivars that are susceptible to FHB and FCR (Xie *et al*., 2006; Moya-Elizondo and Jacobsen, unpublished data).

Seedling and adult plant tolerance (partial resistance) to some members of the FCR complex, such as *F. pseudograminearum*, has been reported (Collard *et al*., 2005; Bovill *et al*., 2006; Li *et al*., 2010; Cook, 2010) and is associated with reduced damage to stem base tissue and increased wheat yield (Wildermuth *et al*., 2001). Seedling resistance, but not adult-plant resistance, has been associated with the phenotypic expression of a genetically determined trait, the depth at which crown tissue is formed for each wheat cultivar or breeding line (Wildermuth *et al*., 2001). Collar *et al*. (2005) used molecular markers associated with partial seedling resistance to FCR disease in populations of double haploid lines constructed from crosses between '2-49' (partially resistant) and 'Janz' (susceptible) parents. The authors demonstrated that the trait is quantitatively inherited and that none of the QTLs identified as conferring resistance to FCR were located in the same region as resistance QTLs that were identified as segregating for FHB caused by *F. graminearum* in other populations. Seedling resistance has been linked to QTLs located on chromosomes 2B, 2D and 5D in progenies obtained from a cross between 'W21MMT70' (partial resistance) x 'Mendos' (susceptible) (Bovill *et al*., 2006). These loci are different from those associated with crown rot resistance in other wheat populations that were examined by Collar *et al*. (2005), who determined that resistant QTL's were located on chromosomes 1D and 1A. Bovill *et al*. (2006) suggested that these loci may represent an opportunity for pyramiding QTL to provide stronger resistance to FCR. Recent studies on the effects of plant height on FCR disease severity in near-isogenic lines (NILs) have shown that dwarf isolines had better FCR resistance when compared with their respective tall counterparts and that this resistance was not associated with enhanced defense gene induction (Liu *et al*., 2010). These authors suggested that the difference in FCR severity between the tall and dwarf isolines might be due to their height difference *per se* or to some physiological and structural consequences of reduced height.

According to Smiley *et al*. (2003), genetic tolerance to FCR is important during years when disease pressure is moderate, and it is ineffective when disease pressure is high. In the PNW, Smiley and Yan (2009) conducted a study with winter wheat cultivars, and screened for tolerance to FCR in naturally infested and inoculated soils. The phenotypic tolerance response in individual cultivars was highly variable over years and test sites. In addition, these authors - in a cooperative effort between Australian and USA researchers - have identified significant differences among

spring wheat entries in the PNW (Smiley and Yan, 2009).

Losses caused by FCR pathogens are significant. Therefore, active wheat screening and breeding programs for dryland root rot resistance and tolerance have been actively initiated in different locations worldwide with the support of CIMMYT (Nicol *et al*., 2004; Smiley *et al*., 2003; Phil Bruckner, Montana State University, Bozeman, USA, personal communication).

Effect of crop nutrition. Soil fertility must be adequate to support vegetative growth but it needs to be balanced with water supplies to avoid FCR. Excessive nitrogen under low-rainfall conditions promotes vegetative growth and especially tiller formation that could be sustained by the remaining water stored in the soil. These conditions favor water stress on the plants during heading and grain fill, which predisposes the crop to severe foot and crown rot caused by FCR (Papendick and Cook, 1974; Cook, 1980; Burgess *et al*., 2001; Cook, 2010). Cook (1980) recommended nitrogen application rates to be based on a soil test for residual nitrogen. Nitrogen fertility should not exceed 60-75 kg ha^{-1} in areas with <240 mm average annual precipitation. Moreover, zinc deficiency has been linked with higher levels of infection caused by *F. pseudograminearum* on wheat in glasshouse trials (Sparrow and Graham, 1988). In addition, wheat genotypes with a more efficient capacity to extract zinc from soils with poor zinc availability have been associated with a reduction of FCR severity as well as increased plant vigor (Grewal *et al*., 1996).

