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Fusarium–Plant Interaction: State of the Art – a Review

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Abstract

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One of the most important genera able to develop diseases in cereals is *Fusarium* which not only produces losses by the fungal presence but also mycotoxin production harmful to human and animal consumers. In the environment, plants are continuously threatened by abiotic and biotic stresses. Among the latter, pathogens gained importance mainly due to their ability to affect the plant fitness. To protect against potential attacks, plants have developed strategies in which phytohormones have an essential role. In plant–pathogen interactions, salicylic acid, ethylene, and jasmonates are the most important, but there are also auxins, gibberellins, abscisic acid, cytokinins, brassinosteroids, and peptide hormones involved in plant defence. The interaction between *Fusarium* species and plants used as models has been developed to allow understanding the plant behaviour against this kind of pathogen with the aim to develop several strategies to decrease the *Fusarium* disease effects.

Keywords: phytohormones; signalling pathways

Fusarium importance

A disease is the main cause of losses produced by biotic factors in crops used in the agricultural and food industry thus posing a threat to favourable production.

Among fungal diseases, Fusarium head blight (FHB) is one of the most important diseases that affect cereal grains. Although this was firstly considered as a secondary disease, due to its increased occurrence enhanced by the use of a zero tillage system (reduced soil disturbance), use of susceptible genotypes and low crop rotation, it is today considered as one of the most devastating diseases that reduce the quality and yield of cereals (McMullen *et al.* 1997). FHB has been responsible for great economic losses worldwide. For example, in 1993 wheat production showed a reduction of 33% in Minnesota with economic losses estimated at 1 billion dollars (Dill-Macky 1997). In Uruguay, a serious outbreak occurred in 1977 showing a decrease of 50% on wheat production (Díaz de Ackermann & Kohli 1997). In Argentina, yield losses were estimated to 20–30% in 1945–1946, 1978, 1985 and 1993 (De Galich 1997). In the last years, an increase in FHB occurrence has been evidenced in Argentina, Brazil, Canada, China, USA, Japan, Paraguay, Uruguay, and some countries of Central and Western Europe (Mazzilli *et al.* 2007).

The genus *Fusarium* comprises a high number of fungi with recognisable capacity to be plant pathogens of cereal grains such as barley, wheat, and oat. Several researchers have found the presence of different *Fusarium* species that colonise diverse substrates. One of them, *Fusarium graminearum,* the main

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causal agents of the FHB disease, has been isolated from barley (Leslie & Summerell 2006), wheat (Gilbert & Fernando 2004), soybean (Pioli *et al.* 2004), potatoes (Ali *et al.* 2005), maize (Leslie & Summerell 2006), sorghum (Menkir *et al.* 1996), and rice (Nyvall *et al.* 1999). Moreover, other species have been isolated from FHB symptoms such as *F. poae*, *F. avenaceum*, and *F. culmorum* (Nicholson *et al*. 2003).

The presence of *Fusarium* species on grains is accompanied by the ability of some of them to produce a large number of secondary metabolites called mycotoxins which are not essential for the fungus life but may provide certain advantages in diverse environmental conditions. Trichothecenes belong among the most important groups of *Fusarium* mycotoxins in which type A (diacetoxyscirpenol – DAS, HT-2 toxin, T-2 toxin, and deoxynivalenol – DON) and B trichothecenes (nivalenol – NIV) are found. Besides the trichothecene mycotoxins, *Fusarium* species are able to produce fumonisins, enniatins, zearalenone, beauvericins, moniliformins, fusarins, fusaric acids, and fusaproliferin (Desjardins 2006). Mycotoxins are harmful for animal and human consumers. Moreover, some of them are stable at high temperatures, being possible to find them not only in primary agricultural crops but also after food manufacturing (Hazel & Patel 2004).

