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RESEARCH ARTICLE

Identification and gene expression analysis of mating type (*MAT*) *1-1-1* gene in *Fusarium oxysporum* f.sp. *cubense* Tropical Race 4

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Abstract

Fusarium oxysporum f.sp. *cubense* Tropical Race 4 (*Foc* TR4) is a soil-borne fungal pathogen that impacts banana production. It is a member of the *F. oxysporum* species complex (FOSC), whose members are predominantly asexual. However, the FOSC members, including *Foc* TR4, retain mating type (*MAT*) loci, suggesting functions that are different from mating. This study identified and characterized the MAT1-1 locus in *Foc* TR4 and the expression of *MAT1-1-1*, the key gene in the MAT1-1 locus, during its interaction with susceptible bananas *in vitro*. The open reading frame of the identified *MAT1-1-1* perfectly matched the reference sequence, and the corresponding MAT1-1-1 protein (367 amino acids) was predicted to localize to the nucleus, which matches its previously reported function as a transcriptional regulator. Based on the phylogenetic analysis of MAT1-1-1 protein sequences, *Foc* TR4 was grouped closely with other *F. oxysporum* formae speciales and clearly separated from other *Fusarium* species. The expression level of *MAT1-1-1* was negligible in the absence of the host but was significantly induced when the host was present within a close range (at 2cm away) and at four to eight hours after being exposed to the host. These data reveal that the *MAT1-1-1* of *Foc* TR4 is possibly associated with host sensing, allowing the pathogen to recognize specific signals from the host and activating genes required for directed hyphal growth and colonization. Overall, this study sheds light on the other potential roles of *MAT* genes, particularly *MAT1-1-1* in *Foc* TR4.

Keywords: asexual, cavendish, *Foc* TR4, host sensing, pathogenicity

INTRODUCTION

Fusarium oxysporum f.sp. *cubense* Tropical Race 4 (*Foc* TR4) is a filamentous pathogenic fungus that attacks bananas (Musa spp.), reducing banana production and causing a substantial economic loss (Staver et al., 2020). *Foc* TR4 infects bananas from the opening in the roots following the germination of infectious chlamydospores in the soil, and the hyphae then travel through the xylem vessels, blocking the water transport (Pegg et al., 2019). The infection will cause yellowing and wilting in the leaves, which is why the name of the disease is called Fusarium wilt. Internally, the disease symptoms can be seen as brown discoloration in the rhizome and pseudostem. Chlamydospores are the survival structures of *Foc*

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TR4, and they can remain dormant in the soil or plant debris for an extended period, even without a host plant (Pegg et al., 2019).

Foc TR4 belongs to the *F. oxysporum* species complex (FOSC), which comprises multiple phylogenetic lineages with complicated taxonomic relationships within its members (Maryani et al, 2019). The FOSC members are responsible for causing various diseases in many agronomically important crops, including bananas (Nag et al., 2022). Like many of the FOSC members, *Foc* TR4 has no known sexual stages and reproduces by producing asexual spores that include conidia and chlamydospores (Chen et al., 2024). However, it retains the mating type (*MAT*) genes in the *MAT* locus that function in sexual reproduction and mating compatibility (Fourie et al., 2009). Different fungal species may contain different sets of genes in their *MAT* loci, but sequences of *MAT* genes are identified as highly conserved across the species (Casselton, 2022).

The *MAT* loci in filamentous ascomycetes comprise *MAT1-1*, characterized by an alpha-box domain, and *MAT1-2*, with a high mobility group (HMG) domain, which is known as idiomorph and can exist within a single individual (heterothallic) or different individual (homothallic) of a fungal species (Turgeon and Yoder, 2000). *Foc* TR4 is a heterothallic species with either *MAT1-1* or *MAT1-2* locus (Magdama et al., 2020). Different MAT lineages of *Foc* TR4 seldom appear in the same field, and the *MAT1-1* lineage is often more abundant (Fourie et al., 2009; Magdama et al., 2020; de la Parte et al., 2024). The uneven spread of *MAT1-1* and *MAT1-2* lineage in the same plantation has been linked to the absence of sexual reproduction in *Foc* TR4.

