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REVIEW

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Transcription factor control of virulence in phytopathogenic fungi

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Abstract

Plant-pathogenic fungi are a significant threat to economic and food security worldwide. Novel protection strategies are required and therefore it is critical we understand the mechanisms by which these pathogens cause disease. Virulence factors and pathogenicity genes have been identified, but in many cases their roles remain elusive. It is becoming increasingly clear that gene regulation is vital to enable plant infection and transcription factors play an essential role. Efforts to determine their regulatory functions in plant-pathogenic fungi have expanded since the annotation of fungal genomes revealed the ubiquity of transcription factors from a broad range of families. This review establishes the significance of transcription factors as regulatory elements in plant-pathogenic fungi and provides a systematic overview of those that have been functionally characterized. Detailed analysis is provided on regulators from well-characterized families controlling various aspects of fungal metabolism, development, stress tolerance, and the production of virulence factors such as effectors and secondary metabolites. This covers conserved transcription factors with either specialized or nonspecialized roles, as well as recently identified regulators targeting key virulence pathways. Fundamental knowledge of transcription factor regulation in plant-pathogenic fungi provides avenues to identify novel virulence factors and improve our understanding of the regulatory networks linked to pathogen evolution, while transcription factors can themselves be specifically targeted for disease control. Areas requiring further insight regarding the molecular mechanisms and/or specific classes of transcription factors are identified, and direction for future investigation is presented.

KEYWORDS
disease, fungi, gene regulation, phytopathogen, transcription factor, virulence

1 | GENERAL INTRODUCTION

The symptoms of plant diseases such as rusts, blasts, smuts, blotches, blights, and mildews, along with various prescriptions for their mitigation, have been recorded since antiquity (Dark & Gent, 2001; Dugan, 2008; Wu et al., 2019). Until the establishment of the germ theory of disease in the 19th century, the nature of the causal agents remained obscure (Kelman & Peterson, 2002). Subsequently, numerous plant-pathogenic microorganisms have been identified (Crous et al., 2015; Lucas, 2020). Consequences of disease outbreaks range

from economic to humanitarian and environmental, the threat of which is heightened by increased migration and transport, allowing diseases to spread (Fones et al., 2017; Kamoun et al., 2019; Santini et al., 2018; Savary et al., 2019).

Crop pathogens pose a distinct challenge, as they exploit the lack of diversity in agroecosystems to rapidly proliferate (Brown, 2015; McDonald & Stukenbrock, 2016; Möller & Stukenbrock, 2017). While modern agricultural practices and technologies have enabled substantial yield increases, continued population growth tied with limited arable land is placing pressure on necessary production (Cole et al., 2018; Fones et al., 2020; World Food Program, 2019). Therefore, disease management forms an integral component of food and resource security and the economic security of producers (Avery et al., 2019; Islam et al., 2019; Kettles & Luna, 2019). A lack of durable resistance in many crops and evolved pathogen resistance to available chemical controls provide further challenges, meaning novel solutions must be developed (Burdon et al., 2016; Fisher et al., 2018; Nelson et al., 2018). Hence, an important goal in fungal plant pathology is to characterize the molecular mechanisms of disease that can be exploited for plant protection (Fones et al., 2020; Oliver, 2012; Sacristan & Garcia-Arenal, 2008).

Fungi represent the majority of pathogens posing a severe threat to plant health, with bacteria, oomycetes, and viruses largely making up the rest (Doehlemann et al., 2017; Hawksworth & Lücking, 2017; de Wit, 2015). Nevertheless, most fungi are nonpathogenic and most plants are resistant to all but a few species, begging the question, what is it that allows a disease to develop? Recent advances have shed light on various aspects of fungal virulence by highlighting the role of microbial effector–host receptor interactions (Han & Kahmann, 2019; Kanja & Hammond-Kosack, 2020; de Wit et al., 2017), secondary metabolite (SM) biosynthesis (Chooi et al., 2014; Collemare et al., 2019; Macheleidt et al., 2016), signal transduction/cellular metabolism (Bielska et al., 2014; Ikeda et al., 2019), cellular trafficking/secretion systems (Le Marquer et al., 2019; Park et al., 2018; Rascle et al., 2018), and the channelling of noncoding RNAs (Cai et al., 2019; Hua et al., 2018; Sesma, 2016). However, a universal strategy does not appear to exist. While the detection of positive selection and the development of machine learning approaches such as EffectorP have assisted the identification of pathogenicity-related genes, such genes have been difficult to functionally annotate (Aylward et al., 2017; Feurtey et al., 2020; Haridas et al., 2020; Sperschneider et al., 2018). Moreover, an organism may be mutualistic or symbiotic until a change in conditions renders it pathogenic (van der Does & Rep, 2017; Lo Presti et al., 2015). Therefore, understanding what regulates those aspects pertaining to fungal virulence is critical to understanding the nature of plant diseases.

Transcription factors (TFs) are sequence-specific DNA-binding proteins required to modulate gene expression (Caramori et al., 2019; Charoensawan et al., 2010; Hughes, 2011). Consequently, an organism relies on a set of suitably operating TFs to orchestrate the expression of genes involved in phytopathogenicity. Characterization of such regulators provides an avenue to identify virulence factors, informing research strategies aimed at building durable resistance into plants (Jones et al., 2019; Keller, 2019; Nejat et al., 2017; Zhang et al., 2018). In addition, their direct inhibition is considered an effective method for targeted disease control (Bahn, 2015; Cho, 2015; Sang & Kim, 2019; Tietjen & Schreier, 2013). In recent years, molecular characterization of TFs has proceeded at a rapid rate and it has become difficult to navigate the wealth of published material concerning aspects of phytopathogenicity. Therefore, the purpose of this review is to provide a systematic overview of what has been established through functional investigation in plant-pathogenic fungi (Table S1 catalogues published studies, indicating TFs involved in virulence). The classification of TFs into families is first detailed to provide insight into some of the distinct mechanisms of gene regulation. This precedes an analysis of TF orthologues belonging to several extensively characterized families from the perspective of fungal virulence and pathogenicity (summarized in Table 1). After establishing where investigations have focused, recommendations for future research efforts are proposed to better characterize disease regulatory pathways for the ultimate goal of better plant protection.

2 | TRANSCRIPTION FACTOR CLASSIFICATION

TFs are classed into families based on their DNA-binding domains (DBDs), which bind through distinct mechanisms (Charoensawan et al., 2010; Hughes, 2011; Wong, 2018). While TFs of a family tend to share affinities for particular core DNA sequences, active binding depends on additional variables, including the presence of cofactors/coregulators, posttranslational modifications, epigenetic states of the DNA, and target site synergists/antagonists (Levo et al., 2017; Sri Theivakadadcham et al., 2019; Vandel et al., 2019; Zabet et al., 2013). With this considered, some conserved DNA-binding features have been elucidated for each family.

The largest class of TFs in fungi are the zinc-coordinated "zinc fingers", which comprises several families. These include TFs harbouring the fungal-specific zinc cluster (Zn2Cys6), Cys2His2 (C2H2), and Cys4 (GATA) DBDs (Iuchi, 2005). The Zn2Cys6 DBD is characterized by two zinc ions, each interacting with three cysteine residues. This structure stabilizes a pair of alpha helices within the protein that interacts with DNA via the major groove and exhibits an affinity for CGG triplets. Zn2Cys6 TFs predominantly bind as homodimers or homotypic dimers (same TF family members) (Joshua & Höfken, 2017; MacPherson et al., 2006; Todd & Andrianopoulos, 1997). C2H2 zinc finger TFs generally harbour multiple C2H2 DBDs that can flexibly bind DNA of diverse nucleotide composition and length outside the major groove (Fedotova et al., 2017; Iuchi, 2005; Klug, 2010). The GATA zinc finger domain is named for the canonical DNA target sequence and comprises four zinc-coordinated cysteines. In fungi, GATA TFs often contain additional zinc finger domains that actively bind other regulatory molecules, leading to more precise DNA-binding activity (Chen et al., 2012; Hasegawa & Shimizu, 2017; Scazzocchio, 2000).

The basic leucine-zipper (bZIP) and basic helix-loop-helix (bHLH) TFs are obligate homo(typic) dimer-forming proteins that

TABLE 1 The transcription factors (TFs) and their families detailed in this review

