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Abstract

Most classical plant hormones are also produced by pathogenic and symbiotic fungi. The way these molecules favor the invasion of plant tissues and the development of fungi inside plant tissues is still largely unknown. In this review, we examine the different roles of such hormone production by pathogenic fungi. Converging evidence suggest that these fungal-derived molecules have potentially two modes of action: (i) they may perturb plant processes, either positively or negatively, to favor invasion and nutrient uptake and (ii) they may also act as signals for the fungi themselves to engage appropriate developmental and physiological processes adapted to their environment. Indirect evidences suggest that abscisic acid, gibberellic acid and ethylene produced by fungi participate to pathogenicity. There is now evidence that auxin and cytokinins could be positive regulators required for virulence. Further research should establish whether or not fungal-derived hormones act like other fungal effectors.

Introduction

Many fungi interact with plants in a beneficial manner as in mycorrhizal symbiosis (Sanders, 2011) or in an harmful manner in the case of fungal diseases (Dean et al., 2012). In order to obtain nutrients, both symbiotic and most pathogenic fungi penetrate their host without breaking the plant cell plasma membrane. The fungal membrane is protected by a cell-wall composed of chitin that can be recognized by plants through membrane receptors which then activate basal immunity. Chitin perception modulates responses during both mutualistic and pathogenic fungi-plant interactions (Gust et al., 2012). Fungi have evolved a repertoire of tools such as protein effectors and metabolites to impede such plant immunity and/or to establish favorable conditions for their establishment in plant tissues (Kamoun, 2007). Besides the production of canonical effectors, fungi also produce compounds that are similar to plant hormones like auxins, cytokinins (CKs), gibberellic acids (GAs), ethylene (ET), abscisic acid (ABA), jasmonates (JA) and salicylates (SA). These hormones are well described to control plant development and to trigger important plant signaling events during biotic and abiotic stresses (reviewed in (Spence and Bais, 2015; Pozo et al., 2015; De Vleesschauwer et al., 2013; Robert-Seilaniantz et al., 2011; Peleg and Blumwald, 2011)).

There are now many examples showing that some pathogen protein effectors trigger hormone regulation to favor infection (Robert-Seilaniantz et al., 2007). By contrast, the involvement of hormonal compounds derived from microorganisms in plant-fungus interactions is poorly documented. Fungal-derived hormones were first suspected to be involved in the virulence of gall-forming pathogens (Robert-Seilaniantz et al., 2007; Denancé et al., 2013). For symbiotic fungi, such production of hormones is consistent with root modifications often required in these interactions (Hirsch et al., 1997). However, many pathogens that do not induce organ deformations can also produce and secrete plant hormones, suggesting a role of these molecules in other biological processes than organ deformation.

The role of plant-derived hormones in plant disease resistance has been extensively reviewed (Robert-Seilaniantz et al., 2011; De Vleesschauwer et al., 2014). In this review, we summarize the current knowledge on the role of fungal-derived plant hormones in plant-pathogen interactions with a focus on their putative role in virulence. When relevant, some information on plant-mycorrhiza interactions is also provided as it often sheds some light on the role of these molecules in plant-fungus interactions.

Auxins from fungi play a positive role in plant-fungus interactions

Auxins are indole-derived hormones involved in plant development processes such as cell division differentiation and organ formation (Oka et al., 1999; Vanneste, 2005; Benjamins and Scheres, 2008) and senescence (Kim et al., 2011). Auxins also control biotic and abiotic stress responses in plants (Peleg and Blumwald, 2011). In plants, auxins is synthetized from tryptophan which is converted into indole-3-acetamide by tryptophan-2-monooxygenase enzymes (Zhao, 2010). Indole-3-acetamide is hydrolyzed to form indole-3-acetic acid (IAA) which is the major auxin active form in plants. These genes were also identified in fungi, e.g. *Fusarium* sp., and were confirmed for being involved in fungal auxin production (Tsavkelova et al., 2012). However, several auxin synthesis pathways were described in fungi. In some of them, like *Fusarium sp.* and *Colletotrichum gloeosporioides* (Tsavkelova et al., 2012; Gruen, 1959; Robinson et al., 1998), auxins is synthesized from the same precursor than in plants (indole-3-acetamide) but as observed in other fungal genus, for instance *Ustilago* (Reineke et al., 2008) and *Rhizoctonia* (Furukawa et al., 1996), auxins can also be produced from indole-3-pyruvate. Auxins could also be produced in a tryptophan-independent manner but the corresponding pathways are still not well described.