MAT genes are reported to evolve under strong purifying selection, which removes deleterious or harmful mutations to maintain the gene's functionality (O'Donnell et al., 2004). *MAT* genes are also functionally constrained even in asexual species, suggesting additional roles beyond sexual reproduction. Besides their critical role in modulating sexual development and mating, recent reports showed that *MAT* genes also play essential roles in stress response, conidiation, mycelial development, and pathogenicity (Beckter et al., 2015; Zhang et al., 2013). The *MAT1-1* locus of *F. oxysporum* is occupied by *MAT1-1-1, MAT1-1-2* and *MAT1-1-3* genes (Yun et al., 2000). Among them, *MAT1-1-1*, which contains the alpha-box domain, is the most studied.

Zheng et al. (2013) showed that mat1-1-1 and mat1-2-1 deletion mutants in *F. graminearum* exhibited defects in pathogenicity assays, hinting at a possible role for the *MAT* genes in plant infection. In a separate study, deletion of only *MAT1-1-1* in *F. graminearum* provided evidence for the involvement of the genes in modulating the expression of pheromone, a signal produced by a cell in response to appropriate mating conditions and pheromone receptor genes in the sexual fungus (Kim et al., 2015). In the asexual *F. oxysporum*, the presence of genes that code for pheromone precursors and their cognate receptors (Ma et al., 2010) has been puzzling until Turrà et al. (2015) elegantly showed that the pheromone response pathway appeared to have acquired a new function in host roots sensing. The finding was supported by Liu et al. (2023), who reported that *Foc4-PP1*, a gene orthologous to the α-pheromone precursor, is indispensable for the complete virulence of *Foc* TR4. The repurposing of the pheromone response pathway for host sensing in *F. oxysporum* highlights its evolutionary significance, suggesting that *MAT1-1-1*, as a transcription regulator, could be pivotal in regulating this process. However, the study of the *MAT* genes in *Foc* TR4 has been limited to population biology studies (Magdama et al., 2020; de la Parte et al., 2024), and research on the expression of the *MAT* genes is lacking. Therefore, investigating the expression of *MAT1-1-1* during *Foc* TR4-banana interaction could uncover its potential regulatory functions beyond mating, particularly in modulating virulence and host recognition.

The present study reports the isolation of *MAT1-1-1* from *Foc* TR4 and its spatiotemporal expression pattern during interaction with a susceptible host. Profiling the dynamic expression of the *MAT1-1-1* gene during host-pathogen interaction is essential to uncover its potential regulatory influence, particularly on host sensing and its contribution to virulence towards banana plants. The findings could provide critical insights into how *Foc* TR4 adapts to its host environment and facilitates infection.

MATERIALS AND METHODS

Fungal and plant materials

The *Foc* TR4 culture was obtained from the Mycology Lab, Faculty of Science, Universiti Putra Malaysia, and maintained on potato dextrose agar (PDA) (Oxoid, UK) at room temperature for seven days for a full-colony plate. *Musa accuminata* var. Cavendish plantlets with 7-9 leaves in an individual polybag were used for the pathogenicity assay in this study. The plantlets were obtained from Simple Farm Sdn. Bhd., Johor, Malaysia, and maintained in a greenhouse at the Faculty of Biotechnology and Biomolecular Sciences, Universiti Putra Malaysia, under natural light with daily watering. Tissue-cultured Cavendish banana plantlets at the rooting stage with an average height of 10cm and 5-7 small leaves were used for the *in vitro* experiments. The plantlets were established by the Biodiversity Unit, Institute of Biosciences, Universiti Putra Malaysia, and maintained in the culture room in light condition at 25°C.

Isolation and bioinformatic analysis of MAT1-1-1 sequence

The mycelia of *Foc* TR4 were harvested from potato dextrose broth (PDB) after one week of culture in a shake flask at 25°C. The extraction of genomic DNA was done using the cetyltrimethylammonium bromide (CTAB) method following the protocol by Poon et al. (2019). To locate the *MAT1-1-1* gene in the *Foc* TR4 genome, the mating-type protein MAT alpha 1 HMG-box (Pfam ID: PF04769) sequence was searched against the *Foc* TR4 database (taxid:2502994) using the tblastn function on the National Center for Biotechnology Information (NCBI) page. The neighboring *MAT1-1-2* and *MAT1-1-3* genes in the *MAT1-1* locus were initially identified based on their position with respect to the *MAT1-1-1* gene and further confirmed through functional domain analysis.