Effect of tillage practices and stubble management. Preceding cropping sequences and agronomic practices can affect the level of inoculum of the FCR pathogens and its distribution in the field, thus defining the incidence of infected plants by FCR (Burgess *et al*., 2001). FCR has shown higher incidence and severity where stubble is retained than where it is removed (Wildermuth *et al*., 1997; Paulitz *et al*., 2002; Cook, 2010). Management of infected stubble through post-harvest burning, fire plus harrowing in the fall season, stubble incorporation by disc cultivators that invert the soil and surface residue, or stubble retirement from the field will greatly reduce the sources of inoculum for FCR (Burgess *et al*., 2001). On the other hand, plowing that promotes the fragmentation and decomposition of stubble reduces infection by FCR pathogens, such as *F. pseudograminearum* or *F. graminearum* (Burgess *et al*., 2001; Steinkellner and Langer, 2004), but has a lesser effect on the persistent chlamydospores of *F. culmorum* (Windels and Wiersma, 1992). In dryland agriculture, the use of summer fallow to conserve soil moisture and release organic nitrogen has caused widespread adoption of moisture-conserving minimum tillage systems (Padbury *et al*., 2002). The use of no-till and conservation tillage system practices in a wheat-fallow production system has been associated with higher levels of *Fusarium* infections (Smiley *et al*., 1996; Bailey *et al*., 2001) and a population change from *F. culmorum* to *F. pseudograminearum* (Sitton and Cook, 1981; Paulitz *et al*., 2002). It has also been suggested that *F. pseudograminearum* is more aggressive than *F. culmorum*, which may explain the increase in FCR severity under conservation tillage systems (Paulitz *et al*., 2002; Smiley *et al*., 2005a). *F. pseudograminearum* is strictly a residue-born pathogen that depends on infesting late season tillers for survival between cropping periods (Sitton and Cook, 1981; Pereyra and Dill-Macky, 2004). This fact could increase the selection pressure on the pathogen to capture residues in order to survive a prolonged non-cropping period (Dyer *et al*., 2009). According to Bailey (1996), prior to the adoption of conservation tillage, the impact of these factors on FCR was largely unknown and could not have been properly considered in making predictions about the impact of conservation tillage practices on this disease. Studies conducted for six years by Paulitz *et al*. (2010) in an irrigated cropping systems experiment in east-central Washington State determined that inoculum concentration of *F. pseudograminearum*

was higher than that of *F. culmorum* after three continuous years of winter wheat cultivation; in one of three years, the former was higher after treatments with standing stubble and mechanical straw removal compared to burned treatments. However, burning stubble is a very controversial practice due to the pressure to reduce CO_2 emissions to prevent global climate change.

Effect of other cropping practices. Cook (1980) recommended increasing the distance between rows to reduce crown and root rot infection in semiarid areas. The wide-row spacing results in a reduced seedling density and hence a slower rate of soil water use per unit of field area (Papendick and Cook, 1974; Cook, 1980). Cultural practices to reduce moisture loss from the soil would logically be associated with a reduction of crown and root rot diseases (Papendick and Cook, 1974). Improving infiltration and reducing water runoff during precipitation or snow melt by working the field with a chisel plow is thought to reduce crown and root rot diseases by making more water available (Cook, 1981). Controlling weeds in summer fallow land and during crop development should also reduce infection by these diseases, because weeds deplete soil moisture that predisposes plant roots to infection in fall. However, studies conducted in the Northern Great Plain of Canada have determined that previous glyphosate applications in summer-fallow were associated with lower B. sorokiniana and higher Fusarium spp. levels in barley and wheat grown under minimum-till management (Fernández *et al*., 2005; Fernández *et al*. 2007a-b, Fernández *et al*., 2008; Fernández *et al*., 2009).

