agriculture

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Co-Cultivation of *Schizosaccharomyces japonicus* and *Fusarium graminearum* Reveals the Biocontrol Effect of Yeast and Its Potential Genes for Detoxification

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Abstract

Fusarium graminaerum causes *Fusarium* Head Blight (FHB) on wheat, reduces yield, and contaminates food and feed. It is therefore of paramount importance to control its growth or convert its harmful mycotoxins. This study aimed to find yeasts with biocontrol activity against *F. graminearum*, and to identify genes with potential detoxifying activities, using microbiological, molecular methods and bioinformatics. Co-cultivation tests showed that *Schizosaccharomyces japonicus* was able to inhibit the growth of *F. graminearum*. Transcriptomic analysis of the yeast cells co-cultured with *F. graminearum* highlighted differentially expressed genes (DEGs) encoding various enzymes, such as oxidoreductases, transferases, hydrolases, or genes involved in transmembrane transport. Three *trichothecene-3-O-acetyltransferase* homologous genes, which can convert trichothecenes to less toxic forms, were also among them. A database search showed that several yeast species contained this gene, including *S. japonicus*, which unexpectedly had seven copies. Real-time PCR analysis and mycotoxin tolerance tests confirmed that some of these genes could be induced by deoxynivalenol (DON), and *S. japonicus* had stronger DON tolerance than the related *S. pombe*, whose genome did not contain such a gene. This study is the first to report the biocontrol efficacy of *S. japonicus* against *F. graminearum* and the identification of its potential detoxification genes, offering promising new avenues for biotechnological applications in food safety.

Keywords: *Fusarium graminearum*; *Schizosaccharomyces japonicus*; mycotoxin; biological control; biotransformation; detoxification genes; biosecurity; crop protection

Received: 10 January 2026
Revised: 15 February 2026
Accepted: 19 February 2026
Published: 24 February 2026

https://doi.org/10.3390/agriculture16050494

1. Introduction

The plant pathogenic fungus *F. graminearum*, the main causal agent of *Fusarium* Head Blight (FHB), which causes bleached spikelets, is spread worldwide and reduces yields in most countries [1–3]. In addition, it often produces mycotoxins such as trichothecenes and zearalenone (ZEA), depending on the environmental conditions [4–8], which can enter the food chain through food and feed contamination [3,9,10]. Previous studies have shown that these mycotoxins have several negative effects on cells, such as inhibiting protein and DNA synthesis [11,12]. Trichothecenes can alter the membrane structure or cell division of infected cells [13] or induce apoptosis (programmed cell death) [14–16]. Deoxynivalenol (DON), also known as a vomitoxin, can activate neurons [17] and disrupt important signaling pathways and reactive oxygen species (ROS) production, thereby turning important biological functions on or off [18]. It has been shown that ZEA is hepatotoxic and immunotoxic; furthermore, it has estrogenic and carcinogenic effects in animals [11]. These phenotypic changes may be the result of altered gene functions, as mycotoxins can affect the expression of various genes, e.g., MAPK-pathway genes [19], and membrane-associated [20], immune [21], or cancer-promoting genes [16].

Because of these adverse effects, various agricultural practices have been developed to ensure food safety, including the use of resistant crop varieties, burial of crop residues, crop rotation, proper harvesting procedures, well-adjusted combine harvesters, appropriate soil management, and chemical control. However, since these approaches have not produced fully satisfactory results, alternative strategies—such as biological control—have also been investigated [8,10,22]. Biological control is an alternative form of defense where the ability of microorganisms to inhibit the growth of other microbes is exploited [23–27]. This process includes competition for nutrients or the production of metabolites and volatile compounds [22,28], resulting in a reduction in the number of harmful microorganisms.

In addition to inhibiting the growth of moulds, the removal or transformation of mycotoxins is another possible way to ensure food safety when food and feed are contaminated. Physical, chemical, and biological methods can be used for mycotoxin reduction [29]. In the latter case, microbes are used, as there are some, such as yeasts, whose cell walls can bind mycotoxins and thus reduce their concentration [30–33]. Other microbes can produce enzymes that convert mycotoxins into less toxic forms [33–36]. *Bacillus*, *Lactobacillus*, or *Saccharomyces* strains, for example, can be used to detoxify ZEA [37]. *Sphingopyxis* species can produce fumonisin B-degrading enzymes, while *Sphingomonas* species may be good for degrading trichothecenes [29]. The trichotechene-3-*O*-acetyltransferases can modify DON and reduce its toxicity [38], while the *Trichomonascus* clade is capable of bioconversion of T2 toxins [39]. These types of microbes can be suitable for post-harvest detoxification, as has been shown in small-scale silage fermentations [40]. In addition to using the microorganisms themselves for detoxification, their genes can also be exploited. If a microorganism produces enzymes suitable for detoxification, the corresponding enzyme-encoding genes (once identified) can be cloned and introduced into a host cell to enable the production of recombinant enzymes. Examples include chitinase from *Metschnikowia fructicola* [41] and peroxidase from *Bacillus subtilis* [42,43]. These results have also led to the development of commercially available biotransforming feed additives, such as FUMzyme and Biomin Mycofix [29].

As the control of Fusaria is still a challenge and different agricultural strategies have little effect on their infectivity, our primary goal was to find a potential yeast species with antagonistic (growth-inhibitory) ability against *F. graminearum*. We were also interested in the transcriptomic changes caused by *Fusarium* in yeast cells, as the latter data could lead to the identification of genes encoding enzymes involved in the detoxification and biotransformation of mycotoxins. Since *S. japonicus* was isolated from soil [44], it was hypothesized that this yeast may have encountered soilborne pathogenic fungi, including *F. graminearum*, and therefore, this yeast species may have a higher tolerance and/or inhibitory effect against *Fusarium*. To test this hypothesis, we used molecular and in silico approaches to investigate *S. japonicus* and *F. graminearum* co-cultures.

2. Materials and Methods

2.1. Strains and Media

S. japonicus var. *japonicus* (7-1) (CCY-44-5-1, CBS354, ATCC 10660) (hereafter referred to as *S. japonicus*) and *F. graminearum* (FGSC9075) strains were used in this study. The strains were purchased from the American Type Culture Collection (ATCC, Manassas, VA, USA) and the Fungal Genetic Stock Center (FGSC, Manhattan, KS, USA), respectively. *S. japonicus* var. *japonicus* was isolated by Yukawa and Maki [45], while the depositor of *F. graminearum* was F. Trail [46].