To amplify *MAT1-1-1*, primers F 5'-TTCTCTCA CTCGTCGCTGT-3' and R 5'-GAACAATCGGAG TTTCTGAAC-3' that amplify regions flanking the open reading frame (ORF) of the gene were designed and the primer specificity was confirmed by checking against *F. odoratissimum* (alternative name for *Foc* TR4) II-5 (NRRL 54006) genome (NW_022158709). The primers were used in a PCR reaction to amplify 1216 bp of *MAT1-1-1* gene sequence using DreamTaq PCR Master Mix (2×) (Thermo Scientific, Lithuania) with an annealing temperature of 55°C. The PCR products were purified using NucleoSpin Gel and PCR Clean-up kit (Macherey-Nagel, Germany) and sequenced at Apical Scientific Sdn. Bhd., Malaysia. The protein sequence of MAT1-1-1 from *Foc* TR4 (XP_031057603) was aligned with the annotated MAT1-1-1 sequence from *Fusarium* species and formae speciales available in the NCBI database and used to construct a phylogenetic tree using "One Click" on "https://www.phylogeny.fr/simple_phylogeny.cgi" (accessed on 2 July 2024). The same protein sequence was also used to predict the subcellular localization via MULocDeep (Jiang et al., 2021), https://www.mu-loc.org/ (accessed on 1 September 2024).

In vitro experiments

The *in vitro* experiments were divided into two parts: distance and time-point. For the distance experiment, tissue-cultured Cavendish plantlets were subcultured individually into a 250mL conical flask containing freshly prepared Murashige and Skoog (MS) medium (Sigma-Aldrich, USA) and positioned close to the wall of the flask. The plantlets were allowed to grow for 1 week. A conidial suspension was prepared by rinsing *Foc* TR4 mycelia from PDA using sterilized deionized water, and the concentration was adjusted to 1×10^6 conidia/mL. The conidial suspension (100μL) was pipetted onto the MS medium opposite the growing banana plantlet, and the fungal mycelia was allowed to grow toward the banana plantlets until it reached certain distances (2cm, 4cm, 6cm, and 8cm). The distances were selected to capture the gradual progression of fungal response dynamics as it approaches the host and to provide a good resolution for detecting changes in *MAT1-1-1* expression and fungal growth behavior. The mycelia were then harvested according to distance away from the plantlets. The mycelia in contact with the host plant at harvest was regarded as 0cm (control). The experiment was conducted in a plant tissue culture room at 25°C.

For the time-point experiment, 100μL of the conidial suspension with the same concentration was pipetted onto PDA in a 250mL conical flask and allowed to grow for 10 days at room temperature until it formed a lawn. Individual tissue-cultured banana plantlets were transferred onto the lawn and incubated for 2, 4, 8, and 12 hours under light at 25°C to capture the early-stage interactions between *Foc* TR4 and banana roots. Then, the plantlets were removed, and the mycelia were harvested using a sterile microspatula for RNA extraction. The mycelial lawn without banana plantlets harvested at the start of the experiment was treated as a control (0 hours). All the *in vitro* experiments were run in triplicate.

Analysis of MAT1-1-1 expression

The total RNA was extracted from *Foc* TR4 mycelia without any treatment and from the *in vitro* experiments using the CTAB method according to the protocol by Poon et al. (2019). The synthesis of cDNA was completed using the ReverTra AceTM qPCR RT Master Mix with gDNA Remover (TOYOBO, Japan) using 1μg of the total RNA and served as a template in a qRT-PCR. The qRT-PCR was performed using THUNDERBIRDTM Next SYBR® qPCR Mix (TOYOBO, Japan) on a Mx3005P quantitative Real-Time PCR machine (Agilent, USA) using primers specific for *MAT1-1-1* gene (Alphabox) F 5'-GCTTGATCTGTTCGGT CAT-3' and R 5'-CAGGAAACCGGAGGCATTCT -3' and the internal control gene, *FocEF1a* (qFocEF1α primers), F 5'-GCTGGTGACTCCAAGAACGA-3' and R 5'-CATCTTGACGATGGCGGAGT-3' from Liu et al. (2019). All samples were analyzed in triplicates, and the changes in gene expression were determined using the $2^{-\Delta\Delta Ct}$ method (Livak and Schmittgen (2001). The expression data from qRT-

PCR were analyzed using a two-way ANOVA followed by Tukey's post-hoc tests ($p<0.05$).

