Antagonistic yeasts can inhibit fungal growth. In our previous research, Meyerozyma guilliermondii, one of the antagonistic yeasts, exhibited antagonistic activity against Penicillium expansum. However, the mechanisms, especially the molecular mechanisms of inhibiting activity of M. guilliermondii, are not clear. In this study, the protein expression profile and transcriptome characterization of P. expansum induced by M. guilliermondii were investigated. In P. expansum induced by M. guilliermondii, 66 proteins were identified as differentially expressed, among them six proteins were upregulated and 60 proteins were downregulated, which were associated with oxidative phosphorylation, ATP synthesis, basal metabolism, and response regulation. Simultaneously, a transcriptomic approach based on RNA-Seq was applied to annotate the genome of P. expansum and then studied the changes of gene expression in P. expansum treated with M. guilliermondii. The results showed that differentially expressed genes such as HEAT, Phosphoesterase, Polyketide synthase, ATPase, and Ras-association were significantly downregulated, in contrast to Cytochromes P450, Phosphatidate cytidylyltransferase, and Glutathione S-transferase, which were significantly upregulated. Interestingly, the downregulated differentially expressed proteins and genes have a corresponding relationship; these results revealed that these proteins and genes were important in the growth of P. expansum treated with M. guilliermondii.

1. Introduction

Penicillium expansum is one of the most common pathogens in pears which cause blue mold decay and is able to secrete toxic secondary metabolite patulin (PAT), causing serious food safety problems and harming human health [1]. Recently, there are many strategies that have been employed to control the postharvest diseases of pears; among them chemical and physical methods are contribute the major part. However, both methods have some drawbacks. Therefore, safe and efficient antagonistic yeasts have been a research hotspot in the control of postharvest diseases of pear. Cryptococcus laurentii, Rhodotorula glutinis, Rhodotorula mucilaginosa, and Rhodotorula paludigenum [2–5] are some effective biocontrol agents against P. expansum in pears.

Meyerozyma guilliermondii was reported as an effective antagonistic yeast, which significantly controlled blue mold decay of pears [6] and controlled rice blast disease, cabbage black leaf spot disorder, and bacterial wilt caused by Ralstonia solanacearum, a tomato pathogen [7]. It also showed significant biocontrol of gray mold disease on table grapes caused by Botrytis cinerea [8] and reduced the severity of rot in mangoes during storage [9]. Our previous study showed that blue mold decay caused by P. expansum was significantly inhibited by M. guilliermondii without any change in the fruit quality [6]. The biocontrol efficacy increased with increasing yeast concentrations. M. guilliermondii colonized in pears rapidly and maintained relatively higher numbers to compete for nutrient and space with pathogen. M. guilliermondii also enhanced the defense to pathogens in pears [6]. The proteomics and transcriptomics analysis conducted in pears induced by M. guilliermondii revealed that M. guilliermondii could upregulate the expression of defense-related proteins and genes of pears [6, 10].
Several proteins intervene during the interaction of pathogens with antagonistic yeasts and many of them are crucial to explain the inhibition mechanism of antagonistic yeast. Our previous research reported that more than one-third of the proteins differentially expressed in Talaromyces rugulosus in response to Yarrowia lipolytica were associated with essential metabolism, like phosphoglycerate kinase, nucleoside diphosphate kinase, and so on, which showed that the mechanisms by which Y. lipolytica inhibited T. rugulosus involved in the essential metabolism [11]. In the same manner, a general analysis of transcriptome and proteome modification of P. expansum spores during germination was conducted by Zhou et al. using RNA-Seq and iTRAQ approaches. The corresponding result showed a statistic of 3026 genes and 489 proteins which were differentially expressed [12]. However, as far as we know, the molecular mechanism of M. guilliermondii against P. expansum has not been studied yet. In the present work, we explored the differentially expressed proteins and several defense-related genes of P. expansum cocultured with M. guilliermondii through proteomics and transcriptomics analysis and tried to establish the molecular mechanism of M. guilliermondii inhibiting the growth of P. expansum.

### 2. Materials and Methods

#### 2.1. Yeast

The antagonist yeast M. guilliermondii (preserved in the China Center for Type Culture Collection, No. M2017270) was isolated from unsprayed orchards. The yeast was cultured in nutrient yeast dextrose broth medium (NYDB, nutrient broth 8 g/L, yeast extract 5 g/L, and glucose 10 g/L) on an incubator shaker (180 rpm, 28°C) for 20 h. After incubation, yeast cells were collected by centrifugation (6918 × g for 10 min); the pellets were resuspended in sterile water and adjusted to 1 × 10⁷ cells/mL concentration with a hemocytometer.