Besides the FHB complex, there are other *Fusarium* species that cause damage in several crops. *Fusarium oxysporum*, an important component of the soil microflora, is responsible for losses around the world. Considered as one of the most important soil-borne plant pathogens, *F. oxysporum* pathogenic isolates produce wild and rot diseases by fungal proliferation on root systems of the plants of economic importance such as tomato, cotton, and banana (Leslie & Summerell 2006; Laurence *et al.* 2012).

Fusarium verticillioides is responsible for stalk rot and cob rot in maize, thus producing significant yield losses and reduction of grain quality. Moreover, some mycotoxins such as fumonisins produced by this pathogen have negative effects on consumers since they cause leukoencephalomalacia in horses (Leslie & Summerell 2006; Silva *et al.* 2006).

Several strategies have been evaluated to control diseases caused by *Fusarium* including cultural, biological and chemical control and the use of cultivars with resistance to *Fusarium* (Pirgozliev *et al.* 2003). Despite efforts focused on reducing *Fusarium* effects, the proposed methods are very limited.

Phytohormones involved in plant–pathogen interactions

In their interaction with the environment, plants are often exposed to different types of stress such as abiotic stress caused by temperature or water conditions, and biotic stress such as diseases caused mainly by viruses, bacteria or fungi that make plants be continuously threatened by pathogens affecting their fitness. Accordingly, plants produce several hormones essential for the regulation of plant growth, development, reproduction and survival. Phytohormones include auxins (AUX), gibberellins (GA), abscisic acid (ABA), cytokinins (CK), salicylic acid (SA), ethylene (ET), jasmonates (JA), brassinosteroids (BR), and peptide hormones which change their levels during infection as strategies to prevent the pathogen colonisation (Adie *et al*. 2007; Bari & Jones 2009). Regarding the pathogen life cycle, specific signalling pathways are activated. Biotrophic pathogens which are fed from live plant tissues lead to activate SA accumulation essential for the systemic acquired resistance (SAR) as primary defence against the pathogen invasion (Alvarez 2000; Thomma *et al*. 2001). SAR is characterised by the increase of pathogenesis-related genes known as PR whose proteins have antimicrobial activity that immunises plants against future pathogen attacks (Durrant & Dong 2004). Cell death is the most effective plant event against this type of pathogen which is carried out by the hypersensitive response (HR) caused by reactive oxygen species (ROS) that produce tissue necrosis preventing the pathogen development. The use of mutant or transgenic plants has allowed knowing several intermediates in the SA signalling pathways. The non-expressor of pathogenesis-related genes (NPR1) is one of the most critical SA transducers. In the pathogen absence, NPR1 is oligomeric in the cytoplasm, but a pathogen invasion increases SA levels and NPR1 becomes monomeric and enters the nuclei to activate several transcription factors (Grant & Lamb 2006; Pieterse *et al.* 2009). Among them, TGA, a family of conserved plant bZIP transcription factors, and WRKY transcription factors with WKRY domain interact with NPR1 and promote the expression of PR genes (Vlot *et al*. 2009) (Figure 1). On the other hand, regarding necrotrophic pathogens, the cell death could only benefit the pathogen survival. Therefore, other responses leading to activate the JA and ET signalling pathways have been developed as other plant defence strategies against this type of pathogen. Previous studies suggested that JA is