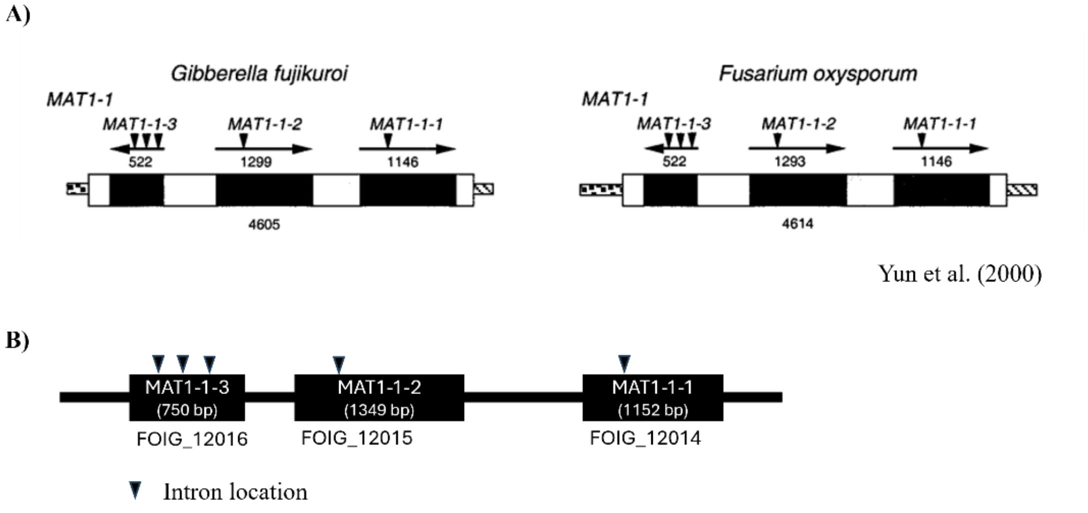
RESULTS AND DISCUSSION

In silico analysis of *MAT1-1* locus and *MAT1-1-1* sequence of *Foc* TR4

The genome of *Foc* TR4 contains the *MAT1-1* locus, but the identity and the potential role of *MAT* genes in the asexual pathogenic fungus are yet to be characterized. In this study, we showed that the *MAT1-1* locus in the reference genome of *Foc* TR4, *F. odoratissimum* II5, contains typical genes present in the *MAT1-1* idiomorph of *F. oxysporum*, which include *MAT1-1-1* (FOIG_12014), *MAT1-1-2* (FOIG_12015), and *MAT1-1-3* (FOIG_12016) with a conserved gene order as reported previously in *F. oxysporum* by Yun et al. (2000) (Figure 1A). The putative *MAT1-1-1* ORF is 1152bp with one intron and two exons (Figure 1B). The putative *MAT1-1-2* gene also contains a single intron with a gene size of 1349bp and a functional domain that matches the MAT1-1-2 protein family (pfam17043). On the other hand, the putative MAT1-1-3 contains three introns with only 750bp and encodes an HMG box-containing protein (cd01389).

A PCR amplification using specific primers designed outside the *MAT1-1-1* ORF in *F. odoratissimum* II5 and our *Foc* TR4 genomic DNA template generated a PCR product that perfectly matches the ORF sequence in the reference genome. The corresponding MAT1-1-1 protein contains the MATalpha_high mobility-group (HMG) domain and is 367 amino acids in length. The domain, hereinafter called the alpha-box motif, spans the intron region (Figure 2). The presence of an intron in the middle of a protein's functional domain suggests that efficient splicing of the single intron might be critical for proper gene expression levels. The *MAT1-1-1* intron contains the canonical splice sites (5' GU···3' AG), and the gene was reported to be expressed in the asexual fungus with its intron removed (Yun et al., 2000). The MAT1-1-1 protein is predicted to localize to the nucleus, which matches its previously reported function as a DNA-binding protein or transcription activator (Kim et al., 2024).