YEA (2% glucose (J0188), 1% yeast extract (J850), 2% agar (J637); VWR, Radnor, PA, USA), and YEL (YEA without agar) were used as standard culture media. MXGB (malt extract, glucose, and agar (Oxoid, Basingstoke, UK) medium [47] were used for the *F. graminearum* yeast co-cultures. PDA (Potato Dextrose Agar; 01-483-500; Scharlau, Barcelona, Spain) and the PDB (Potato Dextrose liquid; 02-483-500; Scharlau, Barcelona, Spain), as well as YEA, YEL, and MXGB, were used in the antagonistic tests.

2.2. Test of Growth Inhibition

The growth inhibitory capacity of yeast cells was tested on solid PDA medium. *F. graminaerum* mycelium (4-day-old, 5 × 5 mm cube of mycelium prepared with a sterile spatula) was inoculated into 2 mL sterile water. After vigorous vortexing, 20 µL of the suspension was dropped onto the surface of agar plates (PDA) in the center and incubated at 25 °C. After 1 day, *S. japonicus* cells were streaked around *Fusarium* (2.5 cm from the center). The Petri dishes were incubated at 25 °C for 6 days, and the growth of *F. graminearum* was monitored [48].

Growth inhibition was also tested in liquid media (PDB, MXGB, YEL). A total of 200 mL of culture medium was inoculated with a cube of *Fusarium* hyphae (5 × 5 mm). 500 µL *S. japonicus* cell suspension prepared in sterile Milli-Q water (OD_{595}: 0.2, 5×10^6 cells/mL) was added to the cultures [48]. The Erlenmeyer flasks were incubated at room temperature without shaking for 5 days. The growth of *S. japonicus* and *F. graminearum* was monitored, and their wet weight was measured after filtration of *Fusarium* hyphae through Miracloth (Merck, Darmstadt, Germany) and centrifugation of yeast cells. The data are the means of three separate experiments. Within an experiment, the experimental conditions and culture media were identical for the co-culture and monoculture.

2.3. Preparation of Yeast-Fusarium Co-Cultures

F. graminearum cells were cultured in 100 mL MXGB medium for 3 days at room temperature. Hyphal cubes measuring 5 × 5 mm were removed and transferred into 50 mL of fresh MXGB. A volume of 100 µL *S. japonicus* cells from an overnight MXGB preculture was added to the hyphae, and the co-cultures were incubated at 25 °C without shaking. After 2 days, the *Fusarium* hyphae were removed, while the yeast cells (settled on the bottom of the flask) were harvested by centrifugation and used for RNA extraction. The cultures were made in triplicate.

2.4. Analysis of the Supernatants of Co-Cultures

Since yeast cells can produce ethanol, which can have a growth-inhibitory effect, the volatile organic compounds were also measured. The culture supernatants were filtered through pleated filter paper (Ahlstrom-Munksjö, Helsinki, Finland; Grade 292) and with a Spartan 30 mm syringe filter (GE Healthcare Life Sciences, Little Chalfont, UK) (regenerated cellulose, 0.45 μm). A volume of 1 μL was injected into a Varian CP 3800GC gas chromatograph (Varian Inc, Walnut Creek, CA, USA) loaded with Varian CP-Wax 52 CB, 30 m × 0.25 mm ID; 0.25 μm, Colonna and Flame Ionization Detector at 230 °C. The carrier gas was 1.0 mL/min helium in constant flow; the injector set was 230 °C with a 1:30 split. The schedule: 30 °C (3.0 min), 100 °C/min, 80 °C (hold: 1.0 min); methyl acetate, ethyl acetate, methanol, ethanol, and *n*-propanol. LOD (limit of detection) was 0.005 (*v*/*v*)% [48].

2.5. Growth of F. graminearum in the Presence of Ethanol

Since analysis of the supernatant showed that *S. japonicus* produced ethanol, we aimed to determine whether the ethanol produced would inhibit the growth of *F. graminearum*, as has been observed for *Fusarium oxysporum* and *Aspergillus flavus* [49,50]. Therefore, a 5 × 5 mm cube of 4-day-old *Fusarium graminearum* hyphae was inoculated in 2 mL of sterile water. After vigorous vortexing, 100 μL of the suspension was inoculated into 5 mL MXGB; MXGB was supplemented with 0.5, 1, 1.5, and 2% (*v*/*v*) ethanol. The Falcon tubes (15 mL) were incubated at 25 °C without shaking. *Fusarium* hyphae were collected after 5 days, and their wet weight was measured. The cultures were made in triplicate.

2.6. RNA Isolation and Sequencing

The co-cultured yeast cells were harvested, and their RNA contents were extracted according to the Lyne method [51], sent for RNA sequencing, and used for RT-PCR validation. The quantity and quality of the total RNA samples were checked on the Agilent BioAnalyzer using the Eukaryotic Total RNA Nano Kit, according to the manufacturer's protocol (Agilent Technologies, Santa Clara, CA, USA). Samples with RNA integrity number (RIN) value ≥ 7 were used for library preparation. RNA sequencing libraries were prepared from 500 ng total RNA using the Ultra II RNA Sample Prep kit (New England BioLabs, Ipswich, MA, USA) according to the manufacturer's protocol. Briefly, poly-A RNAs were captured by oligo-dT-conjugated magnetic beads, then the mRNAs were eluted and fragmented at 94 °C. The first strand cDNA was generated by random priming reverse transcription, and after the synthesis of the second strand, double-stranded cDNA was generated. After repairing ends, A-tailing, and adapter ligation steps, the adapter-ligated fragments were amplified in enrichment PCR, and sequencing libraries were finally generated. Sequencing runs were performed on the Illumina NextSeq 500 instrument (Illumina, San Diego, CA, USA) using single-end 75-cycle sequencing. A total of 18–20 million passing filter reads were generated per sample, with Q30 > 95% basecalling accuracy [52].

Raw sequencing reads were aligned to the *S. japonicus* reference genome [SJ5-GCF_000149845.2] using the HISAT2 aligner (ver. 2.2.1) with default parameters. The resulting alignment files were processed and assigned to genomic features using featureCounts (ver. 2.1.1), generating a raw count matrix for downstream analysis. Differential gene expression analysis was performed in R (ver. 4.2.1) using the DESeq2 package (ver. 1.38.3). Log_2 fold-change values were calculated for comparisons between experimental conditions, and statistical significance was determined using adjusted *p*-values corrected for multiple testing.

The library preparations and the sequencing run were performed by UD-GenoMed Ltd. and the Genomic Medicine and Bioinformatics Core Facility of the Department of Biochemistry and Molecular Biology, Faculty of Medicine, University of Debrecen (University of Debrecen, Debrecen, Hungary). The data came from two independent biological replicates and three technical replicates. RNA samples were also used for RT-PCR to validate the generated data. The primers were listed in Table S1.