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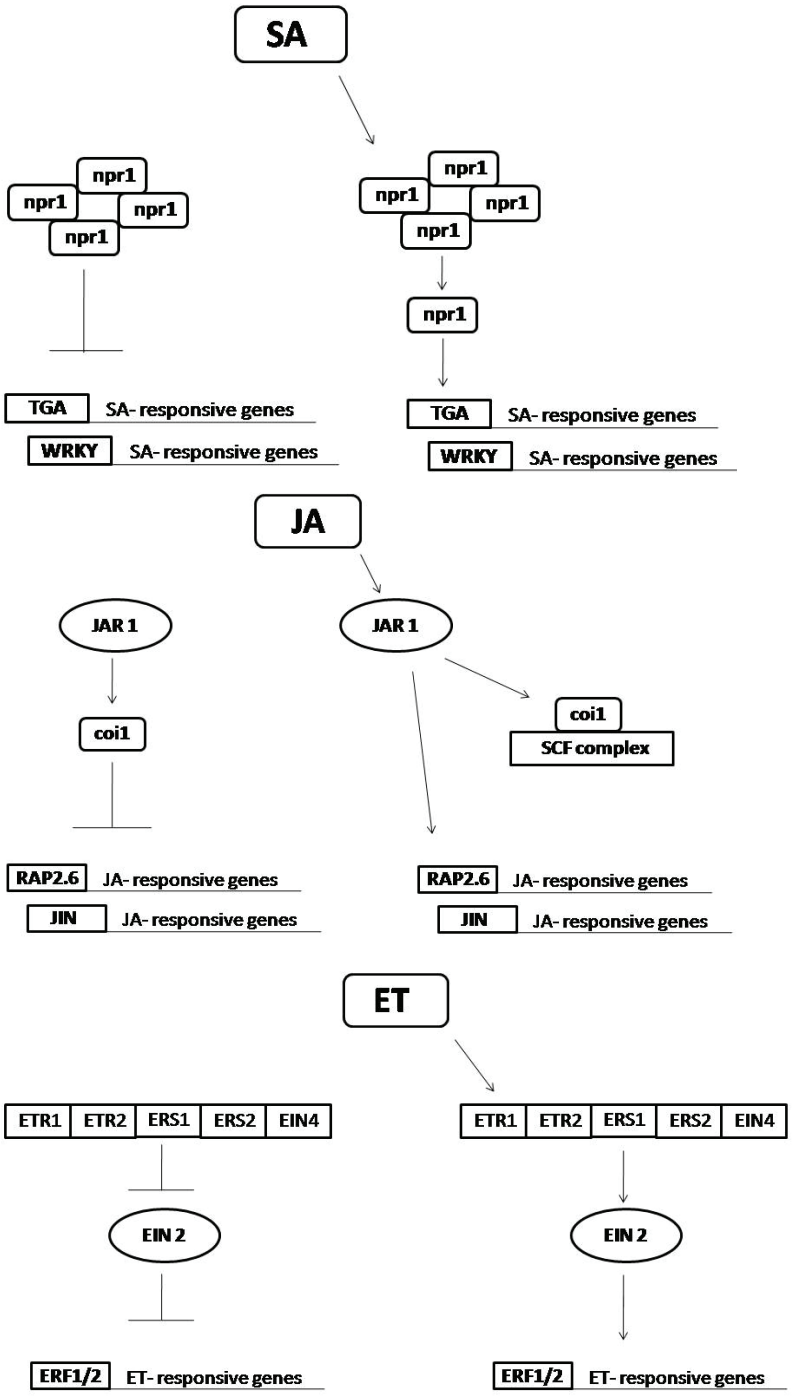

Figure 1. Representation of salicylic acid (SA), jasmonates (JA), and ethylene (ET) signalling pathways

also increased in response to wounds and defence against insects, but ET shows no changes against this kind of attack (Thomma *et al.* 2001). Regarding the JA signalling pathway, several intermediates are necessary to activate the JA depending-response including Jasmonate Resistance 1 (JAR1) with the synthetase function that conjugates JA with several amino acids (Glazebrook 2005). Coronatine Insensitive 1 (COI1) functions downstream JAR1 and acts as a target for degradation by E3 ubiquitin ligase Skp1, cullin, F-box proteins containing a complex (SCF complex) through the ubiquitin-26S proteosome in JA increased levels. The JA depending transcription factors are Ethylene Response Factor 1 (ERF1) and Related to Apetala 2.6 (RAP2.6), another member of ethylene response factors that expresses