#### 2.2. Pathogen

P. expansum was maintained on potato dextrose agar medium at 4°C. Before using, the P. expansum strain was inoculated in PDA plates and allowed to grow for seven days at 25°C in an incubator. After seven days, the spores were removed from the Petri dish and suspended in sterile distilled water. A hemocytometer was used to adjust spore concentrations to 1 × 10⁷ spores/mL.

#### 2.3. Analysis of the Differentially Expressed Proteins of P. expansum and P. expansum Incubated with M. guilliermondii

Initially, 1 mL of spore suspension (1 × 10⁷ spores/mL) of P. expansum was added to 100 mL of PDB inside 500 mL Erlenmeyer volumetric flasks and incubated for two days at 25°C, 120 rpm. Then, 1 mL suspension of M. guilliermondii at 1 × 10⁶ cells/mL was added. After 1 d incubation, the mycelia were collected and the protein was extracted according to the method described by Yang et al. [11].

2-DE and Image Analysis were conducted in accordance with the method delineated by Yang et al. and Zhang et al. with some modifications [11, 13, 14]. Isoelectric focusing was used to separate proteins in GE Ettan IPGphor 3, according to the manufacturer’s instructions [14].

#### 2.4. Transcriptomic Analysis of P. expansum and P. expansum Incubated with M. guilliermondii

RNA from the mycelia was extracted in accordance with the prescription of Sangon Co., Shanghai, China, with little modifications [14]. The concentration of RNA was detected by Qubit® RNA Assay Kit in Qubit® 2.0 Fluorometer (Life Technologies, Carlsbad, CA, USA). Nanodrop 2000 spectrophotometer (Thermo Scientific, Waltham, MA, USA) was used to determine the purity of RNA. RNA Nano 6000 Assay Kit of the Bioanalyzer 2100 system was used (Agilent Technologies, Santa Clara, CA, USA) to assess the integrity of the RNA. The samples that met the experimental requirements were used for the next steps [14].

#### 2.4.1. Transcriptome Analysis

Each RNA sample was used to perform RNA-Seq. RNA-Seq libraries were sequenced on an Illumina HiSeq 2500 platform to generate 125 bp/150 bp single-ended reads [14].

#### 2.4.2. Bioinformatics Analysis of RNA-Seq Data

Transcriptomic data were assembled, after high-quality sequencing data were acquired, using Trinity [14]. The UniGene sequences of P. expansum and P. expansum incubated with M. guilliermondii were searched using BLAST and compared with those obtained using the NR, Swiss-Prot, GO, and KEGG databases for the confirmation of amino acid sequence.

#### 2.5. Validation of RNA-Seq Data by RT-qPCR

RT-qPCR analysis was performed using RNA extracted from P. expansum and P. expansum incubated with M. guilliermondii, in order to validate the data obtained from RNA-Seq. The genes and their specific primers used for RT-qPCR were listed in Supplementary Table 1 and analysis was performed using a Bio-Rad CFX-96 Real-Time PCR System (Bio-Rad, USA). The reaction system that was conducted in accordance with the method delineated by Yang et al. [14] comprised of 12.5 μL SYBR® Premix Ex Taq™ II (2x); 0.5 μL...
50x Rox Reference Dye II; 1 μL Primer-F; 1 μL Primer-R; 2 μL cDNA; and 8 μL ddH₂O. The thermocycler conditions were set at an initial denaturation temperature of 95°C for 30 s, followed by 40 cycles of 95°C for 5 s and finally, one cycle of 60°C for 34 s and 72°C for 30 s. To normalize the gene expression level, Actin gene from P. expansum was used as an internal control. The RT-qPCR analysis was repeated three times with three technical replicates. The relative expression level of the sample gene was calculated using a 2^ΔΔCT method [10].

2.6. Statistical Analysis. The data were analyzed by analysis of variance (ANOVA) using the statistical program SPSS/PC version 8 (SPSS Inc., Chicago, Illinois, USA), and Duncan’s multiple range test was used for mean separation. The statistical significance was assessed at P < 0.05.

3. Results

3.1. Identification of Differentially Expressed Proteins of P. expansum. The whole protein expression of P. expansum and P. expansum treated with M. guilliermondii was shown in Figure 1. In each gel, a total of 66 differentially expressed (average fold change ≥ 2, p < 0.05) proteins were identified. Just 6 of them were significantly upregulated, while 60 proteins were significantly downregulated. Furthermore, 43 spots which showed the best resolution among the significantly differentially expressed proteins were analyzed for identification by mass spectrometry (MS). An elaborated report on lowercase letters about the names of peptides is in Table 1.