2.7. DON Treatment and RT-PCR

The *S. japonicus* cells from an overnight MXGB culture were inoculated into 20 mL of fresh MXGB (OD_{595}: 0.4), and MXGB + 0.5 ppm DON (sublethal concentration of DON was determined in preliminary experiments). The BIOPURE deoxynivalenol was purchased from Romer Labs (Romer Lab, Tulln, Austria). The flasks were incubated at 25 °C, and after 1 h, the cells were harvested for RNA extraction. The isolated RNA was subjected to DNase treatment (M0303; New England Biolabs GmbH, Frankfurt am Main, Germany), while the cDNA synthesis was performed with the High-Capacity cDNA Reverse Transcription Kit (Thermo-4368814; Thermo Fisher Scientific Inc, Waltham, MA, USA) following the manufacturer's protocol.

For the RT-PCR, Bio-Rad IQ5 real-time PCR system (Bio-Rad, Hercules, CA, USA), and SsoAdvanced Universal SYBR® Green Supermix (Bio-Rad, 1725272) reagent were used with the final primer concentration of 0.2 µM. The primers are listed in Table S1. Serial dilutions of genomic DNA (1/10, 1/100, 1/1000, 1/10,000) were prepared to generate standard curves for each reaction. All PCR reactions (toxin-treated and non-treated control) were performed in triplicate. PCR conditions were: 98 °C for 2 min; 40 cycles at 98 °C for 5 s, and 57 °C for 20 s. The melt curve was also generated according to the company's instructions to confirm the amplification specificity. Data were analyzed with the software (Bio-Rad iQ5 2.0) supplied with the qPCR instrument. Gene expression was normalized using a double normalization strategy, using the wild-type non-treated samples and transcription data of the *act1* gene (SJAG_03145.1; internal household gene). Relative expression levels were calculated using the $2^{-\Delta\Delta Ct}$ method. The outlying data were removed during analysis.

2.8. Effect of DON on Yeast-Cell Division

To test the effect of *Fusarium* mycotoxin on the yeast cell division, 1×10^9 yeast cells from a 16 h *S. japonicus* and *S. pombe* pre-culture were inoculated into 2 mL MXGB prepared with DON (0.1–1 ppm). The cells were incubated at 25 °C, at 100 r.p.m. for 24 h. The optical density was measured at 570 nm and compared to the control medium (prepared without toxin) [48]. The experiment was repeated four times.

2.9. Bioinformatics Analyses

2.9.1. Searching for Trichothecene-3-O-Acetyltransferase Homologous Genes

To find the *trichothecene-3-O-acetyltransferase* homologous genes in the yeast species, the protein sequence of the *F. graminearum* Tri101 gene (ACCESSION AB000874, VER. AB000874.1) (ADQ52713.1) was downloaded from the NCBI database and was used for BLASTp analysis as a query. The BLASTp searches were performed on the NCBI website (https://blast.ncbi.nlm.nih.gov/) (accessed on 18 August 2023) after selecting the budding yeasts (taxid:4892) or *Schizosaccharomycetes* (taxid:147554) categories. The BLASTp search was also performed in the Ensemble Fungi database (http://fungi.ensembl.org/) (accessed on 21 August 2023). The reciprocal BLASTp analyses were also carried out, where the homologous protein sequences of the yeasts (listed in Table S3) were used as a query. Sequence alignments were performed at the Clustal Omega website (https://www.ebi.ac.uk/Tools/msa/clustalo/) (accessed on 10 September 2023).

2.9.2. Analysis of the *S. japonicus* Tri101 Homologous Sequences

Chromosomal localisation and coordinates of the *S. japonicus* Tri101 homologs were obtained from the *S. japonicus* database (https://www.japonicusdb.org/) (accessed on 12 May 2024) [53]. Information on the localisation of genes regarding ancestral collinear blocks (aLCBs) was obtained from [54]. To investigate amino acid identity, similarity, and gaps, pairwise sequence alignments were performed using a Needleman–Wunsch algorithm on the EMBL-EBI website (https://www.ebi.ac.uk/jdispatcher/psa/emboss_needle/) (accessed on 13 June 2024) [55].

2.9.3. Phylogenetic Analysis of the *S. japonicus* Tri101 Homologs

Phylogenetic trees were constructed on the Phylogeny.fr website [56] using the "A la carte" option to create a custom workflow. The custom workflow consisted of MUSCLE 3.8.31. for the alignments [57], GBLOCKS v.091b for the curation of alignments [58], and PhyML 3.0 for the phylogenies [59]. The MUSCLE algorithm was adjusted to 'full mode', and the GBLOCKS was set to 'allow smaller final blocks'. For the PhyML phylogeny, the WAG substitution model was used, the gamma shape parameter and the proportion of invariable sites were both estimated, and the number of substitution rate categories was adjusted to 4. The approximate likelihood ratio test (aLRT SH-like) was used for the branch support estimation [59]. The created tree files were downloaded in Newick format and edited in FigTree v1.4.4. (http://tree.bio.ed.ac.uk/software/figtree/) (accessed on 24 July 2024).

2.9.4. Gene Ontology Enrichment Analyses

Functions and GO (Gene Ontology) categories were obtained from the *S. japonicus* database [53]. GO enrichment was performed with the ShinyGO 0.80 (http://bioinformatics.sdstate.edu/go/) (accessed on 2 May 2024) [60], using default settings. Definitions of GO categories were obtained from https://www.ebi.ac.uk/QuickGO/) (accessed on 10 May 2024).

2.10. Statistical Analyses

Normal distributions of the data were tested by Shapiro–Wilk and Anderson–Darling tests. Normally distributed pairwise data were tested with a two-sample *t*-test, and the effect size was measured by Cohen's D. When a two-sample *t*-test was used as a statistical analysis $p < 0.05$ value was regarded as a significant inhibition. In the absence of normal distribution, the non-parametric Mann–Whitney U test was used for related pairwise data, followed by Vargha–Delaney A for testing effect size. All statistical analyses were performed using the Past (v5.2.1) program (https://www.nhm.uio.no/english/research/resources/past/, accessed on 10 July 2025) [61].

3. Results

3.1. S. japonicus Inhibits the Growth of F. graminearum

Since we hypothesized that *S. japonicus* might exhibit antagonistic activity, and our preliminary experiments suggested that this yeast can inhibit *F. graminearum*, we established co-cultures on various media (PDA, MXGB, YEA) and determined the growth of *Fusarium* in the presence of yeast cells. These experiments demonstrated that the yeast significantly inhibited the growth of *F. graminearum* in both solid (Figure 1A,C) and liquid media (Figure 1B), which was confirmed by wet weight measurements. The wet weight of *Fusarium* hyphae produced in the liquid medium was lower in the co-culture than in the control monoculture (average weight was 1.44 g in the co-culture and 6.92 g in the *F. graminearum* monoculture) (Two-sample t test, $p = 7.025 \times 10^{-13}$, Cohen's D effect size = 50.25 (huge effect size).