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defence effector genes. In ethylene response, almost five proteins act as ET receptors known as Ethylene Response 1 (ETR1), Ethylene Receptor 2 (ETR2), Ethylene Response Sensor 1 (ERS1), Ethylene Response Sensor 2 (ERS2) and Ethylene Insensitive 4 (EIN4). Downstream these receptors, Ethylene Insensitive 2 (EIN2) is responsible for further signal transduction that involves several transcription factors such as Ethylene Response Factor 1/2 (ERF1/2) that together with JA induction allow the expression of several defence genes including *plant defensin 1.2* (*PDF1.2*), *thionin 2.1* (*THI2.1*), *hevein-like protein* (*HEL*), and *chitinase b* (*CHIB*) (Bleecker & Schaller 1996; Kunkel *et al*. 2002; Broekaert *et al.* 2006). Besides these main phytohormones involved in plant defence, others such as GA, BR, ABA, CK, and AUX have different roles in the plant–pathogen interactions. For example, ABA is a hormone involved in plant development and allows plants to adapt themselves to different adverse environmental conditions. Although it is a phytohormone mainly related to abiotic stress, its effects on the callose deposition have positive defence effects against pathogens (Mauch-Mani & Mauch 2005; Asselbergh *et al.* 2008). Moreover, Yasuda *et al.* (2008) demonstrated that ABA inhibited SA and vice versa by using several *Arabidopsis* mutants promoting the susceptibility to biotrophic pathogens (Bostock *et al.* 2014). Using tomato as a model, Asselbergh *et al.* (2008) demonstrated that ABA deficiency is needed to activate plant defence response against *Erwinia chrysanthemi*, a necrotrophic plant pathogenic bacterium. According to Walters and McRoberts (2006), CKs play a key role to provide nutrients towards infection sites allowing the biotrophic fungal pathogen development, but considering that some pathogens can produce these phytohormones, the CK origin is undetermined. Moreover, CKs induce the transcription of defence-related genes regulated by SA playing a role in the plant–pathogen interaction (Choi *et al.* 2011). In another pathosystem using tobacco as a plant model, Grosskinsky *et al*. (2014) found that CKs induce resistance against *Pseudomonas syringae* and at the same time, they inhibit the ABA production thus demonstrating a CK-ABA antagonism. On the other hand, the presence of AUX enhances disease susceptibility profiting the pathogen growth and inhibiting JA biosynthesis (Liu & Wang 2006; Chen *et al.* 2007; Bari & Jones 2009). BR can enhance susceptibility or resistance depending on the pathogen and the host evaluated (Lozano-Durán & Zipfel 2015). For example, the Brassinosteroid Insensitive 1 (BRI1) associated receptor Kinase 1 (BAK1), one of the BR intermediates, functions as a co-receptor of several pathogenesis-related receptors like bacterial Flagellin-sensitive 2 receptor inducing plant defence (Wang 2012; Zhu *et al.* 2013). Another phytohormone involved mainly in plant development is the GAs, which allow plants to grow by repressor-DELLA protein degradation (Achard *et al*. 2008). Therefore, DELLA interacts with a JA-signalling repressor known as Jasmonate Zim Domain (JAZ) promoting resistance to necrotrophs and susceptibility to biotrophs by altering the relation between SA and JA (Navarro *et al.* 2008; Song *et al.* 2014). In conclusion, the hormone crosstalk in plant defence is complex and depends on the pathogen and host involved.

Model systems used for plant–pathogen interaction studies

Several plants have been used as system models to study the plant–pathogen interaction. The most recognised system is the crucifer *Arabidopsis thaliana* L. which has several attributes that make it useful for molecular and genetic analysis (Dangl 1993). This system model has advantages from which 150 different available ecotypes can be distinguished, small size of genome and the ability to adapt itself to different environmental conditions (Kunkel 1996; Van Poecke & Dicke 2004). Moreover, this self-fertile plant produces a lot of seeds from a simple individual in a short lifecycle of about 8 weeks of growth (Somerville & Koornneef 2002). All these characteristics facilitate *Arabidopsis* genome manipulations providing different signalling pathway mutants and transgenic lines useful for plant–pathogen interaction studies.