TF family	Orthologue (synonyms)	Pathogens	Reported regulatory functions[a]
Zn2Cys6	Mtf4	*Colletotrichum orbiculare*	Infection-related morphogenesis
	VdFtf1	*Verticillium dahliae*	Carbohydrate metabolism, enzyme secretion
	Ftf1 and Ftf2 (GzZC215, MGG_06243)	*Fusarium graminearum*, *Fusarium oxysporum*, *Magnaporthe oryzae*	Effector regulation, infection-related morphogenesis, sporulation
	Ebr1 (MoCod2)	*F. graminearum*, *F. oxysporum*, *M. oryzae*	SM biosynthesis, hyphal growth, infection-related morphogenesis, sporulation
	Pro1 (AbPro1, GzZC232, MoPro1, UvPro1)	*Alternaria brassicicola*, *Cryphonectria parasitica*, *F. graminearum*, *M. oryzae*, *Ustilaginoidea virens*	Sexual development, sporulation, hyphal growth
	Pf2 (AbPf2 and AbEf1, FgArt1, FvArt1, MoCon1, PnPf2, PtrPf2, Zt107320)	*A. brassicicola*, *F. graminearum*, *Fusarium verticillioides*, *M. oryzae*, *Parastagonospora nodorum*, *Pyrenophora tritici-repentis*, *Zymoseptoria tritici*	Carbohydrate metabolism, effector production, abiotic stress tolerance, infection-related morphogenesis, sporulation
	NirA (Nir1)	*Colletotrichum acutatum*, *Fusarium fujikori*, *M. oryzae*	Nitrogen metabolism
C2H2	CreA (Cre1, GzC2H079)	*A. brassicicola*, *Aspergillus fumigatus*, *Botrytis cinerea*, *F. fujikori*, *F. graminearum*, *M. oryzae*, *Penicillium expansum*, *Sclerotinia sclerotiorum*	Carbon catabolite repression, SM biosynthesis, sporulation
	Crz1 (CrzA, BcCrz1, FgCrz1 & GzC2H013, PdCrz1, VdCrz1)	*A. fumigatus*, *B. cinerea*, *Colletotrichum graminicola*, *F. graminearum*, *M. oryzae*, *Penicillium digitatum*, *V. dahliae*	Ca^{2+}/calcineurin signalling, ionic/cell wall stress response, sporulation, hyphal growth, SM biosynthesis
	PacC (Pac1, BcPacC, Rim1, VmPacC)	*A. brassicicola*, *B. cinerea*, *C. graminicola*, *F. graminearum*, *F. oxysporum*, *M. oryzae*, *P. digitatum*, *P. expansum*, *S. sclerotiorum*, *Ustilago maydis*, *Valsa mali*	pH response regulator, SM biosynthesis, carbohydrate metabolism
	Msn2 (Vf19, Msn1, GzC2H045, MoMsn2/Tdg1, VmSeb1, VdMsn2, ZtVf1)	*A. brassicicola*, *A. fumigatus*, *F. graminearum*, *M. oryzae*, *V. dahliae*, *V. mali*, *Z. tritici*	Hyphal growth, sporulation, enzyme secretion, abiotic stress tolerance
	Con7 (Con7p, GzCon7, Con7-1, PnCon7, Vta2)	*F. graminearum*, *F. oxysporum*, *M. oryzae*, *P. nodorum*, *V. dahliae*, *Verticillium longisporum*	Hyphal growth, cell wall biosynthesis, sporulation, effector regulation, enzyme secretion
	Tri6	*F. graminearum*	SM biosynthesis
	Cmr1 (CmrA, Amr1, Bmr1, Bcsmr1, Pig1, VdCmr1, Zmr1)	*A. alternata*, *A. brassicicola*, *Bipolaris maydis*, *Bipolaris oryzae*, *B. cinerea*, *C. orbiculare*, *M. oryzae*, *V. dahliae*, *Z. tritici*,	Melanization, infection-related morphogenesis, abiotic stress tolerance, sporulation
GATA	AreA (Nrf1, ClnR1, Fnr1, Nut1, Nit2) & AreB (Asd4)	*A. fumigatus*, *Cladosporium fulvum*, *C. graminicola*, *Colletotrichum lindemuthianum*, *F. fujikori*, *F. graminearum*, *F. oxysporum*, *F. verticillioides*, *M. oryzae*, *U. maydis*	Nitrogen metabolism, SM biosynthesis, abiotic stress tolerance, effector regulation
	SreA (Sre1, GzGATA007, Urbs1)	*B. maydis*, *F. graminearum*, *F. oxysporum*, *U. maydis*	Iron metabolism, abiotic stress tolerance
	Wc-1 (LreA, BcWcl-1, Blr1, Crp1, WcoA, FgWc-1, FoWc1, MgWc1) & Wc-2 (BcWcl-2, FgWc-2, Wco2)	*A. alternata*, *B. cinerea*, *B. oryzae*, *Cercospora zeae-maydis*, *F. fujikori*, *F. graminearum*, *F. oxysporum*, *M. oryzae*, *U. maydis*	Light response/tropism, hyphal growth, sporulation, SM biosynthesis
bZIP	Yap1 (Ap1, AgAp1, ChAp1, Bap1, CgApr, FgAp1, MoAp1, ZtAp1)	*A. alternata*, *A. fumigatus*, *Ashbya gossypii*, *B. cinerea*, *B. maydis*, *C. graminicola*, *F. graminearum*, *M. oryzae*, *U. maydis*, *Z. tritici*	Oxidative stress tolerance, metal toxicity, SM biosynthesis, hyphal development
	Atf1(BcAtf1, CpTf1, FgAtf1, Foatf1, MoAtf1, VDAG_08676)	*B. cinerea*, *Claviceps purpurea*, *F. graminearum*, *F. oxysporum*, *M. oryzae*, *V. dahliae*	Oxidative stress tolerance, nitrogen metabolism, sporulation

(Continues)

TABLE 1 (Continued)

TF family	Orthologue (synonyms)	Pathogens	Reported regulatory functions[a]
	Cpc1/Gcn4 (CpcA, CpCpc1)	*C. parasitica*, *F. fujikori*, *Leptosphaeria maculans*, *V. dahliae*, *V. longisporum*	Amino acid biosynthesis, SM biosynthesis
	MeaB (MobZIP12)	*A. fumigatus*, *F. fujikori*, *F. oxysporum*, *M. oryzae*	Nitrogen metabolism, SM biosynthesis
	HapX (FgHapX, MobZIP13, VdHapX)	*B. maydis*, *F. graminearum*, *F. oxysporum*, *M. oryzae*, *V. dahliae*	Iron metabolism, abiotic stress tolerance, hyphal growth, sporulation
APSES (bHLH)	StuA (Stu1, FcStuA, FgStuA, FoStuA, LmStuA, Ust1, Vst1, ZtStuA)	*A. fumigatus*, *F. culmorum*, *F. graminearum*, *F. oxysporum*, *L. maculans*, *M. oryzae*, *P. nodorum*, *U. maydis*, *V. dahliae*, *Z. tritici*	Sporulation, sclerotia formation, melanisation, sexual reproduction, SM biosynthesis, effector regulation
	Swi4 (Mbp1, AfRafA, GzAPSES004, MoAps2) & Swi6 (AFLA_076560, FgSwi6, MOAps1)	*A. fumigatus*, *A. gossypii*, *F. graminearum*, *M. oryzae*	Hyphal growth, infection-related morphogenesis, stress response, sporulation, SM biosynthesis
Ste12 (HD/Hox)	Ste12 (AbSte12, Cst1, Fost, Mst12, Ztf1, Vph1, MgSte12, PstSte12)	*A. alternata*, *A. brassicicola*, *B. cinerea*, *C. orbiculare*, *C. parasitica*, *F. graminearum*, *F. oxysporum*, *M. oryzae*, *P. digitatum*, *P. expansum*, *P. striiformis*, *S. sclerotiorum*, *Setosphaeria turcica*, *U. maydis*, *V. dahliae*, *Z. tritici*	Infection-related morphogenesis, sexual development, nutritional response, hyphal growth, sporulation
Velvet	VeA (Vel1, BcVel1, CsVeA, Fgve1, FoVeA, FvVe1, MoVEA, Umv1, VmVeA, Mve1)	*A. alternata*, *A. fumigatus*, *B. cinerea*, *B. maydis*, *B. sorokiniana*, *Dothistroma septosporum*, *F. fujikori*, *F. graminearum*, *F. oxysporum*, *F. verticillioides*, *M. oryzae*, *P. expansum*, *U. maydis*, *V. mali*, *Z. tritici*	SM biosynthesis, hyphal growth, sporulation, sexual development, abiotic stress tolerance, pigmentation, cell wall integrity
	VelB (Vel2, BcVel2, CsVelB, FgVelB, FoVelB, FvVelB, MoVELB, Umv2, VmVelB, ZtVelB)	*A. fumigatus*, *B. cinerea*, *B. maydis*, *B. sorokiniana*, *F. fujikori*, *F. graminearum*, *F. oxysporum*, *F. verticillioides*, *M. oryzae*, *U. maydis*, *V. mali*, *Z. tritici*	SM biosynthesis, hyphal growth, sporulation, sexual development, abiotic stress tolerance, pigmentation
	VelC (BcVel3, CsVelC FoVelC, FvVelC, MoVELC, Umv3) and VelD	*A. fumigatus*, *B. cinerea*, *B. sorokiniana*, *F. oxysporum*, *F. verticillioides*, *M. oryzae*, *U. maydis*	Hyphal growth, sporulation
	VosA (CsVosA, MoVOSA)	*A. fumigatus*, *B. maydis*, *B. sorokiniana*, *M. oryzae*	SM biosynthesis, hyphal growth, sporulation, sexual development, abiotic stress tolerance, pigmentation
Gti1/Pac2	Wor1 (Gti1, Sge1, BcReg1, CfWor1, FfSge1, Fgp1, MoGti1, Ros1, VdSge1, ZtWor1)	*B. cinerea*, *C. fulvum*, *F. fujikori*, *F. graminearum*, *F. oxysporum*, *F. verticillioides*, *M. oryzae*, *U. maydis*, *Z. tritici*	Infection-related morphogenesis, hyphal growth, effector regulation, SM biosynthesis, sporulation, sexual development
	Pac2 (Fgp2, MoPac2)	*F. graminearum*, *F. oxysporum*, *M. oryzae*, *U. maydis*	Hyphal growth, sexual development

Note: A canonical core DNA target sequence with a strong affinity to the domain is indicated. Numbers represent where members of the family bind as (1) monomer, (2) multiple DBD monomer, (3) homodimer/multimer, (4) homotypic dimer/multimer (TF of same family), (5) coordinated DNA binding complex (either as a heterodimer/multimer, heterochimeric TF or by synergistic binding of separate TFs). SM, secondary metabolite.

[a]Regulatory roles and a direct virulence function are indicated and may not be applicable to all orthologues in the listed organisms. Refer to the corresponding record in Table S1 for species-specific TF details and links to the corresponding publications.

constitute two of the major TF families in fungi. bZIP TFs dimerize through a leucine-rich zipper region and bind to DNA via the major groove with adjacent basic residues (Deppmann et al., 2006; Fujii et al., 2000; Llorca et al., 2014; Reinke et al., 2013; Rodríguez-Martínez et al., 2017). The helix-loop-helix region performs a similar function as the leucine-zipper in the bHLH family (includes the fungal specific "APSES" TFs) (Carretero-Paulet et al., 2010; Sailsbery et al., 2012; Sailsbery & Dean, 2012; Shively et al., 2019). For both families, palindromic half-sites are a feature of target DNA sequences.