The basic information of 43 differentially expressed protein spots, comprising isoelectric point, molecular weight, and peptide matches, was assigned to a class. As reported in Table 1, several proteins were related to secondary metabolism synthesis, which included polyketide synthase (spot 20), enoylreductase (spot 32). Some proteins were associated with ATP synthesis, which included ATP hydrolase (ATPase), delta/epsilon subunit F1, N-terminal (spot 17), ATPase, F1 complex beta subunit/V1 complex, and C-terminal (spot 38). Some proteins were also associated with cellular basal metabolism, which included phosphoesterase (spot 36), glyceraldehyde/erythrose phosphate dehydrogenase family (spot 44), and phosphoglycerate kinase (spot 41) and some proteins were found to be associated with environmental immune response, which included heat shock 70 kDa protein (spot 24); these downregulated proteins were all associated with the basal metabolic process, response, and regulation of P. expansum. Gene ontology (GO) functional annotation examination was performed for the whole identified proteins, which exposed a broad number of molecular functions like biological processes and cellular components (Figure 2). The results indicated that the largest group of biological processes was metabolic process (25 proteins) and cellular process (25 proteins), and the other two biological processes were single-organism process (16 proteins) and biological regulation (7 proteins); these proteins were all related to the basal metabolic process. All identified proteins were annotated to categories. There were 98 and 90 proteins involved in cellular and biological processes as well as 56 proteins involved in molecular functioning, respectively. All the differentially expressed proteins were mainly involved in basic metabolism (30%), binding (23%), catalytic (21%), transporter (7%), and hypothetical (7%) processes (Figure 3).

3.2. Transcriptomic Analysis by RNA-Seq. The transcriptomes of P. expansum and P. expansum cocultured with M. guilliermondii were analyzed using RNA-Seq technology. The transcriptome data indicated a total number of 13 Gb clean data; the Q30 base percentage was 89.75% and 89.92% (Table 2). A total of 434 differentially expressed genes (DEGs) were compiled, among them 408 genes were upregulated and 26 genes were downregulated in the P. expansum treated with M. guilliermondii (|log2 (fold change)| ≥ 2, FDR < 0.05) (Table 3). Using gene ontology (GO), these DEGs were clustered by gene function (Figure 4).

The cellular components and molecular functions were further analyzed, each contained 19 subgroups and the biological processes contained 22 subgroups. The main categories concerning cellular component contained cell (23.9%), cell part (23.9%), organelle (13.9%), and membrane (13.4%). The highest percentage of identified differentially expressed genes under molecular function category included catalytic activity (46.1%) and binding (38.5%), whereas the percentage in the biological process category was as follows: basic metabolism (21.0%), cellular process (20.2%), single-organism process (19.0%), and biological regulation (18.5%). The most enriched KEGG pathway of P. expansum transcriptome analysis was shown in Figure 5. There were four pathways including cellular processes, environmental information processing, genetic information processing, and metabolism. In the cellular processes, there were 5 DEGs in cell growth and death, 16 DEGs in transport and catabolism. In the environmental information processing, there were 22 DEGs in folding, sorting, and degradation, 6 DEGs in transcription, and 6 DEGs in translation. In metabolism, the highest pathway is carbohydrate metabolism (32.14%), energy metabolism (17.26%), amino acid metabolism (16.07%), and lipid metabolism (14.28%).

3.3. Validation of RNA-Seq Data by RT-qPCR. The genes identified as key DEGs of P. expansum, due to M. guilliermondii coculturing, which are involved in basal metabolism were evaluated by real-time-quantitative polymerase chain reaction (RT-qPCR) (Table 4, Figure 6). From the result of RNA-Seq (Figure 6), the expression levels of TRINITY_DN7572_c0_g2 (Phosphoesterase), TRINITY_DN10607_c0_g1 (Polyketide synthase, enoylreductase), TRINITY_DN3524_c0_g2 (ATPase, F0/V0 complex, subunit C), TRINITY_DN7527_c0_g1 (ATPase, F1/A1 complex, alpha subunit, N-terminal), TRINITY_DN5224_c0_g4 (HEAT, type 2) were significantly different. Expression levels of these five genes were significantly decreased, which were 0.53, 0.21, 0.44, 0.41, and 0.32 times lower than those in control group, respectively. The results of RT-qPCR were consistent with the gene expression results of RNA-Seq.
Table 1: Identification of differentially expressed proteins in *P. expansum* after different treatments.