In the family *Solanaceae*, tobacco is another plant used as a system model which was chosen for its plasticity to adapt itself to several environments with broad morphological and chemical phenotypes (Baldwin 2001). Tobacco is a natural allotetraploid that produces a million seeds per plant in three months after germination and is used as the main plant model system until *Arabidopsis* (Ganapathi *et al.* 2004). *Nicotiana benthamiana* has been widely used as a model plant species because it is susceptible to different pathogens such as viruses in the first instance, bacteria, fungi, and aphids. Moreover, *N. benthamiana* is easily transformed and today there are several mutants with different responses to hormones that can be useful for plant–pathogen studies (Bombarely

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et al. 2012). Goddin *et al.* (2008) described several advantages of this system being the most important technology known as virus-induced gene silencing (VIGS) which allows silencing *N. benthamiana* genes of interest and evaluating the gene function in plant–pathogen interactions.

Tomato (*Solanum lycopersicum*) is an ideal crop plant for classical and molecular studies whose genome sequences have been available since 2012 (Tomato Genome Consortium 2012). Among plants, tomato is one of the best mapped crops which is a simple diploid that has few chromosomes and the ability to grow in a broad range of environments. Tomato is also the target of a broad range of fungi, bacteria, and viruses which position it as a favourable model system to study plant–pathogen interactions (Arie *et al.* 2007). Moreover, a lot of morphological, physiological, and enzymatic mutants are available (Rick & Yoder 1988).

One of the most important plant families used for human and animal food production is *Poaceae*, but research using members of this family is complex due to the genome size that makes molecular studies difficult. In recent years, a new pathosystem model has been proposed to study pathogen–grasses interaction known as *Brachypodium distachyon* L. (Peraldi *et al*. 2011, 2014). This model system presents several advantages including self-fertility, simple growth requirements, lifecycle of 2–3 months, small size, and a relatively small genome (Draper *et al.* 2001). Moreover, the complete sequencing genome is available (Vain 2011). Interestingly, *B. distachyon* shares gene family structures with rice, wheat, barley and sorghum, which makes this model attractive to study pathogen-grasses interaction and translate the results to other members of the family (The International Brachypodium Iniciative 2010; Vogel *et al.* 2010). Therefore, some plant physiology characteristics are shared among grasses, for example *B. distachyon* and wheat roots have similarities referred to anatomy and growth, being used to study root pathogen interactions (Chochois *et al.* 2012; Schneebeli *et al.* 2015). Moreover, Goddard *et al.* (2014) demonstrated that the resistance mechanisms have been evolutionarily conserved between *B. distachyon* and barley.

In *Brachypodium*, few mutants are available compared to *Arabidopsis*, which has a lot of insensitive or deficient mutants in the known signalling pathways. But in *Brachypodium* there are some mutants in ET response and other disease resistance family proteins that will be an important tool for future *Brachypodium*–pathogen studies.

Fusarium species studies

Fusarium species can be potential pathogens of various plants with agricultural and economic importance, not only because of fungal presence but also because of the capacity to produce mycotoxins that affect human and animal consumers. For this reason, different *Fusarium* species have been used as biological material in several plant–pathogen studies in order to understand the interactions among them. Using *Arabidopsis thaliana* as a model system, Urban *et al.* (2002) demonstrated that *F. graminearum* and *F. culmorum* have the capacity to infect the floral tissue and to extend into the stem tissue causing symptoms in infected siliques. However, Chen *et al.* (2006) assayed different ways to inoculate *Arabidopsis* for future analysis. On the one hand, a *F. graminearum* conidial suspension was used to infect rosettes with or without wound in *Arabidopsis thaliana* ecotypes. At 2 dpi, chlorosis was visible in the wounded leaves, while the leaves without wound showed no visible symptoms, therefore the wound allowed the pathogen to enter the host while the intact leaves acted as barriers preventing the pathogen penetration into the leaves. On the other hand, the same conidial suspension with or without DON supplied was used to inoculate detached leaves of several ecotypes of *Arabidopsis* embedded in agar media. The results showed that not only the inoculum produces symptoms but also the presence of DON increases dramatically the disease severity. Moreover, a variation in resistance among ecotypes was shown, the Col-0 ecotype being more resistant to *F. graminearum* than the Ler ecotype (Chen *et al.* 2006).