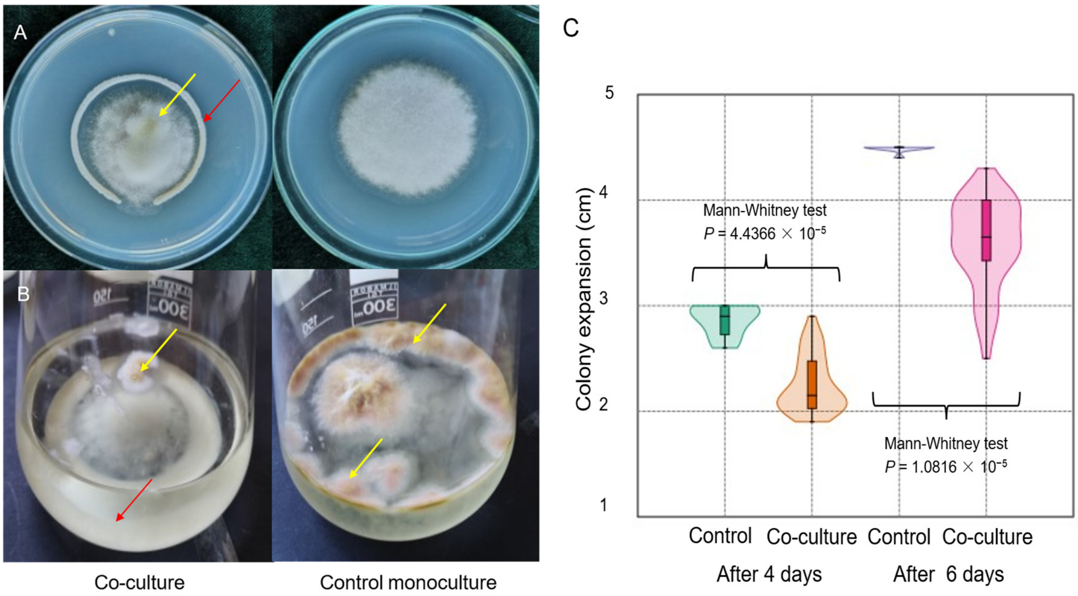

Figure 1. Growth inhibition test. *S. japonicus* was able to inhibit the growth of *F. graminearum*. *F. graminearum* (yellow arrow) did not grow on yeast cells (red arrow) in co-culture and was smaller in size (PDA, at 25 °C, photographed after 5 days) (**A**), which was significant (N = 11) (**C**) (Colony expansion after 4 days: Mann–Whitney test, $p = 4.4366 \times 10^{-5}$, Vargha–Delaney A effect size = 0.9635 (large effect size); Colony expansion after 6 days: Mann–Whitney test, $p = 1.0816 \times 10^{-5}$, Vargha–Delaney A effect size = 1 (large effect size). *F. graminearum* also produced fewer mycelia compared to the control in liquid medium (**B**) (PDB, incubated at room temperature, for 5 days, without shaking) (Similar results were obtained in MXGB and YEL media). The yellow arrows show *F. graminearum*, while the red arrow indicates the yeast cells settled to the bottom of the Erlenmeyer flask.

3.2. *S. japonicus Produces Ethanol, Which Did Not Inhibit the Growth of F. graminearum*

Since yeast cells are generally capable of producing ethanol, which can have a growth-inhibitory effect [49,50], we measured the ethanol content of the supernatant of liquid cultures. The yeast cells produced ethanol (1.46%), (*n*-propanol, *n*-butanol, and methanol were not detected in the supernatants), and slightly reduced the pH compared to *Fusarium* monocultures (Table 1). Interestingly, *F. graminearum* also produced some ethanol in static liquid culture (Table 1).

Table 1. The alcohol concentration and pH of the supernatants.

Species	Ethanol Concentrations (*v*/*v*%)	pH
F. graminearum	0.22 ± 0.17	4.06 ± 0.02
S. japonicus	1.53 ± 0.21	3.41 ± 0.05
S. japonicus + *F. graminearum*	1.46 ± 0.08	3.46 ± 0.04

Average of three experiments; alcohol LOD: 0.005 (*v*/*v*)%.

To test the possible inhibitory effect of ethanol on the growth of *F. graminearum*, *Fusarium* hyphae were inoculated into ethanol-containing MXGB medium (0.5, 1, 1.5, 2 (*v*/*v*) % ethanol), and the wet weight of hyphae was measured. No significant decrease in hyphae production was observed at any ethanol concentration compared to the control.

3.3. *RNA Sequencing of S. japonicus Cells Grown in Co-Culture with F. graminearum Revealed the DEGs*

To determine the yeast genes that are differentially expressed in the presence of *Fusarium*, *S. japonicus*, and *F. graminearum* cells were co-cultured (incubated for two days in MXGB medium, at room temperature), and mRNA levels of *S. japonicus* genes were determined by RNA sequencing. mRNA levels of 135 genes changed significantly during co-culture (109 were upregulated, 24 downregulated) compared to the control yeast culture (Table S2). RNA sequencing data were also validated by RT-PCR, as shown in Figure S1, where randomly selected genes yielded results similar to those obtained from RNA sequencing. Later, the functions and GO categories of genes were obtained from the Japonicus database (JaponicusDB) [53]. According to our data, several transport and membrane-associated genes (e.g., GO:0055085, GO:0022857, GO:0061024) and oxidoreductases (GO:0016491) were among the DEGs (Figure 2, Table S2). Table 2 also shows that most of these genes were upregulated.

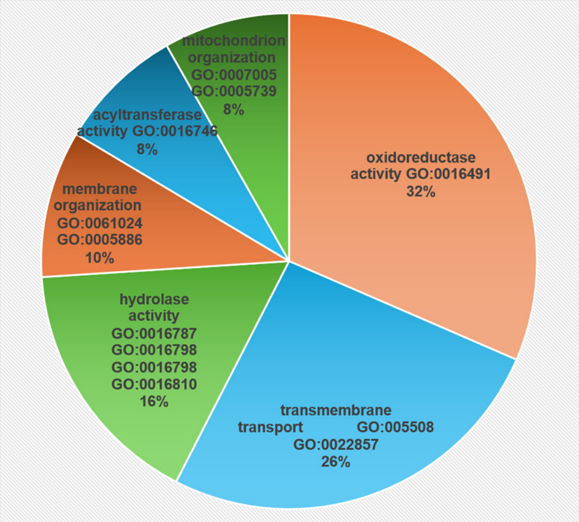

Figure 2. The most important GO categories of differentially expressed *S. japonicus* genes after co-culturing with *F. graminearum*.

Table 2. Genes belonging to transmembrane transport (GO:0055085) and oxidoreductase activity (GO:0016491).