A lot of fungal species, and not only plant-interacting fungi, produce and secrete auxins, suggesting that these hormones could have an endogenous role in these organisms (Gruen,

1959; Ulrich, 1960). A negative correlation between the speed of fungal growth and auxin production was shown in several species (Gruen, 1959). By contrast, auxin treatment promotes cellular elongation and sporulation in the yeasts *Saccharomyces cerevisiae* and *S. ellipsoideus* (Yanagishima, 1965; Kamisaka et al., 1967). Similarly, an aberrant production of auxins leads to morphological transition in *S. cerevisiae* as well as in the human pathogen *Candida albicans*, in which auxin triggers the transition into hyphal growth, a known virulence trait (Rao et al., 2010). The auxin IAA also promotes spore germination of the filamentous fungus *Neurospora crassa* (Nakamura et al., 1978, 1982). When tested on the tomato pathogen *F. oxysporum lycopersici*, auxin reduced spore germination (Sharaf and Farrag, 2004). The effect of auxin on growth could be concentration-dependent: in the case of *F. delphinoides*, a chick pea pathogen, low concentration of exogenous auxin increased fungal growth whereas high concentration decreased it (Kulkarni et al., 2013). Thus the effects of auxins on fungal physiology can strongly differ from one species to another and depends on the dose tested.

Auxins are involved in the symbiotic interactions between plant and bacteria or fungi. They are required for the initiation of nodule formation in the nitrogen-fixative bacterial symbiosis (Hirsch and Fang, 1994) and for the invasion of mycorrhizal fungi (Hanlon and Coenen, 2011; Etemadi et al., 2014). For instance, mutants of the ectomycorrhizal species *Hebeloma cylindrosporum* overproducing auxin showed an increased ability to invade root tissues of *Pinus pinaster* (Gay et al., 1994; Laurans et al., 2001). However, there was no difference between the growth of plants colonized with the mutant and wild-type strains, suggesting that fungal auxin is involved in host invasion but not in the beneficial effects of symbiosis on host development. In most cases, plants interacting with mycorrhizal fungus contain a higher content in auxins than non-mycorrhized ones (Barker and Tagu, 2000; Meixner et al., 2005).

However, the origin of these auxins, whether from the host or the fungal symbiont, is still unclear.

Auxin involvement in plant-pathogen interactions were early suspected and studied when symptoms, like organ deformation, were reminiscent to responses to high auxin level. For instance, *Agrobacterium tumefaciens* and *Pseudomonas savastanoi* are well-known plant pathogenic bacteria that induce tumor formation in their hosts and auxins actively contribute to the virulence of these bacteria (Glass and Kosuge, 1988). Like *Agrobacterium*, some fungi are able to induce tumors, such as the corn smut causal agent, *U. maydis.* However, fungal mutants affected in auxin production were still able to induce tumors in a similar way than wild-type strain even if tumors contained a lower level of auxins (Reineke et al., 2008). This suggests that auxin production by *U. maydis* is not required for the virulence of this pathogen.

In the case of fungal pathogens not triggering organ deformations, functional evidences suggest a role for auxins. By measuring fungal biomass and auxins in plant tissues, it was suggested that *C. gloeosporioides* f. sp. *aeschynomene* produces auxins during early, biotrophic stages of plant colonization (Maor et al., 2004). In *F. oxysporum,* an enhanced expression of auxin biosynthetic genes (tryptophan-2-monooxyngenase and indole-3-acetamide hydrolase) triggers over-accumulation of IAA and an hypervirulent phenotype on Orobanche (Cohen et al., 2002). Consistent with these observations, the transient silencing in *Puccinia graminis* f. sp. *tritici* of a gene required for auxin biosynthesis was obtained in wheat infected leaves. The two-fold reduction of the transcript led to a decrease of pustule formation. Although auxins were not measured after silencing, these results suggest that auxins were required for full fungal pathogenicity (Yin et al., 2014). Thus auxins seem to play a role in pathogenicity and more functional studies with fungal mutants should help better understand how they participate to virulence.