Regarding *F. graminearum*, SA plays a key role. SA mutants impaired in the SA signalling have shown susceptibility to this pathogen; on the other hand, SA applications increased resistance to *F. graminearum.* Moreover, JA signalling contributes to *F. graminearum* susceptibility by SA signalling attenuation during the initial infection but promoting resistance as the disease progresses (Makandar *et al.* 2010, 2012). Not only SA inhibits the *F. graminearum* growth in acidic conditions but also this pathogen has the ability to metabolize SA to SA biosynthesis intermediates such as catechol in basic growth conditions. In conclusion, the SA–*F. graminearum* function depends on the growth conditions (Qi *et al.* 2012). The plant SA response against *F. graminearum* was also confirmed in studies using wheat with known

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resistance or susceptibility to *Fusarium* (Pritsch *et al.* 2000).

Although ET signalling is involved in plant defence against necrotrophic pathogens, *Arabidopsis* mutants impaired in ET signalling have demonstrated resistance to *F. graminearum* while mutants with ET overexpression were susceptible, confirming the ET participation in *Fusarium* interactions not only in *Arabidopsis* but also in wheat and barley (Chen *et al.* 2009).

Fusarium oxysporum is one of the most frequently studied *Fusarium* species in plant–pathogen interaction. Berrocal-Lobo and Molina (2004) evaluated *Arabidopsis–Fusarium oxysporum* f.sp. *conglutinans* and *F. oxysporum* f.sp. *lycopersici* interactions. By using several mutants impaired in the ET, JA, and SA signalling they observed that a positive cooperation between SA, JA, and ET is needed to ensure an effective plant resistance against the evaluated pathogen. Moreover, ERF1, an ET transcriptional factor, was observed to mediate *F. oxysporum-Arabidopsis* resistance (Berrocal-Lobo & Molina 2004). *Fusarium oxysporum* f.sp. *raphani* was evaluated using *A. thaliana* newly as a system model. Interestingly, an ET receptor mutant, named as *etr1-1*, increased resistance to the pathogen, demonstrating that ETR1 is required for this pathogen pathogenicity (Pantelides *et al.* 2013). Recently, Cakir *et al.* (2014) used an *F. oxysporum* isolate with reduced virulence and a wild type isolate as the control and observed that the expression of plant defence genes depends on the pathogen virulence.

Others like *Fusarium solani* induce SA accumulation in tobacco plants during the first three days post infection and then increase the JA levels compared with control plants being both SA and JA essential components to *Fusarium* resistance (Luu *et al.* 2015). *F. sporotrichioides–A. thaliana* assays demonstrated that the SA depending PR1 gene was activated at 24–48 h post inoculation while the JA depending *PDF1.2* gene was transcribed after 48 h post inoculation (Asano *et al.* 2012).

Transgenic wheat expressing *Arabidopsis* NPR1, essential for SA signalling pathways, was inoculated with *F. asiaticum*. Seed inoculation showed that NPR1 increases the pathogen susceptibility, however in floret assays resistance against the pathogen was enhanced, thus demonstrating a dual activity of NPR1 in plant defence (Gao *et al.* 2012).