Gene Symbol	Log_2 FC	Regulation	Function of the Gene
SJAG_02133	1.8282354	up	Amino acid/polyamine transporter
SJAG_01096	1.7833421	up	Amino acid/polyamine transporter
SJAG_02113	1.5267855	up	Amino acid/polyamine transporter
SJAG_03079	1.5025475	up	MFS transporter superfamily
SJAG_02150	−1.5304266	down	Amino acid transmembrane transporter
SJAG_04675	−2.4129047	down	Plasma membrane iron transmembrane transporter Fip1
SJAG_01903	1.8415602	up	Proline dehydrogenase Put1
SJAG_00674	1.7543724	up	Succinate–semialdehyde dehydrogenase
SJAG_00237	1.7031807	up	Hexitol dehydrogenase
SJAG_00704	1.7962087	up	Serine/threonine protein kinase Ppk31
SJAG_02960	1.6098309	up	Methylglyoxyl reductase (NADPH-dependent)
SJAG_01492	1.518742	up	Short-chain dehydrogenase, human DHRS7 family
SJAG_01850	1.5178025	up	Short-chain dehydrogenase, human DHRS7 family
SJAG_04743	−1.6851736	down	Plasma membrane ferric-chelate reductase
SJAG_03266	−2.1648088	down	NADP-specific glutamate dehydrogenase Gdh1
SJAG_04677	−2.8037887	down	Plasma membrane iron transport multicopper oxidase Fio1

Log_2FC: Log_2 Fold Change; up and down: the gene was up-regulated or down-regulated compared to the control.

In addition, genes with hydrolase activity (GO:0016787, GO:0016798, GO:0016788, GO:0016810), or transferases (GO:0016746, GO:0016741, GO:0016769) (Figure 2), including a *glutathione S-transferase* gene (GST) (SJAG_00238) (protects cells from toxins) appeared among the DEGs (Table S2). GO enrichment analysis also confirmed the changes in the gene expression of transporters and oxidoreductases (Table 3).

Table 3. GO enrichment of the differentially expressed *S. japonicus* genes obtained from cells co-cultured with *F. graminearum*.

GO Biological Processes	GO Molecular Function
Upregulated genes	
No significant enrichment was found	Oxidoreductase activity 15/232 (GO:0016491)
Downregulated genes	
Transmembrane transport 8/245 (GO:0055085)	Oxidoreductase acting on metal ions 2/3 (GO:0016722)
Transport 10/652 (GO:0006810) Amino acid transport 4/25 (GO:0006865) Organic acid transport 4/35 (GO:0015849) Transition metal ion transport 3/21 (GO:0000041) Cation transport 4/96 (GO:0006812) Import into cell 4/35 (GO:0098657) Glutamine fam. amino acid metabolic proc. 4/33 (GO:0009064) Glutamine metabolic proc. 3/15 (GO:0006541) Glutamate metabolic proc. 3/7 (GO:0006536) Alpha-amino acid metabolic proc. 4/102 (GO:1901605) Cellular amino acid metabolic proc. 5/156 (GO:0006520) Iron import into cell 2/3 (GO:0033212) Iron ion homeostasis 2/11 (GO:0055072) Iron ion transport 3/9 (GO:0006826) Cellular iron ion homeostasis 2/11 (GO:0006879) Nitrogen utilization 2/4 (GO:0019740) Ammonia assimilation cycle 2/3 (GO:0019676) Dicarboxylic acid metabolic proc. 3/25 (GO:0043648) Establishment of localization 10/690 (GO:0051234)	

Oxidoreductase activity: Catalysis of an oxidation-reduction (redox) reaction. Transport: The directed movement of substances (such as macromolecules, small molecules, ions) or cellular components (such as complexes and organelles) into, out of, or within a cell. Metabolic proc.: metabolic process: A cellular process consisting of the biochemical pathways by which a living organism transforms chemical substances. Iron ion homeostasis: A homeostatic process involved in the maintenance of a steady state level of iron ions within a cell. Nitrogen utilization: A series of processes that form an integrated mechanism by which a cell or an organism detects the depletion of the primary nitrogen source, usually ammonia, and then activates genes to scavenge the last traces of the primary nitrogen source and to transport and metabolize alternative nitrogen sources. Establishment of localization: Any process that localizes a substance or cellular component. Ammonia assimilation cycle: The pathway by which ammonia is processed and incorporated into a cell. (Number of Genes/Pathway Genes) (proc.: processes).

3.4. Study of the Trichothecene-3-O-Acetyltransferase Genes

After a detailed investigation of the DEGs, we noticed that they contain three genes belonging to the CoA-dependent acyltransferase superfamily (marked in red letters in Table S2), whose sequence analysis revealed that they are homologs of the TRI101 *trichothecene-3-O-acetyltransferase* gene. Further BLASTp analyses also showed that several yeast species (*Lipomyces starkeyi*, *Torulaspora delbrueckii*, *Saccharomyces cerevisiae*, *Yarrowia lipolytica*, *Saccharomyces pastorianus*, *Sugiyamaella lignohabitans*, *Debaryomyces hansenii*, *Trichomonascus ciferrii*, *Brettanomyces naardenensis*) possess such a gene (Tables 4 and S3). While these species had only a single homologous gene, *S. japonicus* unexpectedly contained seven copies of the *trichothecene-3-O-acetyltransferase* homologous gene (Tables 4 and S3). In contrast, we did not find homologs in its closely related yeast species, *S. pombe* (Table 4).

Table 4. Yeast species with homologous Tri101 protein sequences.