Cytokinins from fungi: a now clear-cut positive function in virulence

Cytokinins (CKs) are diversified plant hormones derived from ATP/ADP/AMP or from the tRNA degradation pathway. CKs are well described for their role in plant development processes such as root and shoot formation through the regulation of cell cycle and cell differentiation (Barciszewski et al., 1999; Riou-Khamlichi et al., 1999; Carimi et al., 2003; Fosket and Torrey, 1969). CKs are also involved in delaying senescence and in source/sink nutrient distribution (Wingler et al., 1998; Peleg et al., 2011). The first step of CK biosynthesis in plants involves Isopentenyl Transferase enzymes (IPT or tRNA-IPT) which perform the transfer of the isopentenyl chain from the methylerythritol phosphate (MEP) on the adenosine phosphate substrate leading to the formation of the ribosylated phosphorylated CK forms (Sakakibara, 2006). Then, these CKs are activated, in part by the LONELY GUY (LOG) enzymes, into CK free active forms like trans-zeatin and isopentenyladenine (Kurakawa et al., 2007; Frébort et al., 2011). The putative *IPT* and *LOG* genes are present in several fungal genomes and some of them have been recently characterized (see below (Hinsch et al., 2015; Morrison et al., 2015b; Chanclud et al., 2016).

A large diversity of fungal species, whether saprophytic, pathogenic or symbiotic, were shown to produce CKs (Murphy et al., 1997; Cooper and Ashby, 1998) and several studies suggest that they could play a role in several physiological processes in fungi themselves especially in hyphal development and nutrient uptake (LeJohn and Stevenson, 1973). For instance, CKs promote *in vitro* branching of ectomycorrhizal mycelia (Barker and Tagu, 2000) and affect in a dose-dependent manner hyphal membrane viscosity and therefore influence ion and water transport (Gogala, 1991; LeJohn and Stevenson, 1973). Pohleven et al, 1986, demonstrated that some CKs modify the content of K, Ca, P and Na in the mycelia of the basidiomycete *Suillus variegatus* (Gogala, 1991). The effect of CKs on hyphal growth seems to depend on the concentration and on the kind of CK molecule tested (Gryndler et al.,

1998). CKs could also be involved in growth optimization under adverse conditions. For instance, the inhibition of the mycelial growth of *Amanita muscaria* caused by aluminium is significantly correlated with a decrease in CKs amount (Kovač and Žel, 1995). In a recent report, we have shown that endogenous and exogenous CKs are required for oxidative stress tolerance in the rice blast fungus *Magnaporthe oryzae* (Chanclud et al., 2016). In the 60's Lee et al reported that CKs also affect sexual reproduction in the ascomycete *N. crassa* suggesting a role in communication within fungi (Lee, 1961; Elliott, 1967).

During mycorrhizal symbiosis, CKs promote growth of the host and of the symbiont (Allen et al., 1980; Drüge and Schonbeck, 1993; Barker and Tagu, 2000). CK accumulation in the host, root and shoot, were shown in many fungal symbiotic interactions (Allen et al., 1980). A model has emerged since the early 90's about the role of CKs in plant symbiotic interactions, proposing that plants secrete CKs that (i) promote growth of symbiotic microbes that are thus able to detect them, then (ii) this contributes to a better absorption of nutrients through the symbiont and (iii) leads to increase the photosynthesis process in the host leaves (Wullschleger and Reid, 1990; Drüge and Schonbeck, 1993). It is possible that CKs produced by mycorrhizas may initiate this whole process but this awaits the study of CK-deficient symbiotic fungal mutants to confirm this hypothesis.

During interaction with fungal pathogens, CKs content is often affected (Jiang et al., 2013; Devos et al., 2006). Since most of the necrotrophic fungi analyzed do not seem to secrete CKs, in contrast to (hemi)biotrophic ones, it was suggested that fungal CK production and secretion could depend on pathogen lifestyle. CKs are involved in many diseases caused by pathogens that induce tumor formation in their host: protists (e.g. *Plasmodiophora brassicae* (Siemens et al., 2006)), nematodes (e.g. *Heterodera schachtii* (Siddique et al., 2015)), bacteria (e.g. *P. savastanoi* (Barciszewski et al., 2000)*, Agrobacterium* sp.(Barciszewski et al., 2000), *Rhodococcus fascians* (Pertry et al., 2009)) and fungi (*U. maydis* (Mills and Van Staden,

1978), *Claviceps purpurea* (Hinsch et al., 2015)). In the tumor-inducing pathogen *C. purpurea,* deletion of two genes partially abolished CK *de novo* synthesis but did not affect virulence of the fungus. By contrast the mutants exhibited a hyper-sporulating phenotype, implying that CKs are environmental factors influencing fungal development (Hinsch et al., 2015). Recently it was shown that CK accumulation in *U. maydis* infected tissues is correlated to the virulence of this pathogen but there was no direct genetic evidence that fungal-derived CKs are required for full virulence of this pathogen (Morrison et al., 2015a).