| Protein spot | Protein name | NCBI accession | Mass | PI  | Species | Score |
|--------------|--------------|----------------|------|-----|---------|-------|
| 1            | Hypothetical protein PDIG_00280 | gi|425781927 | 10361 | 5.28 | Penicillium digitatum | 397 |
| 2            | Thioredoxin | gi|700488450 | 11987 | 5.12 | Penicillium expansum | 79 |
| 3            | 40S ribosomal protein S21 | gi|584409470 | 10008 | 7.77 | Penicillium roqueforti | 162 |
| 4            | Profiling | gi|768690728 | 13945 | 4.63 | Penicillium solitum | 96 |
| 5            | Pc21g11730 | gi|255954903 | 13188 | 5.59 | Penicillium rubens Wisconsin | 148 |
| 6            | UBI 3 fusion protein (149 AA) | gi|3086 | 18932 | 9.82 | Neurospora crassa | 86 |
| 7            | Cyclophilin-type peptidyl-prolyl cis-trans isomerase Redoxin | gi|700446168 | 43688 | 5.57 | Penicillium expansum | 222 |
| 8            | Elongation factor 1 beta central acidic region, eukaryote Nascent polypeptide-associated complex (NAC) subunit, putative | gi|700447727 | 28161 | 8.91 | Penicillium expansum | 115 |
| 9            | ATPase, F1 complex, delta/epsilon subunit, N-terminal | gi|700458248 | 18736 | 8.69 | Penicillium rubens Wisconsin | 166 |
| 10           | Chaperonin Cpn60 | gi|700452244 | 15646 | 4.92 | Penicillium expansum | 124 |
| 11           | Glucose/ribitol dehydrogenase | gi|700452783 | 28635 | 6.97 | Penicillium expansum | 171 |
| 12           | Ketose-bisphosphate aldolase, class-II | gi|700453533 | 39308 | 4.91 | Penicillium expansum | 116 |
| 13           | Polyketide synthase, enoylreductase | gi|700457792 | 37941 | 5.6 | Penicillium expansum | 390 |
| 14           | Enolase BAC82549-Penicillium chrysogenum | gi|255938796 | 47250 | 5.26 | Penicillium expansum | 316 |
| 15           | Chaperone DnaK | gi|700454561 | 61890 | 5.61 | Penicillium expansum | 313 |
| 16           | Glutamate carboxypeptidase, putative | gi|700452783 | 50668 | 5.18 | Penicillium expansum | 356 |
| 17           | Phosphoesterase | gi|700454353 | 39308 | 4.91 | Penicillium expansum | 356 |
| 18           | ATPase, F1 complex beta subunit/V1 complex, C-terminal | gi|700456999 | 55307 | 5.34 | Penicillium expansum | 356 |
| 19           | Hypothetical protein PDIG_75600 | gi|255948526 | 67030 | 5.32 | Penicillium expansum | 221 |
| 20           | Protein disulfide isomerase | gi|700453960 | 37941 | 5.6 | Penicillium rubens | 420 |
| 21           | Phosphoglycerate kinase | gi|417486 | 44103 | 6.07 | Penicillium citrinum | 96 |
| 22           | Lithostathine precursor | gi|45430003 | 19720 | 5.75 | Bos taurus | 222 |
| 23           | Glyceroldehyde/erythrose phosphate dehydrogenase family | gi|70047332 | 36225 | 6.01 | Penicillium expansum | 126 |
| 24           | Nucleoside diphosphate kinase | gi|425772472 | 16737 | 7.77 | Penicillium digitatum | 259 |
| 25           | FK506-binding protein | gi|584415065 | 13203 | 6.41 | Penicillium roqueforti | 328 |

Figure 1: 2-D gels of differentially expressed proteins of *P. expansum* treated with sterile distilled water and *M. guilliermondii*. (a) *P. expansum* protein expressed after treatment with sterile distilled water. (b) *P. expansum* protein expressed after treatment with *M. guilliermondii*. 
4. Discussion