Species	Protein Name and Length	Score	E-Value	Identities	Positives
Schizosaccharomyces japonicus	CoA-dependent acyltransferase superfamily (predicted) SJAG_00021.1, length: 457	342	4×10^{-113}	182/455 (40%)	254/455 (55%)
Schizosaccharomyces japonicus	CoA-dependent acyltransferase superfamily (predicted) SJAG_02940.1, length: 456	387	2×10^{-130}	208/455 (46%)	278/455 (61%)
Schizosaccharomyces japonicus	CoA-dependent acyltransferase superfamily (predicted) SJAG_00020.1, length: 457	350	8×10^{-116}	193/458 (42%)	265/458 (57%)
Schizosaccharomyces japonicus	CoA-dependent acyltransferase superfamily (predicted) SJAG_00075.1, length: 458	367	8×10^{-123}	196/452 (43%)	273/452 (60%)
Schizosaccharomyces japonicus	CoA-dependent acyltransferase superfamily (predicted) SJAG_01363.1, length: 453	358	2×10^{-119}	193/454 (43%)	276/454 (60%)
Schizosaccharomyces japonicus	CoA-dependent acyltransferase superfamily (predicted) SJAG_02126.1, length: 452	324	5×10^{-106}	182/452 (40%)	261/452 (57%)
Schizosaccharomyces japonicus *	CoA-dependent acyltransferase superfamily (predicted) SJAG_02127.1, length: 457				
Saccharomyces cerevisiae ** YJM1402, YJM1208	Acetyltransferase Ayt1p, length: 474	388	7×10^{-130}	204/454 (45%)	286/454 (62%)
Lipomyces starkeyi NRRL Y-11557	Hypothetical protein LIPSTDRAFT_86407, length:466	454	1×10^{-155}	233/456 (51%)	297/456 (65%)
Torulaspora delbrueckii	Hypothetical protein TDEL_0G04720, length: 427	434	9×10^{-149}	223/450 (50%)	298/450 (66%)
Yarrowia lipolytica	Transferase, length: 443	346	7×10^{-114}	188/450 (42%)	265/450 (58%)
Saccharomyces pastorianus	Trichothecene 3-*O*-acetyltransferase, length: 474	386	4×10^{-129}	203/454 (45%)	286/454 (62%)
Sugiyamaella lignohabitans	Ayt1p, length: 474	373	7×10^{-124}	197/468 (42%)	280/468 (59%)
Debaryomyces hansenii CBS767	Transferase DEHA2D07326p, length: 454	367	8×10^{-122}	203/457 (44%)	280/457 (61%)
Trichomonascus ciferrii	Hypothetical protein TRICI_005126, length: 444	366	1×10^{-121}	194/449 (43%)	276/449 (61%)
Brettanomyces naardenensis	DEKNAAC103449, length: 440	334	2×10^{-109}	183/449 (41%)	266/449 (59%)
Schizosaccharomyces pombe ***	-				

Query: *F. graminearum* Tri101p (ACCESSION AB000874, VERSION AB000874.1) (ADQ52713.1) (14.12.2023 data) (NCBI database, BLASTp). * This gene was found in Ensemble. ** This gene is capable of trichothecene 3-*O*-acetylation [62]. *** BLASTp did not find homologous proteins.

To obtain further information on seven copies of the *S. japonicus trichotecene-3-O-acetyltransferase* homologous genes, their protein sequences were investigated by pairwise and multiple sequence alignments, as well as phylogenetic analyses. The sequences were very similar to each other (Figure 3) and were localized in all three chromosomes of *S. japonicus*, mainly in the subtelomeric regions, which are the DNA segments between chromosomal telomeric caps and chromatin (Table S4). Their phylogenetic analysis also showed that SJAG_01363-SJAG_02940, SJAG_02126-SJAG_00075, and SJAG_02127-SJAG_00021 sequences were more similar to each other than to the others (Figure 3A), while further phylogenetic analysis, extended to other species, confirmed their relationship to Tri101 homologs identified in other yeasts (Figure 3B).

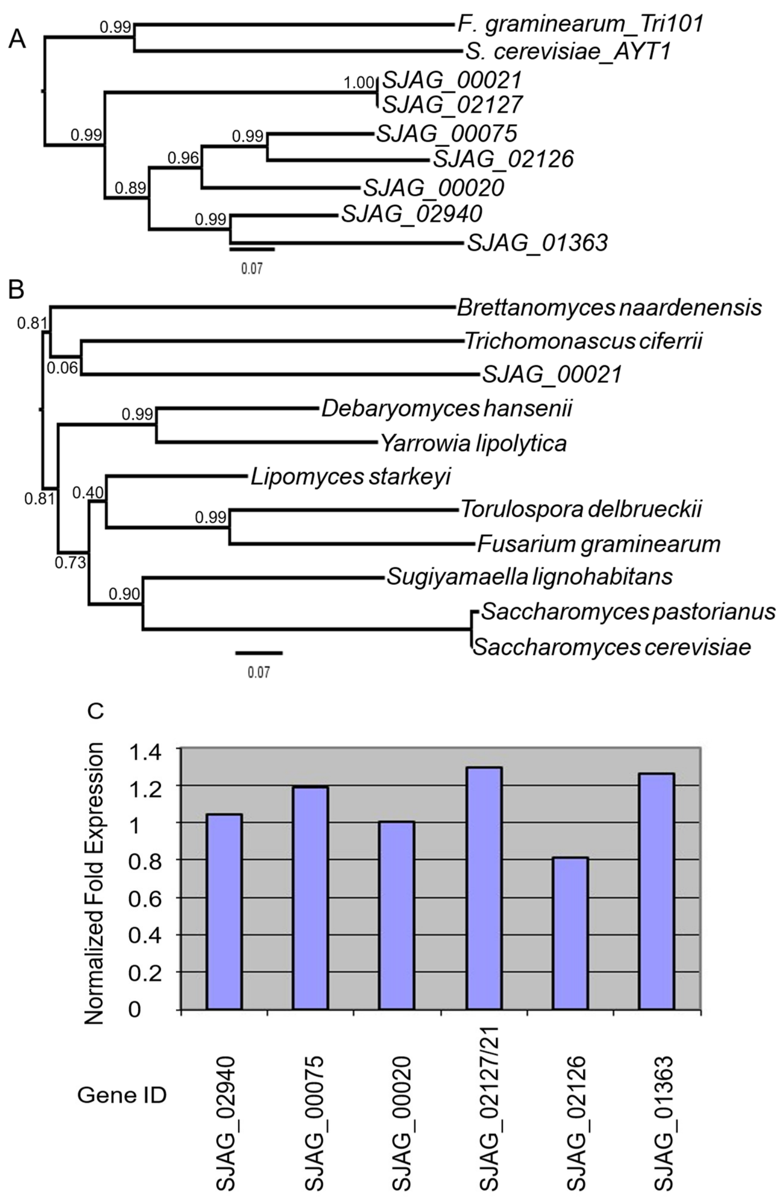

Figure 3. Study of the putative trichothecene-3-*O*-acetyltransferase homologous protein sequences. (**A**) Phylogenetic analysis of the *S. japonicus* protein sequences and the experimentally validated *F. graminearun* and *S. cerevisiae* trichothecene-3-*O*-acetyltransferase protein sequences. The *S. japonicus* genes are clustered together and separated from the *F. graminearum* and *S. cerevisiae* sequences because they are more similar to each other than to the sequences of other species. (**B**) Phylogenetic analysis of the *S. japonicus* SJAG_00021 and Tri101 putative homologous sequences identified in other yeasts. To demonstrate that the identified *S. japonicus* sequences are putative orthologs of the Tri101 gene family, one of the most basally located sequences of *S. japonicus* (SJAG_00021) was included in a phylogenetic analysis comprising many other putative orthologous protein sequences. Although SJAG_00021 is not located on the main branch of the tree, it is clustered with other putative trichothecene-3-*O*-acetyltransferase homologous protein sequences. (**C**) Normalized fold expression of the Tri101 homologs shows that DON treatment of *S. japonicus* cells caused changes in mRNA levels of all but two genes, compared to controls.