Fungal pathogens that do not induce tumors also produce CK compounds and their role in virulence is still poorly understood (see for instance (Murphy et al., 1997; Jiang et al., 2013)). CKs are probably involved in "green island" formation, a photosynthetically active zone often found around lesions caused by biotrophic fungi (Angra and Mandahar, 1991; Choi et al., 2011). In plants CK production is thought to occur in the roots (Rani Debi et al., 2005) and experiments with detached leaves could indirectly address the question of the origin of the CKs in green islands. Using this assay in wheat and maize leaves respectively infected with *Pyrenophora teres* and *Dreschslera maydis*, the increase of CKs content was attributed to the pathogen. The increase in CKs levels in susceptible hosts was also correlated with increased metabolite contents around infection sites (Angra-Sharma and Sharma, 1999). CK secretion was shown by immuno-detection in plant tissues in the case of *P. recondita* f.sp. *tritici* during wheat infection (Hu and Rijkenberg, 1998) but as for most hormones found during infection, it is not possible to unambiguously assign this accumulation to the plant or to the pathogen without characterization of mutants impaired in CK production or perception. A recent study mentioned that CK production by fungi, especially the *cis*- zeatin forms (which seems to be the main one produced by filamentous fungi), could involve tRNA-IPT enzymes that perform modification on tRNA which will then release free CKs after degradation (Morrison et al., 2015b). Among non-tumor inducing fungal pathogens, *M. oryzae* produces and secretes CKs

(Jiang et al., 2013). Knock-out mutants impaired in the only *tRNA-IPT* gene identified in *M. oryzae* were also impaired in CK production, thus confirming the hypothesis of Morrison et al., 2015b that tRNA-IPT are involved in fungal CK production (Chanclud et al., 2016). The interaction between rice and the CK-deficient strain of *M. oryzae* was characterized. This analysis demonstrated that *M. oryzae* derived CKs are required for full virulence by affecting rice defenses, nutrient distribution and fungal oxidative stress tolerance (Chanclud et al., 2016). Since the tRNA-IPT gene identified in *M. oryzae* is well conserved, this mutation could be studied in other fungi as a nice tool for distinguishing fungal CKs to plant CKs in other plant-fungus interactions. Recently, the deletion of a *tRNA-IPT* gene has also been performed in the nematode *H. schachtii* confirming the conservation of the role of this enzyme in CK production among different organisms (Siddique et al., 2015).

Ancient but limited direct evidence for a role of Gibberellic acids from fungal origin

GAs are terpenoid hormonal compounds identified for the first time as being produced by *Gibberella fujikuroi.* This fungus is the causal agent of the “bakanae” or “foolish seedlings” disease of rice in which infected plants are abnormally tall. Following this discovery, the role of GAs on plant physiology started to be studied. GAs have been involved in the control of germination, flowering, cell division and internode elongation (Brian and Elson, 1954; Pimenta Lange and Lange, 2006; Swain and Singh, 2005). The first steps of GA biosynthesis pathways identified in fungi are almost identical with those known in plants. The complex GA biosynthesis pathways were well described by Tudzynski, 2005. GA production was found in several fungal species but their effects on fungal biology are not well described.

In liquid culture, GAs were shown to increase conidial germination and to improve growth of young hyphae of the ascomycete fungus *N. crassa* (Nakamura et al., 1978; Tomita et al.,

1984)(Tomita et al., 1984)(Tomita et al., 1984)(Tomita et al., 1984)(Tomita et al., 1984)(Tomita et al., 1984)(Tomita et al., 1984)(Tomita et al., 1984)(Tomita et al., 1984)(Tomita et al., 1984)(Tomita et al., 1984)(Tomita et al., 1984)(Tomita et al., 1984)(Tomita et al., 1984) . These effects are additive to the effects of auxins, suggesting that these two hormones could act independently to affect *Neurospora* germination and growth (Tomita et al., 1984).