The homeodomain or homoeobox (HD/Hox) family TFs contain a DBD harbouring a conserved helix-turn-helix structure with affinity for a short AT-rich sequence. The HD/Hox family TFs, which encompasses the fungal-specific Ste12 TFs, actively target more specific sequences by forming heteromeric regulatory complexes (Bobola & Merabet, 2017; Bürglin & Affolter, 2016; Mann et al., 2009).

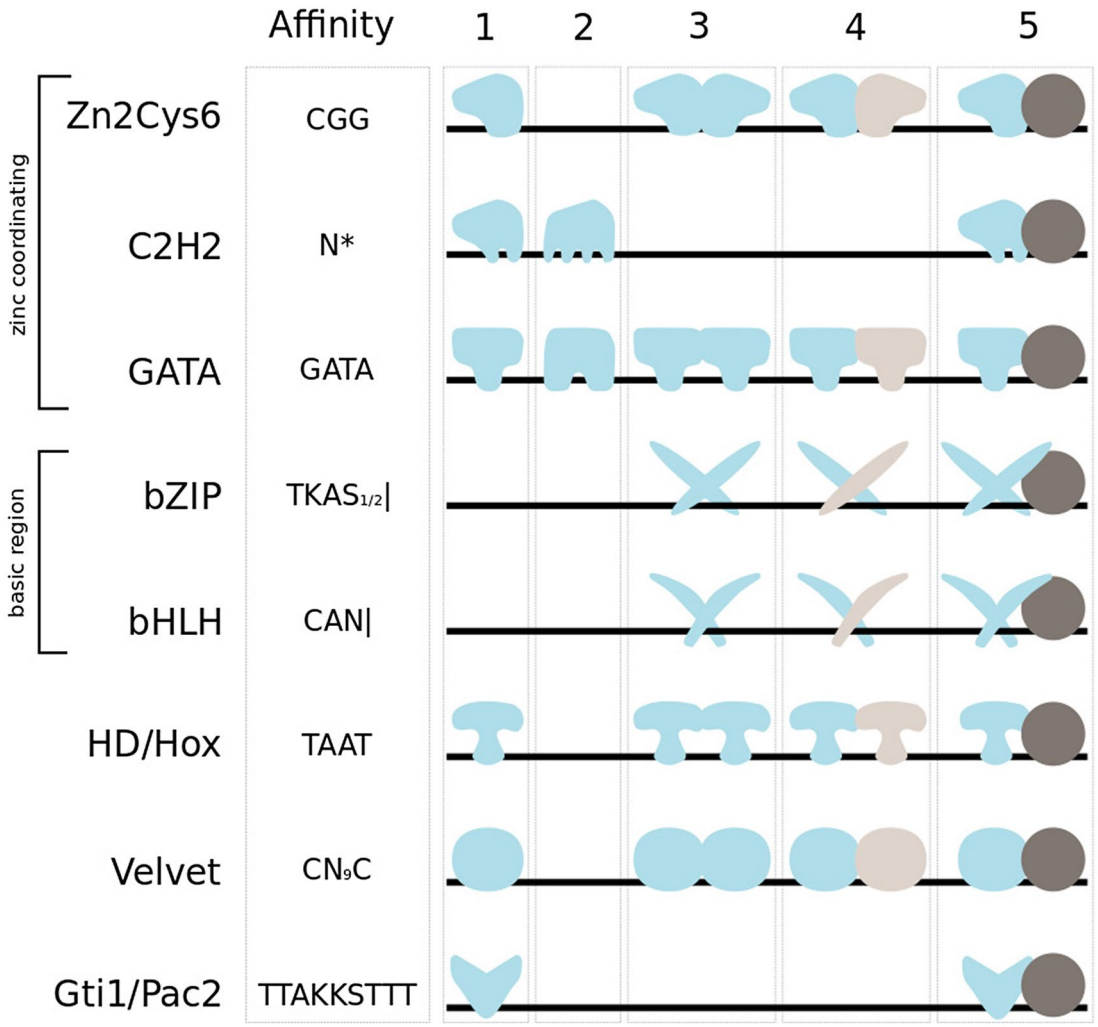

FIGURE 1 Mechanistic overview of transcription factor (TF) families detailed in this review

Less numerous, but well-characterized fungal-specific TFs belong to the Velvet and Gti1/Pac2 DBD families. The Velvet TFs are known to interact with other Velvet TFs and other cofactors, recognizing an 11 bp DNA sequence through two positively charged residue loops (Ahmed et al., 2013; Calvo et al., 2016). In contrast, the Gti1/Pac2 family TFs bind DNA as monomers through two separate but essential globular regions targeting a conserved 9 bp sequence (Cain et al., 2012; Lohse et al., 2010; Tollot et al., 2016). General binding properties for the families that have been presented, on the basis of extensive characterization in plant-pathogenic fungi, are presented in Figure 1.

3 | TFS AND THEIR ROLE IN VIRULENCE IN PLANT-PATHOGENIC FUNGI

3.1 | The Zn2Cys6 family

Zn2Cys6 TFs are fungal specific and the largest family among plant-pathogenic fungi, particularly in ascomycetes (Shelest, 2017; Todd et al., 2014). A significant number of Zn2Cys6 TF encoding genes reside within SM gene clusters, whose activation or functional products have not been resolved (Deepika et al., 2016; Graham-Taylor et al., 2020; Keller, 2019; Romsdahl & Wang, 2019). Nevertheless, diverse and interesting roles for Zn2Cys6 TFs have been reported, some as specific regulators of fungal virulence along with more general developmental regulators.

3.1.1 | Mtf4 + VdFtf1: Host sensors and secretion of virulence factors

Mtf4 and VdFtf1 are distinct Zn2Cys6 TFs specifically regulating fungal pathogenicity in their respective species. Mtf4 belongs to the cucurbit pathogen *Colletotrichum orbiculare* where it was shown to control the development of the appressorium, a mechanical host penetration structure (Kodama et al., 2019). Further analysis revealed Mtf4 is activated via the morphogenesis-related (MOR) kinase signalling pathway in response to cutin monomers derived from the host (Kodama et al., 2019). In the vascular wilt pathogen *Verticillium dahliae*, VdFtf1 was identified through *Agrobacterium*

T-DNA-mediated random mutagenesis as a TF required for full virulence on cotton (Zhang et al., 2018). A comparative RNA-Seq analysis identified a number of putative plant cell wall-degrading enzymes (CWDEs) down-regulated in the *vdftf1* mutant. Subsequent deletion of one of the encoding genes (*VEDA_09651*) revealed that it played a significant role in host infection (Zhang et al., 2018), demonstrating the utility of this approach for characterizing novel virulence factors.

3.1.2 | Ftf1/2: Gene expansion and effector regulation

Gene duplication and neofunctionalization have been recognized as an important process in the evolution of fungal virulence (Haridas et al., 2020; Skamnioti et al., 2008). Ftf1 from the *Fusarium oxysporum* species complex represents an interesting case study for a Zn2Cys6 TF (despite the nomenclature, this TF is not orthologous to VdFtf1). Several accessory chromosomes exist in *F. oxysporum* formae speciales causing vascular wilt on distinct hosts, the acquisition of which can be sufficient to render nonpathogenic strains virulent (Ma et al., 2010). Up to 10 paralogues of *Ftf1* can be found on these chromosomes, the number of which varies depending on the isolate (de Vega-Bartol et al., 2010; Taylor et al., 2019). Ftf1 TF paralogues have been shown to positively regulate a number of key virulence factors such as the SIX (Secreted-In-Xylem) effectors, and increased *Ftf1* gene expression or copy number is positively correlated with virulence (Niño-Sánchez et al., 2016; de Vega-Bartol et al., 2010). It is presumed that *Ftf1* arose from a duplication of *Ftf2*, a paralogue located on the core chromosome 9 (Armitage et al., 2018). Ftf2 shares some conserved regulatory targets with Ftf1 paralogues, many of which are located on the accessory chromosomes with *Ftf1* (van der Does et al., 2016). Interestingly, deletion of the putative *Ftf1*/*Ftf2* orthologue in *Fusarium graminearum*, the cause of fusarium head blight on wheat, did not affect fungal virulence (Son et al., 2011). This was also observed in the rice blast pathogen *Magnaporthe oryzae*, where *fzc76* knockout mutants were fully pathogenic (Lu et al., 2014). Therefore, Ftf1 in *F. oxysporum* demonstrates how TF acquisition (through horizontal gene transfer or duplication followed by neofunctionalization) can enable sufficient expression of host-specific virulence factors important during infection.

3.1.3 | EBR1: Hyphal branching

A virulence function for the enhanced branching TF EBR1 was first reported in *F. graminearum* (Zhao et al., 2011). Detailed phenotypic characterization attributed severe pathogenicity defects in *ebr1* mutants to impaired host penetration as a result of defective growth at the hyphal tip. The orthologue in *F. oxysporum* f. sp. *lycopersici* represents another case of TF gene expansion in this pathogen. Deletion of the core chromosomal *EBR1* orthologue had a moderate effect on hyphal growth and virulence, although this gene fully restored wheat pathogenicity when used to complement the *F. graminearum ebr1* mutant (Zhao et al., 2011). It was proposed that paralogues on *F. oxysporum* accessory chromosomes partially mitigated the effect of *EBR1* gene deletion (Jonkers et al., 2014; Zhao et al., 2011). Further analysis revealed one paralogue, *EBR2*, could fully complement the *ebr1* mutant, but only under the control of an *EBR1* promoter (Jonkers et al., 2014). Compared with *EBR1*, the expression of the respective paralogues during infection was relatively low. Hence the exact significance of these extra functional copies during infection remains to be determined (Jonkers et al., 2014; Yang et al., 2020). In *M. oryzae*, the orthologous gene *MoCod2* was required for proliferation beyond the initial sites of plant infection (Chung et al., 2013). This suggests a conserved EBR1 functional role controlling invasive hyphal growth may also exist in plant-pathogenic fungi.