New strategies for the control of crown and root rot diseases

The management cropping practices previously discussed make controlling the crown and root rot complex challenging and emphasize the need for other control alternatives. Wildermuth *et al*. (1997) have suggested that some form of biological suppression may be operating to limit the maximum incidence of crown and root rot infections in Australia. Biological control agents (BCAs) have shown promise in the control of FCR disease (Huang and Wong, 1998; Dal Bello *et al*., 2002; Johansson *et al*., 2003; Luongo *et al*., 2005; Khan *et al*., 2006; Singh *et al*., 2009). Two approaches have been considered: 1) Manipulation of microbial antagonists to increase the rate of mortality of *Fusarium* spp. in cereal residues (Wong *et al*., 2002; Luongo *et al*., 2005; Singh *et al*., 2009), and 2) seed treatment with BCAs (Dal Bello *et al*., 2002; Khan *et al*., 2006). Assessment of saprophytic fungi obtained from cereal tissues or necrotic tissues of other crops have shown that isolates of *Clonostachys rosea* consistently suppressed sporulation of *F. culmorum* and *F. graminearum* on wheat straw (Luongo *et al*., 2005), while *Trichoderma harzianum*, *F. equiseti*, and *F. nygamai* showed strong antagonism in dual culture interactions with *F. pseudograminearum* (Singh *et al*., 2009). These data have been validated in bio-assays conducted under controlled conditions, but results have been variable for different *Fusarium* spp. (Luongo *et al*., 2005). In addition, BCA performance was strongly affected by temperature and water potential (Singh *et al*., 2009). Seed bio-based treatment has proven promising for enhancing biological control of plant diseases. Huang and Wong (1998), working with *Burkholderia cepacia* (A3R), significantly reduced crown rot symptoms caused by *F. pseudograminearum* on wheat in glasshouse and field experiments and significantly increased grain yield in one of two field experiments. Johansson *et al*. (2003) tested the action of 164 bacterial isolates against both *F. culmorum* and *M. nivale* as causal agents of wheat seedling blight in field experiments during five consecutive growing seasons. Their research determined that three fluorescent pseudomonads and *Pantoea* sp. isolate MF 626 were able to increase the number of established wheat plants under field conditions, when wheat seeds were coinoculated with *F. culmorum*. Del Bello *et al*. (2002) assessed fifty-two bacterial strains and six *Trichoderma* spp. isolated from the wheat

rhizosphere for biocontrol of seedling blight of wheat caused by *F. graminearum*. Among isolates tested, *Stenotrophomonas maltophilia*, three strains of *Bacillus cereus* and one isolate of *T. harzianum* increased the plant stand, height and dry weight in different wheat cultivars, but did not cause a significant decrease in the percentage of diseased plants. Khan *et al*. (2006), working with pseudomonads and chitosan against *F. culmorum*, reported the induction of a wheat class III plant peroxidase gene, which suggested that part of the biocontrol activity of these bacteria and chitosan might be due to the induction of systemic acquired resistance (SAR) in host plants.

One promising strategy to control diseases is induced resistance. In the broadest sense, induced resistance means the control of parasites or pests by activation of genetically programmed plant defense pathways before infection or infestation (Kogel and Langen, 2005). Induced resistance to microbial pathogens, resembling the SAR response, can be obtained by applying defense-signaling compounds that activate the defense signaling pathways (Kogel and Langen, 2005). In cereals, pathways for SAR induction are regulated by salicylic acid (SA) and jasmonic acid (JA) and their cellular targets (Kogel and Langen, 2005). Downstream signaling components, such as nonexpressor of pathogenesis-related gene 1 (NPR1), are deployed during SA-dependent defense and orchestrate cross-talk between the SA and JA pathways (Spoel *et al*., 2003). The antagonistic SA and JA pathways elicit the accumulation of distinct subsets of defense-related proteins. SA-dependent pathways are associated with Pathogenesis-Related proteins (PR-proteins), such as peroxidase, chitinase, β-glucanase and *PR*-1 (Durrant and Dong, 2004). The JA pathway is associated with production of thionins, defensins and proteinase inhibitors (Xu *et al*., 2001). Almost all classes of PR-proteins induced in plants in response to attack by microbial or insect pests have been identified in wheat (Muthukrishnan *et al*., 2001).

Few studies have been conducted to explore the response to infection with crown rot pathogens in wheat. Desmond *et al*. (2006), studying the molecular host-interaction between *F. pseudograminearum* and wheat, showed the induction and expression of eight defense genes in a susceptible and a partially resistant cultivar of wheat when plants were infected by the pathogen. Additionally, they were able to show that the induction of those genes by methyl jasmonate and benzo (1,2,3)thiadiazole-7-carbothionic acid-*S*-methyl ester (BTH, Bion) treatments delayed disease development caused by infection of *F. pseudograminearum*. In two gene expression research projects, induction of chitinase gene expression in wheat seedling has been observed in response to *F. pseudograminearum* (Desmond *et al*., 2006) and *F. asiaticum* (Li *et al*., 2010) infection.