Few studies have reported their role during interaction between fungi and plants (Tsavkelova et al., 2006). In mycorrhizal interaction, GAs content is increased in plants (Barker and Tagu, 2000). Blee and Anderson (1998) have suggested a model where production of fungal GAs is possibly required to initiate a signal leading to enhanced carbon-sink activity of the infected cell (probably combined with CKs and auxins).

In plant pathogen interactions, the role of GAs has been less studied compared to other plant hormonal pathways. Different strains of *G. fujikuroi* were analyzed for their production of GAs and a correlation was found between the quantity of GAs produced and the virulence of the strain (Desjardins et al., 2000). However, in another study, there was no clear link between the production of GAs and the pathogenicity of *Fusarium* (Mańka, 1980). *G. fujikuroi* mutated for two histone deacetylases showed a reduction of GA production. Plants infected with the double deletion mutant resembled the uninfected control plants, suggesting that GA production is required for bakanae disease on rice (Studt et al., 2013). However, the possibility that the introduced mutations have affected other virulence factors cannot be ruled out.

Abscisic acid: converging evidence for ABA used as a virulence factor

In plants, ABA is well known to induce stomatal closure and thus to contribute to plant drought tolerance (Beardsell and Cohen, 1975). ABA is the key hormone for abiotic stress

responses in plants (Peleg and Blumwald, 2011). ABA is also involved in seed dormancy by acting antagonistically with the GAs pathway (Debeaujon and Koornneef, 2000). In plants, ABA is synthesized from both the MEP and the mevalonate pathway (Nambara and Marion-Poll, 2005).

In fungi, it is thought that the mevalonate pathway is mostly involved and that different ABA precursors could be used (Morrison et al., 2015b; Oritani and Kiyota, 2003). Fungal production of ABA was first shown in *Cercospora risicola* (Norman et al., 1983). Since then a lot of fungi with different lifestyles (saprophytic, symbiotic and pathogenic) were described as producing ABA (Crocoli et al., 1991; Esch et al., 1994; Jiang et al., 2010; Morrison et al., 2015b). There are only two reports that ABA affects mycelium growth. In *Ceratocystis fimbriata*, exogenous application of ABA slightly promoted fungal growth. In *M. oryzae*, ABA increased germination and the formation of appressorium, a specialized infection structure differentiated for breaking down the plant cell wall and allowing invasion (Spence and Bais, 2015 and references inside).

The arbuscular-mycorrhizal fungus *Glomus sp.* produces ABA and ABA concentration in the xylem sap is different between mycorrhized plants compared to non-mycorrhized ones. However the origin of this increase of ABA is not established yet (Esch et al., 1994).

In several plant-pathogen interactions, ABA was described to affect plant disease resistance in a positive or a negative manner, depending on the host-pathogen interaction studied (Jiang et al., 2010; Xu et al., 2013; De Vleesschauwer et al., 2010). Kettner and Dorffling, 1995 have inoculated tomato plants with two strains of *Botrytis cinerea* presenting differences in ABA production and showed that ABA increase is higher in leaves inoculated with the ABA-producing strain than with the less-producing ones. This suggests that ABA accumulation in the host during infection could result from or be initiated by this pathogenic fungus. Similarly, ABA was accumulated during the early stages of infection by *U. maydis* and this

accumulation could be correlated with the virulence of the fungus (Morrison et al., 2015a). Even though exogenous ABA triggered a faster development of the necrotic lesion, the role of fungal ABA in virulence was not described until recently. Knocking-out one gene homologous to the *B. cinerea ABA4* gene responsible for ABA biosynthesis, reduced by two-fold ABA levels in *M. oryzae* (Spence et al., 2015; Siewers et al., 2006). Appressorium formation *in vitro* was severely reduced in the *M. oryzae Δaba4* mutant, a phenotype that could be reverted by exogenous application of ABA. The virulence of the *Δaba4* mutant was also strongly compromised suggesting that ABA contributes to the virulence of this fungus. One may then speculate that this production of ABA by *M. oryzae* inhibits the SA-dependent defense response (Jiang et al., 2010), as observed in many other biological situations (Ton et al., 2009). However, since the *Δaba4* mutant did not form appressoria and infect plants at all, it is difficult to conclude on a role of fungal-produced ABA on the plant itself.