3.1.4 | Pro1: Sporulation and development

The Zn2Cys6 TF Pro1 lacks the canonical dimerization domain, indicating it binds DNA as a monomer, an unusual property for this family (Masloff et al., 2002). Originally Pro1 was reported to orchestrate the formation of sexual reproductive bodies in the ascomycete *Sordaria macrospora* (Masloff et al., 1999). This developmental role is conserved for Pro1 orthologues in *F. graminearum* and the chestnut blight fungus *Cryphonectria parasitica* (Son et al., 2011; Sun et al., 2009). In *C. parasitica*, Pro1 was also involved in conidiation, a function that can be extended to the rice pathogens *Ustilaginoidea virens* and *M. oryzae* (Lu et al., 2014; Lv et al., 2016). In several plant pathogens, *pro1* mutants also exhibited perturbed hyphal development. This correlated with impaired virulence on the respective hosts; an exception being *C. parasitica*, where infections were comparable to the wild type (Cho et al., 2009; Lu et al., 2014; Lv et al., 2016; Son et al., 2011; Sun et al., 2009).

3.1.5 | Pf2: CWDEs and effector/effector-like genes

Pf2 has been identified as an important regulator controlling the necrotrophic lifestyle in fungal phytopathogens of the Pleosporales order. In the black spot fungus *Alternaria brassicicola*, AbPf2 was dispensable for normal growth but crucial for virulence on various Brassicaceae species (Cho et al., 2013). Gene deletion of *Pf2* orthologues in *Parastagonospora nodorum* and *Pyrenophora tritici-repentis* resulted in down-regulation of key necrotrophic effector genes including *ToxA* and *Tox3*, leading to the loss of host-specific virulence on wheat (Rybak et al., 2017). A detailed investigation was undertaken in both *A. brassicicola* and *P. nodorum* through RNA-Seq analyses of *abpf2* and *pnpf2* mutants, respectively. This revealed that Pf2 orchestrates the expression of a range of additional targets encoding putative effector-like proteins (small in size, possessing secretion signals and a high cysteine content) and plant CWDEs during early infection in both pathogens (Cho et al., 2013; Jones et al., 2019). A similar motif resembling a Zn2Cys6 binding site was characterized in both mutants, suggesting a conserved nucleotide

target exists for Pf2 (Cho et al., 2013; Jones et al., 2019; MacPherson et al., 2006). In *Zymoseptoria tritici*, a devastating wheat pathogen of the Capnodiales, the putative Pf2 orthologue Zt107320 was reported to regulate carbon sensing/utilization pathways, mediating virulence and sporulation during infection (Habig et al., 2020). This was similar to what was reported in *M. oryzae*, where MoCod1 was shown to be critical for invasive growth on rice (Chung et al., 2013). In both *F. graminearum* and *Fusarium verticillioides*, gene deletion of the respective orthologues *FgArt1* and *FvArt1* impaired pathogenicity, in part through changes to starch hydrolysis and SM biosynthesis (Oh et al., 2016). These reports indicate Pf2 taxonomic orthologues regulate pathways involved in carbohydrate acquisition, which can be tightly linked to the secretion of host-specific virulence factors during invasive growth.

3.2 | The C2H2 family

C2H2 TFs represent a second extensive family of fungal zinc finger regulators. In contrast to the fungal Zn2Cys6 family, C2H2 TFs exist in all eukaryotes (Fedotova et al., 2017). Well-characterized C2H2 TFs are primarily linked to the control of fungal development, stress tolerance, and metabolic activities in plant-pathogenic fungi.

3.2.1 | CreA: Carbon metabolism

The catabolite repressor CreA was originally studied for its regulatory role in central carbon metabolism in the model saprophytic fungus *Aspergillus nidulans* (Dowzer & Kelly, 1989, 1991). In the presence of primary carbon sources such as glucose, CreA blocks the expression of enzymes that break down complex carbohydrates (Adnan et al., 2017; de Assis et al., 2018; David et al., 2005). Since then, studies in a number of fungal phytopathogens have demonstrated a conserved role for CreA in carbon catabolite repression (Cao et al., 2016; Fasoyin et al., 2018; Jonkers & Rep, 2009; Tannous et al., 2018; Tudzynski et al., 2000; Vautard et al., 1999). A role for CreA in pathogenicity was reported during *Aspergillus flavus* infection of peanuts/maize kernels and *Penicillium expansum* colonization of apples. In these species *creA* mutants also displayed severely perturbed vegetative development and capacity to synthesize phytotoxic SMs such as aflatoxin and patulin, which probably contributed to a reduction in virulence (Fasoyin et al., 2018; Tannous et al., 2018). Meanwhile, contrasting reports suggest a significant role for FgCreA in the virulence of *F. graminearum* may or may not exist (Hou & Wang, 2018; Son et al., 2011).

3.2.2 | Crz1: Stress tolerance

The Ca^{2+}/calcineurin responsive zinc finger Crz1 is a key target downstream of Ca^{2+} ion signalling pathways, originally characterized in the yeast model *Saccharomyces cerevisiae* (Stathopoulos-Gerontides et al., 1999; Thewes, 2014). Orthologues in a number of fungal phytopathogens, including *A. flavus*, *Botrytis cinerea*, *Colletotrichum gloeosporioides*, *F. graminearum*, *M. oryzae*, *Penicillium digitatum*, and *V. dahliae*, have been functionally characterized through gene deletion (Choi et al., 2009; Dubey et al., 2016; Lim et al., 2019; Schumacher et al., 2008; Son et al., 2011; Xiong et al., 2015; Zhang, NurAinIzzati, et al., 2013; Zhang, Xu, et al., 2013). In each case, severe defects in development and both ionic/cell wall stress tolerances in *crz1* mutants are accompanied by reduced virulence. These studies demonstrate Crz1 is a fundamental regulator of genes essential for fungal development and stress tolerance in plant-pathogenic fungi of diverse hosts.

3.2.3 | PacC: pH stress tolerance, CWDEs, and SMs

In *A. nidulans* and *S. cerevisiae*, the C2H2 TF PacC/Rim101p is activated following proteolytic cleavage under alkaline conditions, leading to activation of pH-responsive genes (Díez et al., 2002; Lamb & Mitchell, 2003; Li & Mitchell, 1997; Tilburn et al., 1995). In plant-pathogenic fungi, gene deletion of *PacC* orthologues mirrors the phenotypes observed in *A. nidulans* and *S. cerevisiae* where *pacC* mutants exhibit growth defects at high pH (Aréchiga-Carvajal & Ruiz-Herrera, 2005; Caracuel et al., 2003; Chen et al., 2018; Cho et al., 2012; Flaherty et al., 2003; Landraud et al., 2013; Merhej et al., 2011; Miyara et al., 2008; Rascle et al., 2018; Rollins, 2003; Wiemann et al., 2009; Wu, Yin, et al., 2018; Zhang, NurAinIzzati, et al., 2013; Zhang, Sun, et al., 2013). In *B. cinerea*, *Sclerotinia sclerotiorum*, and *Valsa mali*, virulence defects in *pacC* mutants were attributed to an inability to actively acidify the site of host infection (Rascle et al., 2018; Rollins, 2003; Wu, Yin, et al., 2018). For *M. oryzae*, *C. gloeosporioides*, *P. digitatum*, and *P. expansum*, a virulence function for PacC was instead linked to the regulation of CWDEs (Chen et al., 2018; Landraud et al., 2013; Miyara et al., 2008; Zhang, NurAinIzzati, et al., 2013; Zhang, Sun, et al., 2013). In contrast, PacC was shown to suppress the expression of genes involved in the biosynthesis of toxic and protective SMs. These included patulin, bikaverin, fumonisins, and trichothecene biosynthetic genes in *P. expansum*, *Fusarium fujikuroi*, *F. verticillioides*, and *F. graminearum*, respectively (Chen et al., 2018; Flaherty et al., 2003; Merhej et al., 2011; Wiemann et al., 2009). Moreover, PacC suppresses virulence in *F. oxysporum* and was dispensable during infection in both *F. graminearum* and the obligate biotroph *Ustilago maydis* (Aréchiga-Carvajal & Ruiz-Herrera, 2005; Caracuel et al., 2003; Son et al., 2011). Hence in plant pathogens, PacC primarily coordinates pH tolerance along with additional pathways distinct to each species, which are often but not always implicated in fungal virulence.

3.2.4 | Msn2/Vf19: Development and virulence

The Msn2 C2H2 TF was first characterized in *S. cerevisiae* as an important factor coordinating adaptation to environmental

stressors including heat, and hyperosmotic and oxidative conditions (Martínez-Pastor et al., 1996; Schmitt & McEntee, 1996). Host virulence was consistently reduced or abolished following the deletion of *Msn2* orthologues in a number of plant-pathogenic fungi. However, rather than perturbed abiotic stress tolerances, abnormality in vegetative growth and the development of asexual spores or sclerotia were common phenotypic defects associated with *msn2* mutants (Chang et al., 2011; Mohammadi et al., 2017; Son et al., 2011; Tian et al., 2017; Wu, Xu, Yin, Feng, et al., 2018; Zhang et al., 2014). An interesting contrast was for the *A. brassicicola* orthologue Vf19, which was dispensable for normal growth and development, although required for virulence. Following RNA-Seq analysis and growth tests on complex carbon sources, this function was attributed to Vf19 regulation of hydrolytic enzymes (Srivastava et al., 2011).