Blue mold decay caused by *P. expansum* is a serious disease in fruit, in particular pear fruits [6]. Recently, some pathogenic strains developed resistance against synthetic fungicides; therefore, researchers concern about environmental and food safety. Antagonistic yeasts are gaining considerable attention due to their beneficial environmental and food safety characteristics and also controlling postharvest diseases in fruits. Integrating transcriptomic and proteomic data to achieve meaningful insights into *P. expansum* inhibited by *M. guilliermondii* has rarely been reported. Therefore, the present work highlights the protein expression profile and transcriptomic changes of *P. expansum* in order to explore the molecular inhibitory mechanism of *M. guilliermondii*. GO categorization was compared between differentially expressed proteins from 2-DE and differentially expressed genes from RNA-Seq analysis. A majority of differentially expressed proteins and genes were involved in secondary metabolite synthesis, ATP synthesis, cellular basal metabolism, environmental immune response, genetic information processing, and metabolism.

| Protein spot | Protein name | NCBI accession | Mass | PI  | Species         | Score |
|--------------|--------------|----------------|------|-----|-----------------|-------|
| ↑48          | Pc16g13060   | gi|255941672 | 18109 | 6.91 | *Penicillium rubens* Wisconsin | 256   |
| ↑49          | Pc21g22820   | gi|255956993 | 37501 | 8.07 | *Penicillium rubens* Wisconsin | 215   |
| ↓51          | Thiamine pyrophosphate enzyme, C-terminal TPP-binding | gi|700446530 | 63440 | 5.69 | *Penicillium expansum* | 185   |
| ↓52          | Proteasome subunit alpha type 3 | gi|70991357 | 29766 | 5.19 | *Aspergillus fumigatus* | 82    |
| ↓53          | 2-Phosphoglycerate dehydratase Flagellin | gi|74662366 | 47264 | 5.14 | *Penicillium chrysogenum* | 246   |
| ↓54          |              | gi|736787790 | 38621 | 5.09 | *Ewingella americana* | 229   |
| ↓60          | Pc22g17950   | gi|255949874 | 36031 | 9.47 | *Penicillium rubens* Wisconsin | 75    |
| ↓61          | Nucleic acid-binding, OB-fold | gi|700454689 | 58601 | 6.54 | *Penicillium expansum* | 70    |
| ↓62          | Phosphoglycerate kinase | gi|417486 | 44103 | 6.07 | *Penicillium citrinum* | 177   |

Figure 2: GO categorization of differentially expressed proteins in *P. expansum* after different treatments. The proteins were categorized according to the annotation of GO, and the number of each category is displayed based on biological process, molecular functions, and cellular components.
There are many enzymes responsible for synthesis of ATP; ATPase was considered as the most important enzyme in ATP synthesis. In the current investigation, protein ATPase, F1 complex (spots 17 and 38) corresponding with ATPase, F0/V0 complex, subunit C and ATPase, F1/A1 complex, alpha subunit, N-terminal, were all downregulated. Similar trend was observed in transcriptomic analysis; the gene corresponding to ATPase, F0/V0 complex, subunit C (TRINITY_DN3524_c0_g2, TRINITY_DN7527_c0_g1) was downregulated significantly. Yang et al. reported that the poplar buds active fraction (PBAF) depresses ATPase activity of Penicillium italicum and explained that the inhibitory effect of PBAF on fungal growth is due to the inhibition of ATPase by PBAF [16]. Castellote et al. investigated the molecular expression of Geotrichum candidum overripening of Reblochon-type cheese and observed that the genes responsible for F1F0 ATP synthase subunits (ATP1, ATP2, ATP5, and ATP7) were quiescent which leads to the reduced ATP production and consumption, normally less energy needed for quiescent cells [17]. From these reports, we anticipated that ATPase did not only provide energy for the basic metabolism of P. expansum, but also was the main carrier for the life activities of P. expansum. In the present investigation, the ATP activity of P. expansum treated with M. guilliermondii was reduced; thus, the energy supply was prevented and the growth was inhibited.

Heat shock protein 70 (HSP70) was a main part of the cell’s machinery for protein folding and contributed to protection of cells against stress [18, 19]. In addition to the involvement of HSP70 in maintaining and improving the protein integrity, it directly inhibits apoptosis [20]. In our results, the heat shock 70 kDa protein (point 24) corresponded with the transcriptome genes Heat, type 2 (TRINITY_DN5224_c0_g4), and both were downregulated. The intracellular heat shock protein and gene expression of P. expansum was downregulated because of the effect of M. guilliermondii. Zhang et al. studied the underlying molecular mechanisms of HSP70 in the environmental stress response of coral through transcriptome expression and reported that HSP70 (PdHSP70) was an essential stress regulatory protein in the stony coral Pocillopora damicornis; therefore, diverse environmental stress could induce HSP70 mRNA expression and its activity could remain stable under heat stress [21]. Kim et al. identified 10 Calmodulin (CaM)-binding protein in Beauveria bassiana; one of its targets was HSP70 and their results also suggested that ATP was involved in the inhibition of molecular interaction between CaM and HSP70 [22]. From the earlier studies, it was evidenced that downregulation of HSP70 weakens the adaptation ability and immune response of P. expansum to the external environment; the cells were apoptotic and the growth of P. expansum was inhibited by M. guilliermondii.