A phylogenetic analysis using the MAT1-1-1 protein sequence showed that *F. oxysporum* are grouped into a well-supported clade, suggesting significant similarities in their MAT protein sequences and potentially shared evolutionary adaptations (Figure 3). *Foc* TR4 in this study clusters closely with *F. oxysporum* f.sp. *albedinis* and *F. oxysporum* f. sp. *narcissi*, the pathogen of date palm (Khayi et al., 2024) and narcissus (Taylor et al., 2019), respectively (Figure 3). This could reflect similarities in genetic mechanisms linked to pathogenicity, though their host plants differ or conserved regulatory strategies. Outside the *F. oxysporum* complex, a greater divergence in *F. fujikuroi* (also known as *G. fujikuroi*) and other non-*F. oxysporum* species suggest species-specific adaptations in the MAT genes. Despite the striking similarities in the organization of genes in the *MAT* locus of *F. oxysporum* and *F. fujikuroi* (Yun et al., 2000), their protein sequences differ, and this divergence aligns with the broader ecological versatility or host-independent survival strategies of *Fusarium* species outside FOSC.



Yun et al. (2000)

Figure 1. Characteristics of MAT1-1 locus in *F. oxysporum*. (A) MAT loci organization in the asexual *G. fujikuroi* and F. *oxysporum* as published by Yun et al. (2000). (B) Schematic structure of *MAT1-1-1, MAT-1-1-2* and *MAT1-1-1* genes in the MAT1-1 locus of *Foc* TR4. Black rectangles represent genes and black arrowheads represent intron.

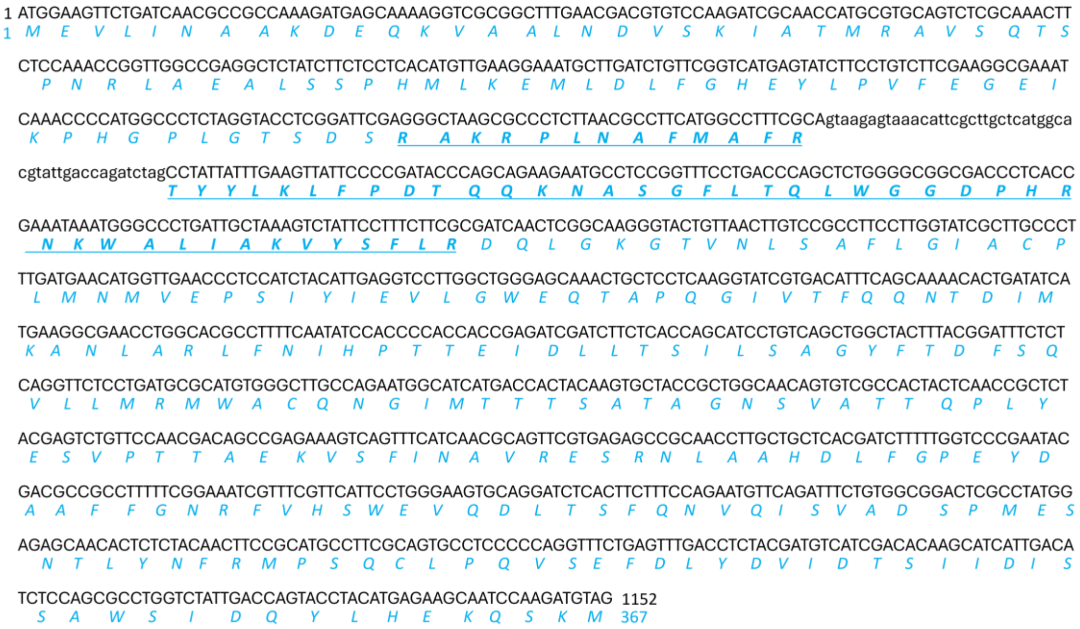


Figure 2: Alignment of the nucleotide (black capital letters) and amino acid (blue capital letters) sequences of MAT1-1-1 in *Foc* TR4. The intron sequences were written in small letters, and the MATalpha_high mobility-group (HMG) domain was bold and underlined.