3.2.5 | Con7: Development and virulence

The C2H2 TF Con7 was originally identified through a random mutagenesis screen for conidiation defects in *M. oryzae*. Since then, orthologues in other plant pathogens have been characterized through gene deletion (Odenbach et al., 2007; Ruiz-Roldán et al., 2015; Shi et al., 1998; Son et al., 2011; Tran et al., 2014). In addition to conidiation, these studies demonstrated Con7 is an important factor controlling hyphal growth and host invasion. In *M. oryzae* and *F. oxysporum* this was largely attributed to the regulation of cell wall synthesis/modulating enzymes (Odenbach et al., 2007; Ruiz-Roldán et al., 2015). *Verticillium* spp. that lacked *Con7* were abolished in their ability to penetrate host tissue. A gene expression analysis and cross-species functional complementation in *S. cerevisiae* revealed cellular adhesins and secreted enzymes were controlled by Con7 in these species (Tran et al., 2014). Although knockout mutants were not obtainable, suggesting a role in viability, gene knockdown of the *P. nodorum* orthologue *PnCon7* revealed it regulates the expression of necrotrophic effector genes and was correlated with reduced virulence on susceptible wheat (Lin et al., 2018). Furthermore, a yeast-1-hybrid analysis indicated PnCon7 directly targeted a promoter element of the necrotrophic effector *SnTox3*. Interestingly, not all differentially spliced isoforms (a common feature of Con7 orthologues) could bind this element (Lin et al., 2018; Ruiz-Roldán et al., 2015). Hence, through alternative splicing Con7 may flexibly regulate both core developmental processes and specific virulence factors in plant-pathogenic fungi.

3.2.6 | Tri6: Toxic SM biosynthesis

Trichothecene SMs are major virulence factors during *F. graminearum* infection of wheat. Deoxynivalenol (DON) is one of the best-studied trichothecenes in *F. graminearum*, where it is synthesized through the action of at least 16 genes situated on four chromosomal locations (Alexander et al., 2009; Amarasinghe & Fernando, 2016). One of these is *Tri6*, encoding a C2H2 TF located within the chromosome 1 core gene cluster and which is crucial for biosynthesis of DON (Hohn et al., 1999; Proctor et al., 1995; Scherm et al., 2011). Interestingly ChIP-Seq and RNA-Seq analyses demonstrate Tri6 possesses broader regulatory roles in *F. graminearum* by controlling the expression directly or indirectly of c.200 genes (Nasmith et al., 2011; Seong et al., 2009). It has since been shown that Tri6 also controls the production of phytotoxic fusaoctaxins and gramillins, demonstrating the TF is a general regulator of SMs involved in the virulence of this pathogen (Shostak et al., 2020).

3.2.7 | Cmr1: Melanization

Melanins refer to a class of dark pigmented, insoluble compounds. They are produced by fungi for cellular protection against physical and chemical environmental stresses or as factors involved in plant penetration and virulence (Eisenman & Casadevall, 2012; Howard & Valent, 1996; Nosanchuk et al., 2015). Melanin regulator Cmr1 is a chimeric TF with both C2H2 and Zn2Cys6 DBDs. It was originally shown to be involved in the biosynthesis of melanins in both *C. orbiculare* (Cmr1) and *M. oryzae* (Pig1) (Tsuji et al., 2000). These pathogens form melanized appressoria to initiate infection; however, Cmr1 and Pig1 were dispensable for melanization at this stage (Howard & Valent, 1996; Tsuji et al., 2000). Instead, Cmr1 orthologues have been reported to induce melanin biosynthetic genes during normal mycelial growth and the formation of sclerotia and conidia, corresponding to later stages of the infection cycle for a number of ascomycetous plant pathogens (Cho et al., 2012; Eliahu et al., 2007; Fetzner et al., 2014; Kihara et al., 2008; Krishnan et al., 2018; Tsuji et al., 2000; Wang, Hu, et al., 2018; Zhou et al., 2017). In an interesting case study, mutations in the *Zmr1* promoter from various wild-type *Z. tritici* isolates and laboratory-induced mutants resulted in changes to melanin production (Krishnan et al., 2018). This had direct implications in a fitness tradeoff. Isolates with reduced melanin grew more vigorously under optimal conditions but were more susceptible to stress induced by succinate dehydrogenase inhibitor fungicides, which are widely used to control this pathogen (Krishnan et al., 2018).

3.3 | The GATA family

GATA zinc finger TFs are named after the core nucleotide sequence they were originally shown to target and are featured across the eukaryotic taxa (Lowry & Atchley, 2000; Scazzocchio, 2000). In plant-pathogenic fungi, the best studied are conserved GATA TFs governing core metabolic pathways involved in nutrient acquisition and responses to light.

3.3.1 | AreA + AreB: Nitrogen assimilation

AreA (syn. NIT2) is a well-characterized TF controlling nitrogen assimilation in filamentous fungi (Marzluf, 1997; Tao & Marzluf, 1999). Other

TFs and signal transduction molecules that modulate AreA activity have also been identified. Briefly, AreB (a GATA TF that interacts with AreA), NmrA (involved in posttranslational modification of AreA), and MeaB (a bZIP TF suppressor of nitrate assimilation) are suppressors of AreA while the Zn2Cys6 TF NirA acts synergistically with AreA on a subset of nitrate assimilation pathways (Bernreiter et al., 2007; Bolton & Thomma, 2008; Michielse et al., 2014; Pfannmüller et al., 2017; Wilson et al., 2010; Wong et al., 2007, 2008, 2009).

Nutritional studies on the tomato pathogen *Cladosporium fulvum* revealed nitrogen starvation resulted in the production and secretion of the avirulence effector Avr9 (Van den Ackerveken et al., 1994). It was therefore hypothesized that nitrogen starvation would act as a general trigger for AreA-mediated expression of pathogenicity genes. However, subsequent investigations revealed the connection was limited to Avr9 and nitrogen scarcity was not a significant factor in this pathosystem (Solomon & Oliver, 2001; Thomma et al., 2006). Interestingly, *AreA* or *AreB/ASD4* gene deletion consistently resulted in perturbed virulence in a wide range of plant-pathogenic fungi (Bi et al., 2017; Divon et al., 2006; Fasoyin et al., 2019; Froeliger et al., 1996; Horst et al., 2012; Kim & Woloshuk, 2008; Marroquin-Guzman & Wilson, 2015; Min et al., 2012; Pellier et al., 2003; Wilson et al., 2010). These results suggest AreA is still an important general factor for fungal growth and development during infection. It has also been shown that specific nitrogen sources can induce SM biosynthesis through the AreA regulatory network (Keller, 2015; Tudzynski, 2014). In *F. fujikori*, this includes gibberellins, a class of phytohormones employed by the fungus to manipulate host physiology (Michielse et al., 2014). In other pathogens AreA also controls the production of a range of phytotoxic SMs (Fasoyin et al., 2019; Kim & Woloshuk, 2008; López-Berges et al., 2014; Min et al., 2012). These factors highlight additional mechanisms through which AreA may be regulating fungal virulence in these pathosystems.

3.3.2 | SreA + HapX (bZIP): Iron homeostasis

Iron is an essential component in fungal metabolism and is strongly linked to the modulation of reactive oxygen species (ROS). Hence, the maintenance of appropriate iron levels ensures optimal cellular function while avoiding iron toxicity (Haas, 2012; Johnson, 2008). In filamentous fungi, iron homeostasis is mediated by the GATA family TF SreA (siderophore regulator). During iron-replete conditions, SreA negatively regulates the production of iron-chelating siderophores (Gerwien et al., 2018; Johnson, 2008). A similar function has been described in the plant-pathogenic fungi *Bipolaris maydis*, *F. oxysporum*, *F. graminearum*, *V. dahliae*, and *U. maydis* (López-Berges et al., 2012; Voisard et al., 1993; Wang, Deng, et al., 2018; Wang et al., 2019; Zhang, NurAinIzzati, et al., 2013). *SreA* expression is suppressed by the bZIP TF HapX, a positive regulator of genes important for iron uptake. Deletion of *HapX* resulted in a loss of virulence in *M. oryzae*, *F. oxysporum*, and *V. dahliae*, and suggests HapX-mediated iron acquisition is critical during infection for these pathogens (Kong et al., 2015; López-Berges et al., 2012; Wang, Deng, et al., 2018).

3.3.3 | WC-1 + WC-2: Light response

The GATA TFs WC-1 and WC-2 interact to form the White-Collar Complex (WCC), one of the best-studied light response regulators in filamentous fungi. In the model *Neurospora crassa*, this complex is directly activated through light-mediated stimulus of a conserved sensory domain that induces transcriptional regulation of downstream response elements (Chen et al., 2010; Fuller et al., 2015; Schumacher et al., 2014). Interestingly, WC-1 orthologues in basidiomycetes lack the GATA DBD but can still form the WCC with WC-2, as demonstrated through a yeast-2-hybrid assay in *U. maydis*, where *wco2* (*wc-2*) mutants are highly susceptible to ultraviolet (UV) light-induced stress (Brych et al., 2016; Fuller et al., 2015). UV stress tolerance is also mediated by the WCC in ascomycete plant pathogens, in addition to conidiation or vegetative growth (Canessa et al., 2013; Estrada & Avalos, 2007; Kihara et al., 2007; Kim, Singh, et al., 2011; Kim et al., 2015; Pruß et al., 2014; Ruiz-Roldán et al., 2015). While the majority of these pathogens did not rely on the WCC for infection, an interesting case was reported for *Cercospora zeae-maydis*, where WC-1 regulated light-dependent infection via stomatal openings (Kim, Ridenour, et al., 2011). Moreover, MGWC-1 from *M. oryzae* acted to suppress infection of rice under light conditions (Kim, Singh, et al., 2011).

3.4 | The bZIP family

The basic region-leucine zipper or "bZIP" family of TFs is prevalent across eukaryotes (Amoutzias et al., 2007; Llorca et al., 2014; Reinke et al., 2013). An ability to readily form homo(typic) dimers with other bZIP TFs renders them flexible regulators of diverse cellular processes (Amoutzias et al., 2007; Deppmann et al., 2006; Miller, 2009). Studies in plant-pathogenic fungi have identified key metabolic and stress response pathways regulated by bZIP orthologues.