3.5. The Closely Related S. japonicus and S. pombe Have Different DON Tolerance

Since, unexpectedly, we have found a large difference in the number of *trichotecene-3-O-acetyltransferase* homologous genes between *S. japonicus* and *S. pombe* (Table 4), we compared the DON tolerance of the two closely related species. The inhibition of their cell division was different, i.e., the DON tolerance of *S. japonicus* was better than that of

S. pombe, whose genome did not contain this gene (Table 5). RT-PCR analysis also revealed that most of the *S. japonicus* TR101 homologous genes can be induced by DON (Figure 3C).

Table 5. Growth inhibition of yeast cells by DON.

	DON Concentrations			
	0.1 ppm	**0.5 ppm**	**0.7 ppm**	**1 ppm**
Species	**Inhibition (%)**			
S. japonicus	<10	<10	<10	<10
S. pombe	<10	20	37	52

LOD: 10%.

4. Discussion

Since *F. graminearum* infection causes significant agricultural problems by reducing crop yields and frequently contaminating food and feed with mycotoxins, and because biological methods are suitable for controlling pathogenic fungi, the objectives of this study were to find a yeast strain that inhibits *F. graminearum* and to identify genes that may be capable of converting *Fusarium* mycotoxins into less harmful compounds.

Here, we provide the first evidence that the fission yeast *S. japonicus* exhibits growth-inhibitory capacity (Figure 1), thereby expanding the range of yeasts known to exhibit antagonistic activity against *Fusarium* species [24,63–66]. To determine whether the yeast produced ethanol (as yeasts are often capable of producing ethanol) and whether this could have caused growth inhibition, as in the case of *Fusarium oxysporum* and *Aspergillus flavus* [49,50], we measured the alcohol concentrations in the supernatant of the co-cultures. As expected, *S. japonicus* cells produced ethanol (1.4%) in static liquid cultures (Table 1); however, when we examined the growth-inhibiting effect of ethanol on *F. graminearum*, we found no significant growth inhibition in the presence of 0.5–2% ethanol. This may also be related to the fact that, interestingly, *F. graminearum* was also able to produce small amounts of ethanol, similar to *F. oxysporum* and *F. verticillioides* [48,67,68]. Therefore, it can be assumed that nutrient competition or other antifungal compounds produced by fission yeast may have caused the growth inhibition. Antifungal compounds can be diverse, including volatile compounds [28] as well as secreted toxic molecules. For example, *Cochliobolus sativus* is able to produce and secrete toxic molecules, one of which is similar to prehelminthosporol, and these compounds were shown to inhibit the growth of *F. graminearum* [69]. Another study reported that the expression of mannosidase and glucosidase genes in *Aureobasidium pullulans* was enhanced in the presence of *F. oxysporum* [68]. These enzymes may contribute to cell wall degradation and, consequently, to growth inhibition. Since growth inhibition may arise from multiple mechanisms and may reflect synergistic effects, further experiments are necessary to identify the inhibitory compounds involved. Nevertheless, our results indicated that *S. japonicus* exhibits antifungal potential and, pending further field evaluation, could be a suitable candidate for the biological control of *F. graminearum*.

Since the co-cultivation of *Fusarium* and a yeast species may induce different gene expression in microorganisms due to numerous biological and environmental factors resulting from the interaction between the species [48,70], we also examined gene expression changes in yeast cells in the hope that the presence of *Fusarium* triggers detoxification and activation of toxin-modifying/defense-related genes in the yeast. According to our results, *S. japonicus* is not only capable of inhibiting the growth of *F. graminearum*, but also presumably biologically transforms its mycotoxins. When we examined the transcriptomic changes induced by the presence of *F. graminearum* in yeast cells (co-culture), we identified several enzyme-encoding genes among the 135 genes whose mRNA levels were significantly altered compared to the control yeast monoculture (DEGs) (Table S2). Most genes were upregulated (109 out of 135) and several of them encoded oxidoreductases (GO:0016491) (Figure 2, Tables 2 and S2), which was also confirmed by GO enrichment (Table 3). In addition, DEGs included genes encoding hydrolases (GO:0016787, GO:0016798, GO:0016788, GO:0016810) and transferases (GO:0016746, GO:0016741, GO:0016769) (Table S2, Figure 2). Since oxidoreductases are generally known as enzymes that can remove contaminants [71], and for example, peroxidases can reduce mycotoxins [70], or hydrolases such as carboxypeptidases degrade ochratoxin [72,73], we assume that these genes may have played an important role in detoxification. This is supported by the fact that several oxidoreductase and hydrolase genes also appeared among the DEGs during the co-cultivation of other species, such as *S. pombe* and *F. verticillioides*, or *A. pullulans* and *F. oxysporum* [48,70]. This means that these genes represent a promising opportunity to identify new *Fusarium* toxin–degrading genes, whose products could later be used as recombinant enzymes following gene cloning. This is important because such enzymes are needed, yet only a few of them are currently commercially available [29]. Potential detoxifying role of these enzymes is supported by the fact that the *glutathione S-transferase* (GST) (SJAG_00238) gene was among them, and its expression was upregulated in co-culture (Table S2) (confirmed by RT-PCR validation; Figure S1). This result is consistent with the enzyme being involved in detoxification [74], and with previous results that showed overexpression of the barley GST13 gene in *Arabidopsis* resulted in an increased resistance to *F. graminearum* [75], or introduction of another GST gene into wheat caused resistance to *Fusarium* Head Blight [76].

The transcriptome analysis also highlighted additional enzyme-coding genes, as three genes belonging to the CoA-dependent acyltransferase superfamily were identified among the DEGs (Table S2). Sequence alignments of the encoded proteins and subsequent phylogenetic analyses revealed that these three acetyltransferases are homologs of the trichothecene 3-O-acetyltransferase Tri101 (Figure 3A).