Ethylene: a gaseous hormone involved in plant physiology and defenses which also affects fungal development

Ethylene (ET) is a gaseous compound first discovered for its role in fruit maturation (Bleecker and Kende, 2000; Payton et al., 1996). ET was later shown to be involved in senescence, germination, flowering as well as in the inhibition of root and shoot growth (Bleecker and Kende, 2000; Grbic and Bleecker, 1995). In *Arabidopsis*, ET has first been described to contribute, with JA, to the induction of defenses against necrotrophic pathogens. However, this dichotomy of responses, to biotrophic and necrotrophic pathogens, is not always clear in the other plants, like in rice, in which hormonal regulation of defenses is slightly different (De Vleesschauwer et al., 2013, 2014). In plants and fungi, ET biosynthesis occurs from methionine that is transformed in ACC (1-aminocyclopropane-1- carboxylic acid) via ACC-synthase enzymes (Esser et al., 2002). Moreover, fungi also produce ET from the 2-keto-4-

methylthiobutyric acid, deriving from methionine, and/or from the 2-oxoglutarate then requiring Ethylene-Forming enzymes (Bockhaven et al., 2015; Hottiger and Boiler, 1991 and references inside). Altogether, studies about fungal ET production show that it is strongly dependent on growth media and confirmed that several pathways exist among fungi (Esser et al., 2002; Strzelczyk et al., 1994). Since the first report of ET production by *Penicillium digdatum* in 1940, ET production has been measured in a lot of fungal species, in both hyphae and spores (Dasilva et al., 1974). These fungi belong to different phylum, have different lifestyles and range from pathogenic like *B. cinerea* to symbiotic ones like *F. oxysporum* f. sp. *pini* (Graham and Linderman, 1980; Dasilva et al., 1974; Arshad and Frankenberger, 1991). Several *in vitro* experiments demonstrated that ET or some precursors (ethephon and ACC) affect spore germination and hyphal growth of the pathogenic filamentous fungi, *Alternaria alternata* and *B. cinerea*, and the symbiotic ones, *Gigaspora ramisporophora* and *G. mosseae* (Kępczyńska, 1994; Chagué et al., 2006). The effects of ET on fungal development seem to be dose-dependent with a promoting effect observed at concentrations below 1mM and a negative effect at or higher than 1mM (Ishii et al., 1996).

In the case of mycorrhiza, the role of ET depends on the type of symbiotic interaction. A low content of ET was measured in mycorrhized roots (McArthur and Knowles, 1992) and an exogenous supply of ET suppressed AM development (Geil et al., 2001; Zsögön et al., 2008). Therefore, it was suggested that a repression of the ET pathway by AM fungi is required to allow the establishment of symbiosis. Indeed, the AM fungus *G. intraradices* secretes a protein (SP7: secreted protein 7) which interacts with an ethylene response factor to suppress ethylene signaling (Kloppholz et al., 2011). In contrast, ET seems to promote ectomycorrhizal symbiosis. Two species of truffles (*Tuber melanosporum* and *Tuber borchii*) were showed to produce ET (and auxin) for manipulating these hormonal pathways in the host and inducing root morphological modifications, a plant developmental process in which these hormones are

involved (Splivallo et al., 2009). Given the roles of ET in plant defense, this fungal ET production by symbionts could also be required for counteracting the establishment of host immunity.

During plant fungal pathogen interactions, ET content often increases at the beginning of the interaction (Broekaert et al., 2006). However, its origin, from plants or fungi, is still unclear. In the case of the *Colletotrichum* sp. pathogens, ET is required for the formation of appressorium (Flaishman and Kolattukudy, 1994). Indeed appressoria formed on ripening tomato whereas none formed in plant mutants affected in ET production. An exogenous supply of ET restored appressorium formation on these plant mutants suggesting that ET produced by fruits during the ripening is perceived by the pathogen and is beneficial to initiate the development of specialized structures required for penetration and thus for full virulence. Furthermore ET production by fungi could be required to disturb host defense induction by affecting the plant hormonal homeostasis, essential for plant immunity establishment(Broekaert et al., 2006). This hypothesis was recently investigated in the interaction between rice and the necrotrophic pathogen, *Cochliobolus miyabeanus,* in which ET increases rice susceptibility (Bockhaven et al., 2015). In this study, the authors have used a specific inhibitor of fungal ET biosynthesis (2,2-bipyridyl), that abolishes fungal ET production and leads to a higher resistance of the host (or a lack of virulence of the fungus). Combined with other results showing that *C. miyabeanus* affects the 2-oxoglutarate (an ET precursor for microbes) pool in rice, the authors suggested that ET accumulation is mainly initiated and caused by the fungus and then contributes to the symptom development (Bockhaven et al., 2015). However, exogenous supplies of hormonal production inhibitors or signaling inhibitors could have side effects on the host and on the fungus, therefore the study of fungal mutants affected in ET perception or production is still missing for understanding the different roles of ET in plant-fungus interactions.