3.4.1 | Yap1/Ap1 + Atf1 and Skn7 (heat shock factor/HSF): Oxidative stress and SM biosynthesis

Yap1 is the representative member of the fungal-specific activator protein lineage of bZIP TFs, which have been extensively characterized in the yeast model *S. cerevisiae* (Moye-Rowley et al., 1989; Simaan et al., 2019). This subfamily targets both distinct and overlapping chemical stress responses (Rodrigues-Pousada et al., 2010). Highly conserved in filamentous fungi, Yap1 is activated by oxidative stressors, which induce cysteine–cysteine intramolecular bond formation leading to rapid nuclear import and transcriptional activity (Fernandes et al., 1997; Rodrigues-Pousada et al., 2019). Given that production of ROS forms a major component of plant immune responses, a role for Yap1 during infection has been explored in a number of phytopathogens (Camejo et al., 2016; Mendoza-Martínez et al., 2019; Segal & Wilson, 2018). Consistent with this connection, Yap1 orthologues were shown to be important for virulence in *Alternaria alternata*, *C. gloeosporioides*, *M. oryzae*, and *U. maydis* (Guo et al., 2011; Li

et al., 2017; Lin et al., 2009; Molina & Kahmann, 2007). However, Yap1 was dispensable for pathogenicity in *B. cinerea*, *B. maydis*, *F. graminearum*, and *Z. tritici* despite contributing to ROS detoxification (Montibus et al., 2013; Shalaby et al., 2014; Temme & Tudzynski, 2009; Yang et al., 2015). Some insight comes from the observation that Yap1 can heterodimerize with Skn7 (a TF of the HSF family, Table 2), a general stress responder downstream of the histidine kinase-based phosphorelay system (Mulford & Fassler, 2011). In *B. maydis*, only the double deletion of both *ChAp1* and *Skn7* genes resulted in reduced virulence on maize (Shalaby et al., 2014). This suggests Yap1 and Skn7 may redundantly target ROS detoxification pathways during plant infection.

Atf1 (also of the bZIP family) is another TF controlling ROS tolerance. Originally characterized in the fission yeast *Schizosaccharomyces pombe*, Atf1, like the human orthologue Atf2, is activated through phosphorylation by the p38/Hog1-mitogen activated protein kinase (MAPK) signalling cascade (Breitwieser et al., 2007; Shiozaki & Russell, 1996). While Atf1 shares some redundancy with Yap1 targets for oxidative stress tolerance, the two act independently (Montibus et al., 2015; Simaan et al., 2019). In plant-pathogenic fungi, Atf1 orthologues were shown to regulate stress response pathways to varying degrees (Fang et al., 2017; Guo et al., 2010; Nathues et al., 2004; Qi et al., 2013; Temme et al., 2012; Van Nguyen et al., 2013). Recently, nitric oxide detoxification and inorganic nitrogen assimilation were novel functions attributed to the Atf1 orthologue in *V. dahliae* that was also extended to *F. graminearum* (Tang et al., 2020). These additional roles may help explain why Atf1 remains an integral component regulating virulence in plant pathogens even while Yap1 is still functional. Induction or

TABLE 2 Research on the transcription factors (TFs) of conserved families not covered in this review

TF family	Orthologue (synonyms)	Pathogens	Reported regulatory functions[a]
bHLH	SreA (GzbHLH013, MoSre1, PdSreA)	*Fusarium graminearum*, *Magnaporthe oryzae*, *Penicillium digitatum*	Fungicide sensitivity (sterol biosynthesis), oxidative stress tolerance, iron metabolism
	SreB (PdSreB, GzbHLH009, FpbHLH9)	*F. graminearum*, *Fusarium pseudograminearum*, *P. digitatum*	Fungicide sensitivity (sterol biosynthesis), oxidative stress tolerance
	Crf1 (GzbHLH005)	*F. graminearum*, *M. oryzae*	Carbon/lipid metabolism, osmotic stress tolerance, hyphal growth, sporulation
HD/Hox	Hbx1 (GzHOME005, Htf1, UvHox2, Vhb1)	*Aspergillus fumigatus*, *F. graminearum*, *M. oryzae*, *Ustilaginoidea virens*, *Verticillium dahliae*	Sporulation, SM biosynthesis, abiotic stress tolerance, sclerotia formation
	Hdp1 & Hdp2 (GzHOME009, MoHox1)	*F. graminearum*, *M. oryzae*, *Ustilago maydis*	Infection-related morphogenesis, hyphal growth, SM biosynthesis, effector regulation
	MatbE1 and MatbW1	*Sporisorium scitamineum*, *U. maydis*, *Ustilago hordei*	Sexual development, infection-related morphogenesis
	MoHOX7 (CoHox3, GzHOME002)	*F. graminearum*, *M. oryzae*, *Colletotrichum orbiculare*	Infection-related morphogenesis, melanization, sporulation, SM biosynthesis
HSF	Skn7 (MoSKN7	*Alternaria alternata*, *Aspergillus fumigatus*, *Botrytis cinerea*, *Bipolaris maydis*, *F. graminearum*, *M. oryzae*	Abiotic stress tolerance, hyphal growth, sporulation, fungicide sensitivity (Hog1 pathway), melanization
	Sfl1 (MoSfl1, GzHSF003, VdSfl1)	*F. graminearum*, *M. oryzae*, *V. dahliae*	Hyphal growth, infection-related morphogenesis, sclerotia formation, abiotic stress tolerance
FH/WH	MoFkh1 (GzWing010, SsFkh1)	*F. graminearum*, *M. oryzae*, *Sclerotinia sclerotiorum*	Hyphal growth, sporulation, sclerotia formation, melanization, abiotic stress tolerance
	MoHcm1 (GzWing015, Fox1)	*F. graminearum*, *M. oryzae*, *U. maydis*	Hyphal growth, sexual development, effector regulation
	MoFox1 (GzWing027, FoxE2)	*F. graminearum*, *M. oryzae*, *S. sclerotiorum*	Sexual development
MADS	Mcm1 (Fgmcm1, Fmt, MoMcm1, PstMCM1-1, SsMads, VdMcm1)	*F. graminearum*, *F. verticillioides*, *M. oryzae*, *Puccinia striiformis*, *S. sclerotiorum*, *V. dahliae*	Hyphal growth, infection-related morphogenesis, sexual development, SM biosynthesis, sporulation
	Rlm1 (BcMads1, GzMADS003, Fmt2, Mig1)	*Ashbya gossypii*, *B. cinerea*, *F. graminearum*, *Fusarium verticillioides*, *M. oryzae*	Hyphal growth, sexual development, SM biosynthesis, sclerotia formation, protein secretion, light response
HMG box	Mat1 loci genes (Mat-1-1-x, Mat-2-1-x, Prf1)	*F. graminearum*, *S. scitamineum*, *U. maydis*	Sexual development
SANT / Myb	Flb4 (BzCon1, GzFlbD, MoMyb1)	*A. gossypii*, *Bipolaris zeicola*, *F. graminearum*, *M. oryzae*	Hyphal growth, sporulation, sexual development, SM regulation

Note: [a]Regulatory roles and a direct virulence function is indicated and may not be applicable to all orthologues in the listed organisms. Refer to the corresponding record in Table S1 for species-specific TF details and links to the corresponding publications. SM, secondary metabolite.

suppression of SM biosynthesis has also been linked to both Yap1 and Atf1 (Guan et al., 2019; Hong et al., 2013; Mendoza-Martínez et al., 2019). SMs can be metabolically taxing to synthesize under stressful conditions, providing an explanation for their suppression, while some exhibit protective properties and are valuable under such circumstances (Keller, 2015).

3.4.2 | Cpc1/Gcn4: Amino acid biosynthesis

A general mediator of amino acid (AA) biosynthetic pathways is the cross-pathway control bZIP TF Cpc1, which binds the TGACTCA sequence (Hoffmann et al., 2001; Paluh et al., 1988; Tian et al., 2007). The DBD is remarkably conserved in eukaryotes, with the yeast orthologue Gcn4 able to functionally complement the human orthologue JUN (Struhl, 1987, 1988). In fungal models including *N. crassa* and *A. nidulans*, AA starvation leads to Cpc1-mediated activation of AA biosynthetic genes (Hoffmann et al., 2001; Paluh et al., 1988; Tian et al., 2011). Reports to date in plant-pathogenic fungi suggest this function is also a conserved feature of Cpc1, which is dispensable for growth under nutrient-rich conditions (Elliott et al., 2011; Schönig et al., 2009; Son et al., 2011; Timpner et al., 2013; Wang et al., 1998). Accordingly, perturbed development on host tissue by *C. parasitica* following *CpCpc1* mutation was attributed to AA starvation (Wang et al., 1998). The vascular wilt pathogens *Verticillium longisporum* and *V. dahliae* were similarly perturbed following *Cpc1* gene deletion (Timpner et al., 2013). In the blackleg pathogen of canola *Leptosphaeria maculans*, gene silencing of the *Cpc1* orthologue led to overproduction of the phytotoxin sirodesmin-PL under AA starvation (Elliott et al., 2011). There it was concluded Cpc1 diverts metabolism towards AA biosynthesis, thereby reducing the available precursors necessary for sirodesmin-PL biosynthesis (Elliott et al., 2007, 2011). However, a strong link between Cpc1 regulation and SM biosynthesis has not yet been reported in other plant-pathogenic fungi. As such, the overall connection between Cpc1 and virulence probably correlates with nutrient availability rather than the induction of host-specific virulence factors.

3.5 | The bHLH family

Like the bZIP TFs, bHLH regulators readily dimerize with other members of the family to bind DNA through the basic residues at the N-termini (Sailsbery et al., 2012; Shively et al., 2019). Thus far, the ASPES subfamily is the best-characterized group of bHLH TFs in plant-pathogenic fungi (others are outlined in Tables 2 and S1).