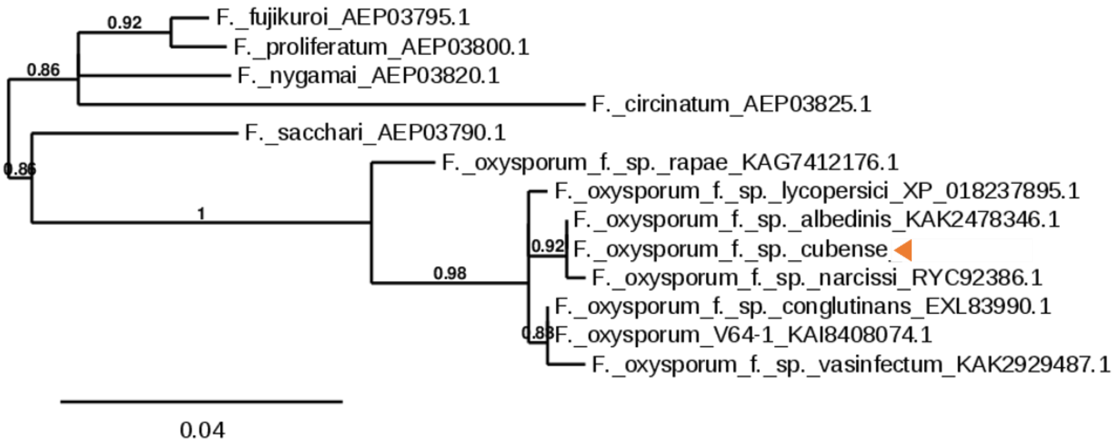


Figure 3: Phylogenetic tree of MAT1-1-1 homologs across different *Fusarium* species and formae speciales. The tree was constructed using the "One Click" pipeline on Phylogeny.fr, which employs a maximum likelihood approach for phylogenetic inference. *Foc* TR4 in this study is marked with an orange triangle. The accession number for each protein sequence is included next to the species name.

Spatiotemporal expression of MAT1-1-1 during interaction with a susceptible host in vitro

The expression profile of *MAT* genes in asexual fungi is not widely investigated compared to the sexual counterpart. Yun et al. (2000) and Kerenyi et al. (2004) reported that *MAT* genes are expressed in several asexual *Fusarium* species, including *F. oxysporum*. This study found that the expression of *MAT1-1-1* was very low and, most of the time, not detected when cultured on PDA in the absence of a host plant or more than 24 hours after infection in banana plants (data not shown). Similar observations were reported for the *MAT1-1-1* gene in *F. graminearum* (Zheng et al., 2013) and *F. asiaticum* (Kim et al., 2012). In both studies, *MAT* gene expression was transiently induced under specific conditions such as sexual development. We postulated that *MAT1-1-1* could be expressed earlier and during interaction with a host plant. Hence, *in vitro* experiments that covered both spatial and temporal expression of *MAT1-1-1* were designed to capture the specific interaction that otherwise cannot be observed in the soil.

In the distance experiment, the introduced *Foc* TR4 spores germinated into hyphae, which developed into a mycelial mat and grew towards the tissue-cultured banana plantlet in the opposite direction. The first detectable expression of *MAT1-1-1* was after the mycelium had grown to within 8 cm of the host plant (Figure 4A). The expression increased gradually as it approached the host plant, where the host signals likely became more concentrated and peaked significantly ($p<0.05$) after it had grown to within 2cm. The fungal mycelia possibly responded most strongly to the host-derived signals at this proximity, which may stimulate pathways controlled by the *MAT* genes, potentially tied to host sensing. Strikingly, the expression level plummeted upon establishing physical interaction with the host, possibly because the fungus has transitioned to other pathways critical for host colonization or nutrient acquisition. The findings showed that *MAT1-1-1* may be critical during the early phases of host sensing and fungal movement toward the plant but less so during the physical colonization of the host tissue.

In the time-point experiment, at 0 hours post introduction (hpi) of banana plantlet to the mycelial lawn, the *MAT1-1-1* expression level was almost negligible. A slight increase in the level of *MAT1-1-1* expression was detected two hours after the introduction of a banana plantlet to the mycelial lawn, suggesting an initial response to the host presence (Figure 4B). The expression increased significantly at 4 and 8 hpi, which supports the role of *MAT1-1-1* in sensing signals from the host during the initial stages of contact. The expression level then decreased at 12 hpi, coinciding with the attachment of *Foc* TR4 hyphae to banana roots, similar to the pattern observed in the distance experiment.