Fusarium graminearum as well as *F. culmorum* have also been used to inoculate *Brachypodium distachyon*, which showed susceptibility to these pathogens confirming the use of this grass as a system model to allow studying the *Fusarium*–grasses interaction (Peraldi *et al.* 2011). Spray inoculation of *B. distachyon* spikes with both pathogens showed that the period around mid-anthesis is the most susceptible and point inoculation allowed determining that *B. distachyon* exhibits susceptibility to spread within the spikelet. Both results were similar to those found in wheat. Finally, not only leaves were used to assay the *Fusarium* pathogenicity but also other plant tissues like stem, stem nodes, leaf sheaths, and root were inoculated with both pathogens and all of them were susceptible to *F. graminearum* and *F. culmorum* (Peraldi *et al.* 2011). Therefore, *F. graminearum* wild type and several mutants with deficient virulence were used to inoculate single florets of *B. distachyon* spikelets and disease symptoms were induced in them (Blümke *et al.* 2015). Considering its participation in plant interactions, the mycotoxins produced by *F. graminearum* have also been evaluated. Desmond *et al.* (2008) inoculated wheat with DON mycotoxin and observed that this mycotoxin functions as elicitors inducing the H_2O_2 production and consequently the cell death. Therefore, DON has been described as a virulent factor because analyses using DON producer and non-producer isolates show differences in the pathogen biomass on *B. distachyon.* Interestingly, by applying DON pretreatment prior to *F. graminearum* infection, Blümke *et al.* (2015) observed that DON induced the priming of the *B. distachyon* spikelet tissue, thus contributing to reduce susceptibility to FHB. Diamond *et al.* (2013) evaluated the effects of DON on the viability of *Arabidopsis* cells and observed that low DON concentrations do not kill cells due to the capacity of DON to disarm the apoptosis-like plant programmed cell death. Recently, carboxylesterase (CXE) genes of *B. distachyon* responsible for deacetylation of trichothecene toxins have been characterised. Interestingly, Schmeitzl *et al.* (2016) found that some of them could play a role as a susceptibility factor in crop plants, due to the fact that they can hydrolyse 3-ADON into DON, thus increasing the toxicity. On the other hand, several detoxifier metabolites are more expressed in the DON presence than in the mycotoxin absence by transcriptional analysis (Pasquet *et al.* 2014). Other *Fusarium* mycotoxins were evaluated to know their capacity to induce defence gene expression. T-2 toxin, HT-2 toxin, and DAS were infiltrated into *A. thaliana* leaves and SA related genes were induced accompanied by the cell death (Nishiuchi *et al.* 2006).

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Regarding other necrotrophic fungal pathogens, Ferrari *et al.* (2003) demonstrated that SA, JA, and ET mediate the defence signalling pathways against *Botrytis cinerea*, a pathogen able to produce losses in grapefruits of nutritional and commercial importance (Wang *et al.* 2015). However, SA is not required to *Alternaria brassicicola* plant defences, able to cause damage in several *Brassica* species, which is mediated by JA (De Vos *et al.* 2005). Similarly, JA has been reported to play a main role in the *Pythium irregulare* plant defence, a soil-borne pathogen able to produce severe economic losses in ornamental plants (Adie *et al.* 2007).

Interestingly, all these researches evidenced that the plant–pathogen interaction is the result of interplay among the main hormones involved that act as positive or negative regulators depending on the pathogen evaluated.

CONCLUSION

The genus *Fusarium* is one of the most important fungi causing great losses in agronomical practices worldwide, therefore strategies that allow decreasing the disease incidence are needed, but the potential tools to achieve this aim require the knowledge of the main components in the plant–pathogen interaction. In our review, all *Fusarium*–plant interaction studies have demonstrated that there is a complex crosstalk among signalling pathways to defend plants against pathogen attacks; however, there is still much to know about the *Fusarium*–plant interaction added to several remaining species comprised in the genus *Fusarium* responsible to produce not only symptoms in diverse substrates but also a range of mycotoxins that could trigger some different plant defence responses.

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