3.5.1 | APSES: Developmental regulators

The Asm1/Phd1/Sok2/Efg1/StuA (APSES) subfamily is unique to fungi and has been divided into four groups, orthologues of StuA, Mbp1/Swi4 & Swi6, Afp1, and Xbp1. Each group is largely conserved across the fungal kingdom (Aramayo et al., 1996; Zhao et al., 2015). Functional investigation in plant-pathogenic fungi has focused on the StuA orthologues. The *A. nidulans* StuA target motif (A/TCGCGT/ANA/C) is enriched in gene promoters regulated by StuA in both *F. graminearum* and *U. maydis*. Consequently, it has been inferred that a functional StuA binding system is conserved, while a diverse set of pathways is known to be controlled by StuA in plant-pathogenic fungi (Dutton et al., 1997; García-Pedrajas et al., 2010; Koch et al., 1993; Lysøe et al., 2011).

In the ascomycete pathogens, gene deletion or silencing revealed *StuA* is broadly required for asexual reproduction (IpCho et al., 2010; Lysøe et al., 2011; Ohara & Tsuge, 2004; Nishimura et al., 2009; Pasquali et al., 2013; Sarmiento-Villamil, García-Pedrajas, et al., 2018; Soyer et al., 2015; Yao et al., 2017; Tiley et al., 2018). Conversely, the *U. maydis* orthologue Ust1 suppresses haploid spore formation (García-Pedrajas et al., 2010). In addition to asexual reproductive pathways, StuA is also important for sexual development in several species (García-Pedrajas et al., 2010; Lysøe et al., 2011; Nishimura et al., 2009; Soyer et al., 2015). Biosynthesis of melanins and phytotoxic SMs, as well as glycolysis are examples of the diverse metabolic pathways regulated in some fungi (García-Pedrajas et al., 2010; IpCho et al., 2010; Lysøe et al., 2011; Pasquali et al., 2013; Tiley et al., 2018; Sarmiento-Villamil, García-Pedrajas, et al., 2018). StuA has also been shown to play a role in effector gene expression in *L. maculans* and *P. nodorum* (IpCho et al., 2010; Soyer et al., 2015). Moreover, deletion or silencing of *StuA* orthologues directly impaired or abolished pathogenicity in all of the fungi studied, with the interesting exceptions of *F. oxysporum* and *V. dahliae*, both pathogens which invade vascular tissue, suggesting this infection route may be independent of StuA regulation.

Aside from StuA, regulatory functions have been attributed to APSES orthologues of Mbp1/Swi4 and Swi6. Early studies in *S. cerevisiae*, replicated in the closely related pathogen of cotton *Ashbya gossypii*, demonstrated the two members of the Mbp1/Swi4 and Swi6 group interact to form a homotypic dimer, regulating cellular division and cell wall integrity (Leem et al., 1998; Lengeler et al., 2013; Nair et al., 2010; Nasmyth & Dirick, 1991). Similar roles may explain the defects in both vegetative and invasive hyphal growth, sporulation, and susceptibility to several chemical stresses observed in *F. graminearum* and *M. oryzae* deletion mutants (Liu et al., 2013; Park et al., 2013; Qi et al., 2013; Son et al., 2011). In *A. flavus* the Mbp1 orthologue AfRafA lacks the conserved APSES DBD but was still crucial for fungal development, pathogenicity, and production of aflatoxin (Yao et al., 2017). These orthologues and the other APSES TFs remain to be explored further in plant-pathogenic fungi.

3.6 | The HD/Hox family

The HD/Hox TF family is the third largest in fungi after the Zn2Cys6 and C2H2 zinc fingers (Shelest, 2017). Aside from the Ste12 regulator, relatively few reports regarding phytopathogenic fungi are

available that describe a role for HD/Hox TFs beyond mating type regulation (Tables 2 and S1).

3.6.1 | Ste12: Invasive growth

In *S. cerevisiae* mating and morphological transitions in response to nutritional scarcity are controlled by Ste12, a target of the Fus3/Kss1-MAPK signal transduction cascades (Cook et al., 1996; Song et al., 1991; Tedford et al., 1997). Ste12 is characterized by a conserved N-terminal HD/Hox domain, but in filamentous fungi orthologues contain additional C2H2 domains at the C-terminus (Rispail & Di Pietro, 2010; Wong Sak Hoi & Dumas, 2010). Despite this difference, largely conserved regulatory functions are described regarding the morphological transition and sexual development. Ste12 is critical for pathogenicity in *A. alternata*, *C. orbiculare*, *F. graminearum*, *M. oryzae*, *Setosphaeria turcica*, and *V. dahliae* (Gu et al., 2014, 2015; Ma et al., 2019; Park et al., 2002; Sarmiento-Villamil, Prieto, et al., 2018; Tsuji et al., 2003), and plays some role in the virulence of several other plant pathogens (Tables 1 and S1). A common underlying factor is that Ste12 promotes the development of invasive hyphae, which allows the pathogen to colonize the host tissue and acquire nutrients. On nutrient-rich media, vegetative growth of *ste12* mutants is mostly unaffected in plant-pathogenic fungi aside from *B. cinerea*, *S. sclerotiorum*, and *S. turcica* (Gu et al., 2014; Schamber et al., 2010; Xu et al., 2018). Beyond morphological transitions, Ste12-mediated virulence has been attributed to reduced CWDE (*A. alternata* and *A. brassicicola*) and protease (*F. graminearum* and *V. dahliae*) secretion (Cho et al., 2009; Gu et al., 2015; Ma et al., 2019; Sarmiento-Villamil, Prieto, et al., 2018). Spliced isoforms and distinct cofactors have also been identified in several *Ste12* orthologues, revealing mechanisms for differential activity (Sarmiento-Villamil, Prieto, et al., 2018; Schamber et al., 2010; Tsuji et al., 2003). Interestingly, host-induced gene silencing of *PstSTE12* in the obligate rust fungus *Puccinia striiformis* f. sp. *tritici* inhibits the growth of the pathogen in wheat and demonstrates Ste12 is a useful target for disease control (Zhu et al., 2018).

3.7 | The Velvet family

The Velvet TF family consists of four conserved members (VeA, VelB, VelC, and VosA) that are unique in filamentous fungi (Bayram & Braus, 2012). The nature of the Velvet domain was only recently elucidated after structural analysis in *A. nidulans* (Ahmed et al., 2013). This confirmed the domain binds DNA and can interact with other Velvet TFs and an associated methyltransferase LaeA (Ahmed et al., 2013; Bayram et al., 2008). The Velvet family is predominantly associated with fungal metabolism and sporulation, functions that have been summarized previously (Bayram & Braus, 2012; Calvo et al., 2016).

Recent reports have extended this understanding in several plant-pathogenic fungi. In the apple canker pathogen *V. mali*, deletion of *VmVeA* and *VmVelB* revealed that they function as suppressors of melanin production and conidiation (Wu, Xu, Yin, Dai, et al., 2018). The two TFs, which interacted in a yeast-2-hybrid assay, were also shown to regulate virulence through pectinase production and the response to several abiotic stresses. In the cereal spot blotch pathogen *Bipolaris sorokiniana*, CsVeA, CsVelB, and CsVelC are all required for full virulence on barley (Wang et al., 2016). Specific functions for CsVeA and CsVelB were reported to include oxidative stress tolerance, conidiation linked to trehalose biosynthesis, hyphal development, pigmentation, and biosynthesis of the host-specific virulence factor ND90Pr (Wang et al., 2016). In a separate study, it was shown that CsVosA shares overlapping functions with CsVeA and CsVelB, as well as a role in regulating ionic/heat stress responses (Wang et al., 2015). These results largely mirror those reported for orthologues in *B. oryzae* (Wang et al., 2014; Wu et al., 2012). In *M. oryzae* MoVeA, MoVelB, and to a lesser extent MoVelC are important for hyphal development and conidiation (Kim et al., 2014). MoVeA and MoVelC were both involved in virulence on rice, controlling appressorium formation, cell wall porosity, and the deployment of ROS. However, MoVosA and MoVelB orthologues were dispensable for virulence, in contrast to what is observed for most plant pathogens (Calvo et al., 2016; Kim et al., 2014). Lastly, an analysis in *P. expansum* found *veA* mutants display perturbed conidiation, invasive growth, and biosynthesis of toxic SMs including patulin and citrinin (Assaf et al., 2018). Together, these reports reveal the extensive involvement of Velvet regulators in biosynthetic pathways, which is linked to the production of both specific virulence factors and the core developmental components of plant-pathogenic fungi.

3.8 | The Gti1/Pac2 family

The last TFs discussed in detail in this review belong to the Gti1/Pac2 family: orthologues of the two respective yeast genes *Gti1* and *Pac2* (Caspari, 1997; Kunitomo et al., 1995). Unlike other TF families, significant duplication/loss events have not been reported for the *Gti1* or *Pac2* genes, which are present ubiquitously as single copies in fungi (Cain et al., 2012). A role in fungal virulence was originally explored in Gti1 orthologs of the human pathogens *Candida albicans* (Wor1) and *Histoplasma capsulatum* (Ryp1), where they function as master regulators of the morphological transition between saprophytic and invasive growth (Huang et al., 2006; Nguyen & Sil, 2008; Zordan et al., 2006). An analogous function in *S. cerevisiae* exists as the switch to pseudohyphal growth exhibited during nutrient starvation (Cain et al., 2012).