Over-expression of the chitinase gene and chitin-binding (*PR-4*) gene in wheat seedlings has been associated with seedling resistance to *F. asiaticum* infection. High expression of a plant cytochrome P450 gene *CYP709C1*, which is involved in detoxification of exogenous compounds, has also been associated with seedling resistance to *F. asiaticum* infection (Li *et al*., 2010). Pathogenesis-related proteins of the *PR-4* family have been shown to have distinct antifungal activities in coleoptiles and roots against *F. culmorum* (Caruso *et al*., 2001; Bertini *et al*., 2003). *PR 4* has chitin-binding activity and it has been demonstrated to possess RNAse activity, which may be part of a mechanism for inhibiting invading pathogens (Caruso *et al*., 2001). Moreover, Desmond *et al*. (2006) also showed that in response to FCR, thaumatin-like proteins (*PR-5*) were highly expressed after inoculation with *F. pseudograminearum*.

By using a GeneChip® Wheat array, Desmond *et al*. (2008a) showed that after one day of stem base inoculation of 2-week-old wheat seedlings with *F. pseudograminearum*, 1248 unique genes were induced compared to mock-controls. Among these genes, the largest classes of induced genes were associated with anti-microbial proteins, such as

chitinase, β-1, 3-glucanase, *PR-1*, *PR-10*, *PR-5*, peroxidases, germin–like proteins, and detoxifying proteins such as glucosyltransferase or cytochrome *P*450. This array of genes involved in the response of the plant to crown rot pathogens indicates that process of resistance to this necrotrophic disease is complex, and demonstrates the necessity of going in depth in the study of genes that correspond to different sources of disease resistance.

In conclusion, FCR disease is an endemic disease in wheat crops caused by different pathogens of the genera *Fusarium*. Predictions associated with global climate change suggest considerable yield loss and widespread distribution of the pathogens associated with this crown and root rot complex on worldwide cereal agro-ecosystems. This concern is especially high due to the changing patterns of rainfall and increasing drought over different regions of the world, which could increase yield losses and the prevalence of the diseases and the pathogens. Field surveys of pathogen species associated with FCR in different wheat crop regions could be an adequate tool to assess changes associated with climate change, especially considering the impact of agroecological zones on the distribution, incidence and prevalence of different *Fusarium* species. Based on the diverse biology involved in the establishment and disease infection of the pathogens of the FCR complex, management strategies are required. The use of certified and chemically disinfected seed, management of seeding date, proper fertilization, the use of tillage, crop rotations avoiding other cereals, the use of cultivars with resistance or tolerance, and/or with resistance to water stress are useful tools to reduce the impact of this disease. However, new practices such as the use of biological control and induction of resistance with chemicals and BCAs could be new alternatives to control this problem.

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Resumen

E.A. Moya-Elizondo. 2013. Fusariosis de la corona: biología, interacción, manejo y un posible sensor de cambio climático global. Cien. Inv. Agr. 40(2):235-252. Bajo condiciones de producción en secano y áreas semiáridas, los cultivos de trigo son comúnmente afectados por el complejo de pudriciones radiculares del secano (DLRRC). Este complejo se asocia con la necrosis de plántulas y pudrición de raíces, coronas y tallos de las plantas de trigo. Varios patógenos están asociados a este complejo, pero la Fusariosis de la corona (FCR) es la enfermedad más comúnmente asociado con DLRRC y tiene importancia en todo el mundo. Incremento en la frecuencia de sequías y los cambios en los regímenes de lluvias asociadas al fenómeno de Cambio Climático Global podría aumentar la prevalencia de este complejo de enfermedades, especialmente de FCR, en las áreas donde se cultiva trigo. Este artículo discute sobre la posible actividad de patógenos asociados con FCR como sensores de este fenómeno global. La presente revisión también analiza las características de las especies de patógenos implicados en esta enfermedad del DLRRC, reporta información sobre la interacción entre los patógenos involucrados, y entrega información sobre las estrategias de manejo de la enfermedad.

Palabras claves: Fusariosis de la corona, trigo, cambio climático.

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