In biological systems, phosphoesterase plays a vital role in DNA fragmentation, RNA replication, human body medicine, metabolism, chemotherapy, and bioremediation [23, 24]. In the present results, the phosphoesterase protein (point 36) that corresponded with the transcriptome genes phosphoesterase (TRINITY_DN431_c0_g2) was downregulated. It could be speculated that the phosphatase activity of P. expansum was reduced and substance metabolism process was blocked due to the effect of M. guilliermondii, which resulted in shortage of phosphate needed for the survival of P. expansum and thus the normal life activity of P. expansum was inhibited by M. guilliermondii.

Polyketide synthases (PKSs) belong to a multidomain-enzyme or complex-enzyme family which are responsible for the production of polyketides, a major class of secondary metabolites, in microorganisms, plants, and some animal lineages [25, 26]. Polyketide synthases also play a definite role in the production of naturally occurring small molecules employed in chemotherapy [27]; many of the commonly used antibiotics and other industrially important polyketides were produced by polyketide synthases [28]. Our results demonstrated that the polyketide synthase, enoylreductase protein (point 20 and point 32), was downregulated. RNA-Seq analysis also showed that the gene responsible for polyketide synthases (TRINITY_DN10607_c0_g1) was downregulated significantly. Moreover, in P. expansum, the polyketide synthases are involved in the synthesis of patulin, a hazardous mycotoxin derived from polyketides [29]. Role of patulin in the pathogenicity and virulence of P. expansum was already proved in postharvest apples infected by P. expansum [30]. Patulin synthesis in P. expansum is carried out by a biosynthetic gene cluster consisted of 15 genes (PatA-PatO) in ten different enzymatic reactions [31]. Among them, the initial seven reactions in patulin synthesis are catalyzed by polyketide synthases [32]. Therefore, our...
results may confirm that the polyketide synthase activity of *P. expansum* was reduced due to the inhibition of *M. guilliermondii*; thus the normal synthesis of patulin and other secondary metabolites of *P. expansum* was prevented. Likewise, Ras-association gene (TRINITY_DN6243_c0_g3) was also downregulated in *P. expansum* treated with *M. guilliermondii*. In most of the pathogenic fungi, Ras pathway signaling is determined as critical virulence factor [33]. The Ras pathway signaling is involved in pathogenesis, morphological transitions, nutrient sensing and acquisition, sexual reproduction, and stress responses of fungi [34]. The results also evidenced that the pathogenicity and virulence of *P. expansum* was weakened, and its growth was eventually inhibited by *M. guilliermondii*.

Phosphatidate cytidylyltransferase is an enzyme, involved in lipid transport and metabolism, that majorly takes part in the phospholipid metabolism in cell membranes. Lipids are essential components in membrane trafficking, cytoskeletal rearrangement, and secretion, which are reported to be the important mechanisms of stress tolerance [35]. In the present transcriptomic analysis, the gene responsible for phosphatidate cytidylyltransferase (TRINITY_DN3203_c0_g2) was upregulated in *P. expansum*. Bernardo et al. reported the upregulation and accumulation of phosphatidate cytidyltransferase during drought stress in the roots of wheat [36]. Other than stress tolerance, phosphatidate cytidylyltransferase was also known for its role in antibiotic resistance mechanism against antimalarial lipopeptides [37]. It was evidenced that in order to overcome the stress created by *M. guilliermondii* and to resist the activity of the yeast, the phosphatidate cytidylyltransferase gene was upregulated in *P. expansum*. In the same way, the upregulation of striatin, N-terminal (TRINITY_DN6439_c0_g1) was observed in the transcriptomic analysis. Striatin orthologs were directly related to the virulence of some filamentous fungi like *Fusarium verticillioides* and *F. graminearum* against plants [38]. Hence, we hypothesized that though some pathogenic related factors were inhibited by *M. guilliermondii*, some other genes related to stress tolerance and virulence were upregulated.