Pathogenic fungi also produce defense-related hormones SA and JA

In most plants, SA and JA trigger defenses against fungal biotrophic and necrotrophic pathogens respectively, in an antagonist manner (Bari and Jones, 2009; Robert-Seilaniantz et al., 2011). Some fungal pathogens may produce one hormone in order to inhibit the defense pathway which is the most detrimental to their growth. In plants, SA is synthesized from chorismate and the corresponding pathway is for instance targeted by the fungal pathogen *U. maydis* which secretes a chorismate mutase that channels chorismate into the phenyl propanoid pathway, preventing SA accumulation during infection and then contributing to its virulence (Djamei et al., 2011). However, the chorismate pathways identified in fungi do not lead to SA biosynthesis. Thus, even if SA (or SA-derivatives) production was measured in different species, to date this pathway is still unknown in fungi (Packter and Steward, 1967).

Some pathogens produce both SA *and* JA, like for instance *Moniliophthora perniciosa* which causes the witches' broom disease of cocoa. In this case, the production of these hormones could (i) contribute to manipulate the hormonal pathways involved in the host defense responses throughout its invasion i.e. causing abnormal shoot development and necrosis and (ii) could have a direct effect on this fungus since both SA *and* JA promote *in vitro* growth (Kilaru et al., 2007; Chaves and Gianfagna, 2006). A few other studies mentioned the effects of SA or JA on fungal physiological processes. SA had a moderate suppressive effect on spore germination and colonial growth rate of *Harpophora maydis* (Degani et al., 2015). In *Aspergillus flavus,* the results obtained from *in vitro* experiments showed that SA significantly reduced hyphal growth at all concentrations tested (Panahirad et al., 2014).

Several studies mentioned the production of JA by pathogenic fungi like *G. fujikuroi* and *Botryodiplodia theobromae* (Miersch et al., 1992, 1991). JAs are derived from lipid

peroxidation, and thus belong to the oxylipins. Some fungal oxylipin biosynthesis pathways were identified and characterized. JA and the other oxylipins could affect both host and fungal physiological processes (Tsitsigiannis and Keller, 2007). The *in vitro* application on *F. oxysporum* f.sp. *lycopersici* of the methyl-JA reduced spore germination and mycelium growth (Król et al., 2015). Recently, *M. oryzae* was shown to secrete a monooxygenase that converts rice endogenous JA into hydroxylated JA (12OH-JA). This 12OH-JA may then inhibit JA signaling and thus impairs JA-dependent host defenses and resistance (Patkar et al., 2015).

Although the number of pathogenic fungi characterized for producing SA and/or JA increases, there is no direct evidence that fungal SA or JA are required for their virulence.

Conclusions

Thus far, most fungi have been shown to produce almost all plant-like hormones *in vitro*. It is noteworthy that some growth medium used in many studies are made with potatoes dextrose agar and/or yeast extract, two compounds that already contain some plant derived hormones including auxins, CKs, ABA and the others, in unknown concentrations. Thus, some confusion exists between the ability of *de novo* production of plant hormones by fungi and their ability to metabolize them from the growth medium. This should be carefully addressed in future studies conducted *in vitro*. The sequencing of many genomes may also help to shed light on the presence of the hormonal biosynthesis pathways already described in some fungal species (Esser et al., 2002).

This overview shows that most known plant-hormonal compounds are produced and perceived by fungi. To date the involvement of fungal hormonal compounds, and the way that they are secreted and act in the plant cell are still poorly understood. Although most of the biosynthesis pathways of hormones in fungi are well described (reviewed in Esser et al., 2002), studies on fungal mutants affected in hormonal production are strikingly missing to confirm the involvement of fungal derived plant hormones in such interactions. In particular, the origin of hormones in colonized tissues is unclear and needs to be established to understand the complex relationships between fungal-derived and plant-derived hormones.