This conserved role can be extended to plant pathogens where several studies have found the Gti1 orthologue positively regulates a suite of genes required for host infection. The first report was in *F. oxysporum* f. sp. *lycopersici* (Michielse et al., 2009). Despite the fungus lacking a distinct morphological transition, the phase transition into parasitism was found to be highly dependent on the Gti1 orthologue. Expression of several key effectors encoded by *SIX* genes was a distinguishing feature, which suggested the name Sge1 (*SIX* gene

expression) (Michielse et al., 2009). In addition, conidiation was reduced and subsequent studies in the banana pathovar *F. oxysporum* f. sp. *cubense* through gene knockout (Hou et al., 2018) and RNAi (Fernandes et al., 2016) identified similar regulatory roles for Sge1 in these contexts. For other members of the *Fusarium* genus, Gti1 orthologues are global regulators of effector gene expression or SM biosynthesis (Brown et al., 2014; Jonkers et al., 2012; Michielse et al., 2015).

Functional analyses of the respective orthologues have also been undertaken in *V. dahliae*, *Z. tritici*, *B. cinerea*, *C. fulvum*, and *M. oryzae*. These studies consistently describe a significant role in fungal development, conidiation, and virulence, in line with a shift in the expression profile of effector-like genes and/or SMs (Brown et al., 2014; Chen et al., 2014; Michielse et al., 2011; Mirzadi Gohari et al., 2014; Ökmen et al., 2014). In the basidiomycete *U. maydis*, the orthologue Ros1 orchestrates a massive transcriptional reprogramming during the late stage of infection (Tollot et al., 2016). This was found to be crucial for karyogamy and teliospore development, both required for completion of the infection cycle. The genes regulated included 80 TFs and 198 effectors, many of which were identified as direct targets through ChIP-Seq analysis (Tollot et al., 2016). The N-terminal DBD of Gti1 orthologues is highly conserved across the fungal taxa along with its cognate DNA target sequence (Cain et al., 2012; Tollot et al., 2016). This is not observed for the C-terminal, evidenced by partial or complete loss of TF function when the region was exchanged between *Fusarium* and *Cladosporium* spp. (Jonkers et al., 2012; Ökmen et al., 2014).

Fewer studies have been conducted on the other member of the Gti1/Pac2 family (i.e., Pac2 orthologues). Originally described as a suppressor of sexual development in *S. pombe*, this function was also reported in *U. maydis* (Elías-Villalobos et al., 2011; Kunitomo et al., 1995). In this pathogen, sexual development is crucial to the infection process and *Pac2* overexpression mutants were abolished in pathogenicity, in contrast to the *pac2* knockout mutants (Elías-Villalobos et al., 2011). Targeted gene knockout in *Fusarium* species indicates that *Pac2* plays only a minor role if any in fungal pathogenicity and development (Jonkers et al., 2012; Michielse et al., 2009). *M. oryzae pac2* mutants were impaired in hyphal growth and displayed some reduced virulence but, unlike *gti1* mutants, were not involved in sexual development (Chen et al., 2014). As these studies did not test *Pac2* overexpression, a potential role as a suppressor of sexual development in plant-pathogenic ascomycetes remains unknown.

3.9 | Additional TF families of plant-pathogenic fungi

In this review, several of the major fungal TF families have been covered. Priority was given to those encompassing TFs that have been the subject of extensive functional research efforts. However, the breadth of the topic means that it is not possible to cover each family in detail. Hence, a summary of research efforts until the time of writing into several other conserved classes is provided in Table 2. Along with those already detailed, this highlights the extent to which TFs that bind DNA through a wide range of mechanisms regulate diverse pathways implicated in fungal virulence. However, many are yet to be thoroughly investigated in plant-pathogenic fungi. Previous reviews annotating TF families across the fungal taxon provide further scope on the extent to which this remains the case (Park et al., 2008; Shelest, 2008, 2017; Todd et al., 2014).

4 | FUTURE PERSPECTIVES

A question was raised at the beginning of this review: what is it that allows a disease to develop in plant-pathogenic fungi? This review outlined the extent to which the functional characterization of TFs has provided insight into the regulation of pathogenicity. The aim was to systematically summarize these studies to highlight what is known and which areas remain to be explored for the ultimate goal of plant protection.

So far, functionally conserved TFs have been shown to control fundamental pathways such as iron, nitrogen and carbohydrate metabolism, oxidative, pH, osmotic and UV light stress tolerance, as well as vegetative growth, differentiation, and both asexual and sexual development. Many of these TFs were first identified based on homology to well-characterized saprophytic fungal models and functional investigation provided useful insight into the extent these pathways operate in the respective pathosystems. Some of these well-characterized regulators, such as Ste12, StuA, Gti1, and the Velvet TF orthologues, are fungal specific and broadly required for pathogenicity. As such they represent promising targets for the control of fungal diseases. Indeed, this was already effectively demonstrated through host-induced gene silencing of *PstSTE12* in *P. striiformis* f. sp. *tritici* as well as *V. dahliae Sge1* (Song & Thomma, 2018; Zhu et al., 2018). TFs continue to be explored as effective targets through gene silencing measures (Guo et al., 2019; Sang & Kim, 2019). TFs would also seem to be good targets for chemical intervention, which must be safe for nontarget organisms including the host plants, animals, humans, and beneficial microbes such as mycorrhizal fungi to be commercially viable (Bahn, 2015; Tietjen & Schreier, 2013). The design of screens for inhibitors of such fungal-specific TFs could be optimized using engineered strains, where activity could be measured by TF-controlled expression of a reporter gene.

While the core fungal TFs present robust targets for broad-spectrum disease control, regulators specifically controlling the expression of virulence factors would allow an even more targeted approach. Candidates such as VdFtf1, Ftf1/2, Pf2, and Tri6 could be targeted with conceivably few off-target effects on beneficial fungi. It is the novel identification and characterization of these TFs that warrants further effort, not only for direct pathogen control, but to better elucidate specific disease pathways. This would assist the discovery of novel effectors and damaging SMs, useful tools for improving plant protection (Vleeshouwers & Oliver, 2014). Genome sequencing

TABLE 3 Molecular methods to analyse transcription factor (TF)–DNA binding applied to plant-pathogenic fungi

Molecular method	Description	Examples
Chromatin immunoprecipitation (ChIP)	In vivo system, antibody-mediated pull down of TF followed by enrichment analysis of bound DNA by sequencing or quantitative PCR	MoCrz1 (Kim et al., 2010), Tri6 (Nasmith et al., 2011), FgSR (Liu et al., 2019), Ros1 (Tollot et al., 2016), FgAreA (Wang et al., 2019)
Protein binding microarray (PBM)	Binding affinity for purified TF measured against an array of DNA sequences in vitro	Ftf1 + Ebr1 (van der Does et al., 2016), MAT-1-2-1 (Kim et al., 2015), Fct1 + Fct2 (Kim et al., 2020)
Electrophoretic mobility shift assay (EMSA/gel shift)	Binding affinity for purified TF against a predetermined DNA sequence measured as shift in migration along a gel	BcabaR1 (Wang, Hu, et al., 2018), VdPf (Luo et al., 2016), FgSR (Liu et al., 2019), Tri6 (Nasmith et al., 2011), ZEB2 (Park et al., 2015), MAT-1-2-1 (Kim et al., 2015), SsFdh1 (Zhu et al., 2019), Ust1 (Baeza-Montañez et al., 2015), ClSte12 (Hoi et al., 2007), AreA (Mihlan et al., 2003), FgHapX (Wang et al., 2019)
Yeast-1-hybrid (Y1H)	TF expressed in yeast. TF target determined by mating a compatible strain containing candidate sequence upstream of selectable marker gene system.	Con7 (Lin et al., 2018), Pf2 (Jones et al., 2019), BcYOH1 (Simon et al., 2013), Rua1 (Teichmann et al., 2010), BcabaR1 (Wang, Hu, et al., 2018)

Note: Detailed reviews on these and other methods not yet widely used in plant-pathogenic fungi can be found (Levati et al., 2016; Orenstein & Shamir, 2017; Slattery et al., 2014; Viola & Gonzalez, 2016).

revealed the huge number of TFs from a range of families that have yet to be characterized (Aylward et al., 2017; Shelest, 2017). Hence, the scope for exploring the TF control of virulence in plant pathogens remains large. Moving forward two broad approaches seem pertinent:

- Continue to identify novel TFs that are regulators of specific virulence and pathogenicity-related functions. Random mutagenesis, or the large-scale TF knockout studies conducted on *F. graminearum*, *A. brassicicola*, and *M. oryzae* are examples of such approaches (Cao et al., 2016; Cho et al., 2012; Lu et al., 2014; Son et al., 2011). Phylogenetic approaches may also identify cases evolutionarily linked to pathogenicity, such as the Ftf1/2 TFs in *F. oxysporum* (Niño-Sánchez et al., 2016).
- Harness molecular techniques to determine TF–DNA binding to characterize the precise targets for known regulators of virulence. Some use cases in plant-pathogenic fungi are provided (Table 3). Further adoption of these techniques will allow us to distinguish direct target genes specific to fungal pathogenicity from pleiotropic effects resulting from gene deletion. It is also of interest to determine the interactions with other regulatory molecules and cofactors. This has already been achieved through yeast-2-hybrid screens, protein arrays, coimmunoprecipitation, and bimolecular fluorescence complementation, identifying interactions with signal transducers and other regulatory molecules (Brych et al., 2016; Li et al., 2011; Liu et al., 2018, 2019; Schumacher et al., 2015; Zhu et al., 2019). When these methods are used in concert with RNA-Seq, proteomics, and epigenetic tools, the fundamental mechanisms orchestrating the disease regulatory networks for specific pathogens can be established.

Considering the current technological and genomic resources, both avenues are sound approaches that will extend our understanding of the mechanisms, and thereby enhance both monitoring and management of the diseases caused by plant-pathogenic fungi.

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DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created of analysed in this study.

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[Correction added on 07 June 2021, after first online publication: new reference "Marroquin-Guzman, M. & Wilson, R.A. (2015)" has been included in this version.]

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

[Correction added on 07 June 2021, after first online publication: Table S1 has been updated in this version.]

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