To sustain cellular redox homeostasis, the thioredoxin system assures a crucial function and the thioredoxin protein (point 2) was downregulated in the present study. Viefhues et al. indicated that thioredoxin had a strict influence on virulence of *Botrytis cinerea*, proving that redox processes were determinant for host-pathogen interactions in this pathogen; in addition, the balanced redox status established by the thioredoxin system was vital for growth and pathogenesis of *B. cinerea* [39]. Ianiiri et al. investigated the modification of gene expression in *Sporobolomyces* sp. under patulin exposition; they noted the major increase in transcript levels of antioxidant molecules glutathione and thioredoxin in *Sporobolomyces* genes. The research team further subclassified the metabolic process of patulin exposed group and found that 6 DEGs were involved in glutathione biosynthesis, and 3 DEGs were involved in the thioredoxin system [40]. In contrast, by downregulation in the present study, we speculated that the thioredoxin system, which is involved in the defense response to ROS, was inhibited by *M. guilliermondii* and the growth of *P. expansum* was controlled.

| Samples | JSHY-ID | Read number | Base number | GC content (%) | %≥Q30 |
|---------|---------|-------------|-------------|----------------|-------|
| CK      | T01     | 23336546    | 7000963800  | 54.33          | 89.75 |
| Y       | T02     | 20001194    | 6000358200  | 53.89          | 89.92 |

**Table 2:** Transcriptome sequencing data of *P. expansum* treated with *M. guilliermondii* (Y) and *P. expansum* (CK).

| DEG set | DEG number | Upregulated | Downregulated |
|---------|------------|-------------|---------------|
| CK vs. Y | 434        | 408         | 26            |

**Table 3:** The number of differentially expressed genes of *P. expansum* treated with *M. guilliermondii* (Y) and *P. expansum* (CK).
### Table 1: GO and KEGG Categorization of Differentially Expressed Genes in *P. expansum*

| GO Classification                  | Number of Genes |
|------------------------------------|-----------------|
| Cellular component                 |                 |
| Cell part                          | 14030           |
| Organelle part                     | 140            |
| Extracellular matrix               | 14             |
| Cell junction                      | 3               |
| Cellular component organization or biogenesis | 35   |
| Molecular function                 |                 |
| Nucleic acid binding transcription factor activity | 100  |
| Structural molecule activity       | 358            |
| Transporter activity               | 35             |
| Electron carrier activity          | 3               |
| Guanyl-nucleotide exchange activity | 1              |
| Channel regulatory activity        | 1              |
| Guanyl-nucleotide exchange activity | 1              |
| Channel regulatory activity        | 1              |
| Metabolic process                  |                 |
| Carbohydrate metabolism            | 54 (32.14%)    |
| Energy metabolism                  | 29             |
| Amino acid metabolism              | 27             |
| Metabolism of cofactors and vitamins | 24            |
| Metabolism of other amino acids    | 14             |
| Metabolism of terpenoids and polyketides | 1           |
| Nucleotide metabolism              | 9              |
| Genetic information processing     |                 |
| Amino acid metabolism              | 27             |
| Metabolism of terpenoids and polyketides | 1           |
| Metabolism of cofactors and vitamins | 24            |
| Metabolism of other amino acids    | 14             |
| Metabolism of terpenoids and polyketides | 1           |
| Nucleotide metabolism              | 9              |
| Environmental information processing |            |
| Metabolism of terpenoids and polyketides | 1           |
| Metabolism of cofactors and vitamins | 24            |
| Metabolism of other amino acids    | 14             |
| Metabolism of terpenoids and polyketides | 1           |
| Nucleotide metabolism              | 9              |

### Figure 4: GO Categorization of Differentially Expressed Genes in *P. expansum*.

### Figure 5: KEGG Categorization of Differentially Expressed Genes in *P. expansum*.
was upregulated. Ouyang et al. showed that citral possibly triggered a reduction in the mitochondrial membrane potential (MMP), intracellular ATP, and glutathione content, in contrast to an increase in the glutathione S-transferase activity and the accumulation of reactive oxygen species (ROS); these results indicated that the addition of citral probably leads to the oxidative damage of *Penicillium digitatum* and inhibited the growth of *P. digitatum* [50]. Hence, from the upregulation of GST, it could be postulated that the GST activity was activated in order to overcome the increased ROS in the presence of *M. guilliermondii*. The results also evidenced that *M. guilliermondii* created oxidative stress against *P. expansum*; hence, the level of GST (antioxidative enzyme) was increased. Overall, we have hypothesized that though some stress tolerance mechanism of *P. expansum* was activated, *M. guilliermondii* inhibit the growth and pathogenesis of *P. expansum* by downregulating certain pathways of virulence mechanism, cellular signal transduction, mycotoxin production, and cell organization.