Some plant hormones have been shown to affect fungal development, nutrition and reproduction processes suggesting that these molecules trigger some signals in fungi (Nakamura et al., 1982; Gryndler et al., 1998; Esch et al., 1994; Elliott, 1967; Nakamura et al., 1978; LeJohn and Stevenson, 1973; Kępczyńska, 1989). The Figure 1 non-exhaustively summarizes the main effects of hormones known to date on fungal biology. However, the perception systems of hormones by fungi, as well as the signaling pathways triggered and the physiological responses induced, still remain to be discovered.

These plant hormone compounds are also produced, and very probably perceived, by other microbes including bacteria and nematodes (Denancé et al., 2013; Siddique et al., 2015; Kisiala et al., 2013). Moreover, some of these compounds have some effects on animal cells (Jiang et al., 2002; Slaugenhaupt et al., 2004; Ishii et al., 2003), suggesting that "plant" hormones not only participate to plant-microbe dialogue but might also contribute to communication in other host-microbe interactions involving widely different organisms (animals, plants and all kind of pathogenic, saprophytic and symbiotic microbes). However, to date there is no report on the involvement of such compounds in these interactions.

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Figure 1. Schematic representation of the effects of hormones on fungal biology.

A schematic view of yeast-like (light grey background), infecting and sporulating filamentous fungus is given. This model summarizes the effects of hormones on fungal biological processes reported to date; the effects due to the dose, the molecule tested, other environmental factors as well as the specie studied are provided in the text and could differ among fungi. Arrows and « T » bars respectively represent positive and negative effects. AUX : Auxins, ABA : Abscisic Acid, ET : Ethylene, CKs : Cytokinins, GAs : Gibberellic Acids, JA : Jasmonic acid, SA : Salicylic Acid.

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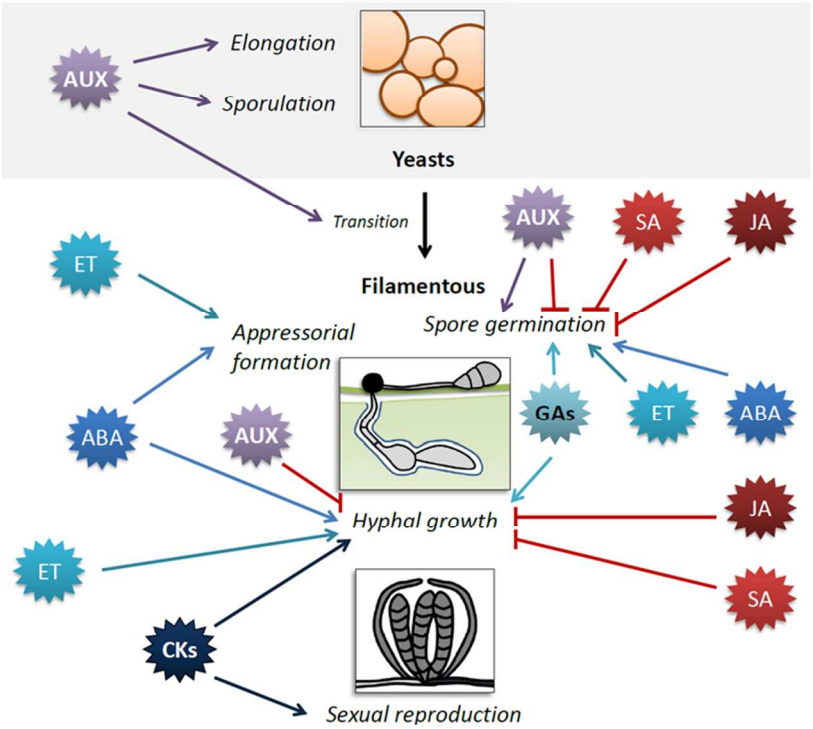

Figure 1. Schematic representation of the effects of hormones on fungal biology.
A schematic view of yeast-like (light grey background), infecting and sporulating filamentous fungus is given. This model summarizes the effects of hormones on fungal biological processes reported to date; the effects due to the dose, the molecule tested, other environmental factors as well as the specie studied are provided in the text and could differ among fungi. Arrows and « T » bars respectively represent positive and negative effects. AUX : Auxins, ABA : Abscisic Acid, ET : Ethylene, CKs : Cytokinins, GAs : Gibberellic Acids, JA : Jasmonic acid, SA : Salicylic Acid.

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