Collectively, the results suggest a possible involvement of *MAT1-1-1* in directed hyphal growth towards the host plant and/or the infection process upon detecting cues from the hosts. Fungi are constantly attuned to their surroundings, detecting various chemical and physical signals. In pathogenic fungi, the perception of these signals activates signal transduction pathways that regulate cellular processes essential for infection. Soil-dwelling fungal hyphae, in particular, exhibit a phenomenon known as chemotropism, where they respond directionally to plant root exudates and other compounds (Srivasta et al., 2024). Root exudates from the host and nonhost plants have different effects on spore germination among the FOSC members (Ren et al., 2016; Li et al., 2013). Turrà et al. (2015) proved that the chemotropism of *F. oxysporum* towards the host roots is activated by peroxidases, which involve a mitogen-activated protein kinase (MAPK) cascade and a sex pheromone receptor. The study demonstrated the repurposing of a pheromone receptor in asexual fungus to sense host signals, which aligned with the findings of this study. Reports have shown that *MAT1-1-1* modulates the expression of pheromone-associated genes (Zhang et al., 2024, Zheng et al., 2013). The spatiotemporal responsiveness of *MAT1-1-1* in this study could initiate transcriptional activation of genes in the pheromone pathway, allowing *Foc* TR4 to sense and move toward host signals. The transient nature of *MAT1-1-1* expression also aligns with its role as a transcriptional regulator.

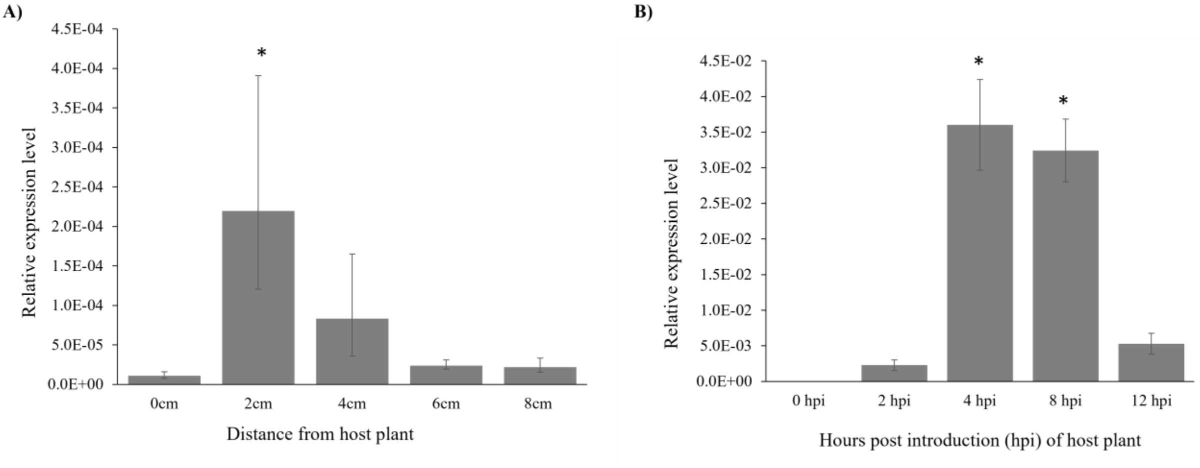


Figure 4: Relative expression ($2^{-\Delta\Delta C_t}$) of the *MAT1-1-1* gene at varying A) distances from the host plant and B) duration after contact with the host plant. Data analysis was conducted using a two-way ANOVA and Tukey's post-hoc tests. Bars denote mean expression levels (± standard error) for three biological replicates. Significant differences among groups are shown by asterisks ($p<0.05$).

CONCLUSION

This study identified and characterized the *MAT1-1* locus in *Foc* TR4, revealing the presence of the typical *MAT1-1* genes with conserved gene order and structural features, as reported in other *F. oxysporum* species. The amplified *MAT1-1-1* ORF in *Foc* TR4 matches the reference genome, encoding a 367 amino-acid protein with an alpha-box motif predicted to be localized to the nucleus. The phylogenetic analysis of the MAT1-1-1 protein clustered *Foc* TR4 with the other formae specialis within *F. oxysporum*. The gene expression data revealed that *MAT1-1-1* might play an essential role in the initial stages of banana-*Foc* TR4 interaction by responding to both spatial (proximity to the host) and temporal (early time points after contact) cues. Analysis of *MAT1-1-1* through targeted overexpression or deletion is essential to verify its predicted function and identify the downstream genes. These findings support the evidence that *MAT1-1-1*, as a transcriptional regulator, controls the expression of genes beyond its originally ascribed function in regulating mating-related pathways, in this case, enabling *Foc* TR4 to sense and respond to host-derived signals. Unraveling these mechanisms may pave the way for novel strategies to disrupt fungal virulence and improve disease management.

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CONFLICT OF INTEREST

The authors have declared that no conflict of interest exists.

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