On the other hand, the biocontrol efficacy of *M. guilliermondii* and pathogenic ability of *P. expansum* might be altered under availability of different nutritional sources

**Table 4:** Differentially expressed genes of *P. expansum* treated with *M. guilliermondii* (Y) and *P. expansum* (CK). FDR < 0.05 and log₂ fold change ≥ 2 were considered statistically significant.

| Functional classification                                                                 | Gene ID                  | Gene annotation                          | Fold change | FDR       |
|-------------------------------------------------------------------------------------------|--------------------------|------------------------------------------|-------------|-----------|
| Secondary metabolites biosynthesis, transport, and catabolism                             | TRINITY_DN10607_c0_g1    | Polyketide synthase                      | -9.638      | 0.0144304 |
| ATP hydrolysis coupled proton transport                                                  | TRINITY_DN3524_c0_g2     | ATPase, F0/V0 complex, subunit C         | -9.654      | 0.0498454 |
| ATP hydrolysis coupled proton transport                                                  | TRINITY_DN7527_c0_g1     | ATPase, F1/A1 complex, alpha subunit, N-terminal | -9.882      | 0.0450140 |
| Signal transduction mechanisms                                                           | TRINITY_DN6243_c0_g3     | Ras-association                          | -10.069     | 0.0414577 |
| Cell wall/membrane/envelope biogenesis                                                  | TRINITY_DN431_c0_g2      | Phosphoesterase                          | -10.667     | 0.0296615 |
| Cell organelle organization                                                             | TRINITY_DN5224_c0_g4     | HEAT, type 2                             | -10.048     | 0.0415417 |
| Ascospore formation                                                                      | TRINITY_DN6439_c0_g1     | Striatin, N-terminal                      | 12.128      | 0.0144304 |
| Lipid transport and metabolism                                                          | TRINITY_DN3203_c0_g2     | Phosphatidate cytidylyltransferase       | 10.235      | 0.0381777 |
| Secondary metabolites biosynthesis, transport, and catabolism                           | TRINITY_DN5730_c0_g1     | Cytochrome P450, E-class, group          | 13.040      | 0.0138044 |
| Posttranslational modification, protein turnover, chaperones                             | TRINITY_DN8139_c0_g1     | Glutathione S-transferase/chloride channel, C-terminal | 11.707      | 0.0138044 |

**Figure 6:** Verification of differentially expressed genes by RT-qPCR. Treatments: CK: *P. expansum* treated with sterile distilled water, Y: *P. expansum* treated with *M. guilliermondii*. Values are means of two independent experiments. Error bars represent the standard error of the mean. (a) Phosphoesterase. (b) Polyketide synthase, enoylreductase. (c) ATPase, F0/V0 complex, subunit C. (d) ATPase, F1/V1 complex, alpha subunit, N-terminal. (e) HEAT, type 2.
such as carbon (C), nitrogen (N), and environmental factors such as pH value, temperature, and water activity. Jianjie et al. studied the effect of nutrition and environmental factors on the biocontrol potential of *Esteya vermicola* and reported that both of them have great influence on the biocontrol potential [51]. Similarly, the growth and myco-toxin producing ability of *P. expansum* was altered by different glucose-containing sugars, complex N sources, and acidic conditions were favorable conditions for patulin production [52]. Since the stress tolerance of *M. guilliermondii* in extreme salinity stress was proved already [53], we speculated that the antagonistic potential of *M. guilliermondii* might be worthy in a diverse range of nutritional supplements and environmental factors. However, in the future prospect, the effect of various nutritional sources and environmental factors in the biocontrol mechanism of *M. guilliermondii* are needed to be studied.

In conclusion, several genes, such as HEAT, Phosphoesterase, Polyketide synthase, and ATPase, disclosed a corresponding relationship between the transcript and protein levels and revealed that those genes could play an important role in the growth regulation of *P. expansum*. Moreover, the data from transcriptomic and proteomic analysis discussed in the present study have not only underlined a set of genes and proteins that were essential in the growth of *P. expansum*, but also gave fundamental knowledge of molecular mechanism behind the inhibitory activity of *M. guilliermondii* against the growth of mold.

**Data Availability**

The data used to support the findings of this study are included within the article.

**Conflicts of Interest**

The authors have no conflicts of interest to declare.

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**Supplementary Materials**

Supplementary Table 1: primer design of basal metabolism and response regulation genes in *P. expansum*. (*Supplementary Materials*)

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