Their functions may also be supported by the fact that the homologs included the *S. cerevisiae* Ayt1 protein (Figure 3B), which is capable of trichothecene-3-*O*-acetylation [62]. In addition, it was also demonstrated that expressing a *trichothecene-3-O-acetyltransferase* gene in *S. pombe* and in plant cells could protect the host cells from DON [77–79]. Therefore, we further investigated these *acetyltransferase* genes. In silico analyses also revealed that, unexpectedly, the genome of *S. japonicus* contained seven copies of the *trichothecene-3-O-acetyltransferase* homologous gene sequence, in contrast to other yeast species and the closely related *S. pombe* (Table 4). While the genomes of several yeast species, such as *Lipomyces starkeyi*, *Torulaspora delbrueckii*, *Saccharomyces cerevisiae*, *Yarrowia lipolytica*, *Saccharomyces pastorianus*, *Sugiyamaella lignohabitans*, *Debaryomyces hansenii*, *Trichomonascus ciferrii*, *Brettanomyces naardenensis*, contain only a single TRI101 homologous gene, the *S. pombe* genome contains no homologous gene (Table 4). This latter data is also remarkable because, in general, the gene content and order of the two closely related fission yeast species (*S. japonicus* and *S. pombe*) are highly conserved [54,80]. One possible explanation for the difference in copy number of *trichothecene 3-O-acetyltransferase* homologous genes is that the two related species occupy different habitats. *S. pombe* is frequently detected on fruits, whereas *S. japonicus* is mainly found in soil [44], where it may encounter *Fusarium* species and therefore needs to defend itself. This assumption is supported by the observation that several species possessing TRI101 homologs—such as *Debaryomyces hansenii*, *Yarrowia lipolytica*, *Saccharomyces pastorianus*, *Lipomyces starkeyi*, and *Torulaspora delbrueckii*—have also been isolated from soil [81–86].

Further examination and alignment of the *S. japonicus* TRI101 homologous gene sequences and their encoded proteins indicated that some of these genes are more similar to each other, and are localized in subtelomeric regions (Figure 3A, Table S4). These findings suggest that segmental duplication and translocation events may have contributed to the high copy number observed in the examined strain. Consequently, this strain represents a non–genetically modified yeast that naturally harbors a *trichothecene 3-O-acetyltransferase* gene at high copy number, without the involvement of artificial genetic modification.

The question then arose as to whether these genes are functional or not. To obtain further evidence for the functionality of *trichothecene-3-O-acetyltransferase* genes, *S. japonicus* cells were treated with purified DON, and changes in mRNA levels were measured by RT-PCR. DON treatment caused changes in mRNA levels of all but two genes, compared to controls (Figure 3C). Based on these data, we hypothesized that at least five of the seven *trichothecene-3-O-acetyltransferase* copies would be functional, and that *S. japonicus* cells should have greater DON tolerance than *S. pombe* cells lacking the TRI101 homolog gene. Experiments on DON-supplemented media confirmed that *S. japonicus* has a stronger DON tolerance than *S. pombe* (Table 5). This is in good agreement with previous studies, which showed that yeast and plant cells exhibit increased resistance to DON when the *trichothecene 3-O-acetyltransferase* gene is overexpressed [77,78].

Our results not only highlighted the genes encoding the above-mentioned enzymes (which may offer good opportunities for data mining and further gene cloning) but also showed that genes related to transport and membranes (e.g., GO:0055085, GO:0022857) were strongly influenced by the presence of *F. graminearum* or its mycotoxin (Figure 2, Tables 2 and S2). This is consistent with the findings of Kosawang, who also identified several transporter genes in the transcriptome profile of *Clonostachys rosea* after treatment with *Fusarium* mycotoxins [87], as well as with our previous findings, which suggested that transporters are important components of mycotoxin defense in yeasts [48].

In summary, we demonstrated that the fission yeast *S. japonicus* exhibits antagonistic activity against *F. graminearum*. In addition, we identified genes that are differentially expressed in the presence of *Fusarium* and may be involved in the detoxification and biotransformation of mycotoxins, including genes homologous to the *trichothecene-3-O-acetyltransferase* gene. We also showed that there are seven such genes in the *S. japonicus* genome and that this species displays high tolerance to deoxynivalenol (DON). Although gene expression may differ depending on whether yeast cells are cultured with *F. graminearum* under in vivo or in vitro conditions, and therefore further experiments in plants are required, we believe that these findings contribute to a better understanding of the mechanisms underlying interactions between *Fusarium* (and *Fusarium*-derived mycotoxins) and yeast, and may ultimately lead to promising biotechnological approaches for the production of safer foods.

5. Conclusions

S. japonicus may be suitable for the biological control of *F. graminearum*. Transcriptomic results from co-cultivation showed a sophisticated genetic response and highlighted genes sensitive to *Fusarium graminearum* or its mycotoxins, while bioinformatic analyses indicated the presence of multiple *trichothecene 3-O-acetyltransferase* homologs.

These findings represent more than just a list of genes; the differentially expressed enzyme-encoding genes identified in this study offer data mining opportunities. By using this data set to identify and clone new genes, we are paving the way for the next generation of highly efficient, biotransforming feed additives.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/agriculture16050494/s1, Figure S1. RT-PCR validation of RNA sequencing data. The randomly selected upregulated (SJAG_00238, 02988,03723,03526,03640, 04796) and down–regulated genes (SJAG_03266, 04677,04675,03724) gave similar results as in RNA sequencing. Their normalized gene expression was above 1 or below 1, respectively; Table S1: Primers used for RT-PCR; Table S2: Differentially expressed *S. japonicus* genes in the presence of *F. graminearum*; Table S3: Tri101 homologous protein sequences; Table S4: Chromosomal localization and characteristic data of the *S. japonicus* Tri101 homologs.

Author Contributions: Conceptualization, L.A.P., L.A.-S. and I.M.; investigation, H.C. and C.A.; validation, G.B.; supervision, I.M.; writing—original draft preparation, I.M.; writing—review and editing, T.P. and I.P.; project administration and funding acquisition, I.P. All authors have read and agreed to the published version of the manuscript.

Funding: The project no. 2019-2.1.13-TÉT_IN-2020-00056 has been implemented with the support provided by the National Research, Development and Innovation Fund of Hungary, financed under the 2019-2.1.13-TÉT_IN funding scheme. Project no. TKP2021-EGA-18 has been implemented with the support provided by the Ministry of Culture and Innovation of Hungary from the National Research, Development and Innovation Fund, financed under the TKP2021-EGA funding scheme. This project has received funding from the HUN-REN Hungarian Research Network and was supported by the University of Debrecen Program for Scientific Publication and for Scientific Research Bridging Fund (DETKA).

Data Availability Statement: All data generated or analyzed during this study are included in this published article and its Supplementary Information Files. The transcriptome data sets are also available in the Gene Expression Omnibus database (GEO; http://www.ncbi.nlm.nih.gov/geo; accessed on 25 July 2024) with the following accession number: GSE273231. Data collection: 2024.

Acknowledgments: We thank Ilona Lakatos for her technical assistance. The authors thank Sebastien Santini (CNRS/AMU IGS UMR7256) and the PACA Bioinfo platform for the availability and management of the phylogeny.fr website. The authors apologize to the authors whose articles have not been cited for reasons of length.

Conflicts of Interest: The authors declare no conflicts of interest.

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https://doi.org/10.3390/agriculture16050494