Within the frame of this project we managed to reach the following main goals: (i) Isolation, identification and quantification of secondary metabolites and pigments produced by *Aspergillus nidulans* (a widely used filamentous fungus model organism, which is known to produce the aflatoxin precursor molecule sterigmatocystin) *ΔatfA*, *ΔmnSOD*, *ΔAN7872* and *AN7872*OE mutants as well as *Fusarium verticillioides* (a cosmopolitan plant pathogenic fungus causing major losses in corn production world-wide and also threating the feed and food chain through its fumonisin production) *ΔFvatfA* and *ΔFvmnSOD* mutant strains under various culture conditions *via* the application of advanced analytical/structural chemistry tools. (ii) Collecting and analyzing large-scale transcriptomics data in various environmental stress-exposed cultures of *A. nidulans* and *F. verticilloides* wild-type and mutant strains and construction of fungal stress database.

(i) Secondary metabolites, pigments

Secondary metabolites produced by fungi are a valuable source of molecules with a wide range of chemical structures and versatile biological activities. Fungal genes required for the production of secondary metabolites are mostly organized in gene clusters, some of which are silent or barely expressed under laboratory conditions. Therefore, the determination of any causal connections between genes and metabolites is mostly difficult and, as a consequence, the unceasing development and application of efficient methods for the discovery and chemical analysis of either known or unknown molecules are needed to identify the secondary metabolite production pathways themselves and the gene clusters behind them. Our primary aim was to apply the molecular biological and chemical analytical tools available for us to uncover metabolites produced by *A. nidulans* and *F. verticillioides* mutant strains under various culture conditions.

1. We hypothesized that the *A. nidulans* AN7872 putative transcription factor would regulate a function-unknown secondary metabolite gene cluster with a non-ribosomal peptide synthase key biosynthetic gene in its center. We constructed the *ΔAN7872* gene deletion and the *AN7872*OE overexpression strains and tested several culture conditions and culture media to elicit the possible production of new secondary metabolites. As a result, we found significant differences in the secondary metabolite profiles between the control, *ΔAN7872* and *AN7872*OE mutants

under the following culture conditions: **(a)** 1 % glucose, 2 % maltose and 1 % mycological peptone; 25 ^{o}C, 220 rpm shaking frequency, 3 d incubation time, and **(b)** Czapek-Dox medium, 25 ^{o}C, static culture, 14 d incubation in the dark.

Secondary metabolite profiles in the freeze-dried and 70 % acetone:water extracted mycelial samples cultivated in the **(a)** medium were studied by QTOF-MS (Department of Inorganic and Analytical Chemistry, Faculty of Science and Technology, University of Debrecen). The samples from *AN7872*OE mutants contained a component of 875.3977 m/z which was a Na^+ adduct ($[M+Na]^+$) and this was absent in both the control and the *ΔAN7872* samples. The most probable formula was $C_{35}H_{56}N_{12}O_{13}Na$ and the corresponding neutral formula was $C_{35}H_{56}N_{12}O_{13}$ (neutral molecular mass: 852.4084). The measured and the simulated mass spectrum with isotopic patterns agreed well. The MS/MS study of this component showed a fragment ion at 591.2587 m/z, and similar results were received by capillary zone electrophoresis (CZE) coupled to mass spectrometric detection. Spectrum analysis and comparison with databases and literature enabled us to identify the molecule N,N',N''-triacetylfusarinine (TAFC), which is composed of three N^5-cis-anhydromevalonyl-N^5-hydroxy-N^2-acetyl-L-ornithine residues. Considering the chemical groups involved in iron binding, TAFC is a hydroxamate siderophore utilizing negatively charged oxygen atoms to form a hexadentate octahedral complex with ferric ion but have somewhat lower affinity for iron than other siderophore families. Spectrum analysis revealed further metabolites, which were found in different concentrations in the control, *ΔAN7872* and *AN7872*OE mutants, and the identification of these components are in progress. Summing it up, the AN7872 putative transcription factor seems to regulate the production of various secondary metabolites including the important siderophore TAFC, which plays a pivotal role *e.g.* in the pathogenesis of the important opportunistic human pathogenic fungus *Aspergillus fumigatus*. A manuscript based on these original observations is now in preparation.

From the freeze-dried and methanol extracted mycelial samples cultivated in **(b)** medium were measured by HPLC and detected by high-resolution Orbitrap mass spectrometry (HR-MS, Department of Plant Anatomy, Faculty of Science, Eötvös Loránd University, Budapest). We managed to extract a red colored compound, which was later proved to be the pigment asperthecin (M=318.23, formula: $C_{15}H_{10}O_8$). In the *ΔAN7872* mutant, the asperthecin

concentration was higher than in the control and *AN7872*OE strains, which result will also be published in the near future.

2. Secondary metabolite production was also influenced by the deletion of the *gfdB* gene encoding a glycerol 3-phosphate dehydrogenase in *A. nidulans*. Sterigmatocystin production was significantly higher in the *ΔgfdB* mutant than in the control strain and oxidative stress treatment induced by *tert*-butyl hydroperoxide (*t*BOOH, elicits lipid peroxidation) decreased the sterigmatocystin production but still remained higher in the *ΔgfdB* mutant than in the control strain (Király et al. 2020a). In another study, *Aspergillus glaucus* was supplemented successfully with *A. nidulans gfdB*, which increased the environmental stress tolerance of *A. glaucus* (Király et al. 2020b).

3. It is widely known that tyrosol (2-(4-hydroxyphenyl) ethanol), which is a quorum-sensing molecule in a number of *Candida* spp., affects the growth and virulence of these pathogenic yeasts. Tyrosol added at 35 mM concentration also hindered the growth of *A. nidulans* and concomitantly elicited the production of some new metabolites in this fungus, including a new one with a 439 molecular mass according to the MS spectra (Department of Organic Chemistry, Faculty of Science and Technology, University of Debrecen). Even though the molecular mass is known the structure of the metabolite was needed to be characterized further since the chemical diversity of secondary metabolites is very high in *A. nidulans*. Therefore, the next step was to isolate the metabolite and, for this purpose, a scale-up cultivation was carried out (in altogether 5 L medium) following by extraction with ethyl acetate and purification steps by standard organic chemistry silica gel chromatography. Extracts were filtered and concentrated in vacuum than purified by column chromatography with 9:1 dichloromethane methanol eluent. Because the semi-pure isolate resulted in low yield (0.1 %) and showed impurities by LC-MS analysis further purification by preparative HPLC became impossible.

Considering alternatives, we prioritized techniques for comparison without the need for full component identification. For this purpose, LC-MS and HRMS analyses allowed us to compare the resulted data with data presented in literature. Fortunately, in collaboration with the Research and Development Service Unit of the ELKH Research Centre for Natural Sciences, Budapest, we gained the accurate m/z mass range of the metabolite (440.1677). This encouraging result

prompted us to search for similar known secondary metabolites of *A. nidulans* in the literature and we reached the conclusion that no identical metabolite has been described yet.

Meanwhile, we also investigated a procedure applied previously for the isolation and recovery of tyrosol from phenolic extracts. This method was based on chemical acetylation reaction resulting in alkyl carbonate derivatives of tyrosol. The aim of this reaction was to eliminate the tyrosol, as a bulky compound present in the crude extract. Acetic anhydride 0.66 mL (0.71 g, 7 mmol) was added dropwise to 100 mg of the crude extract for 2 hours under reflux conditions. The residue was dissolved in dichloromethane and washed with a solution of $NaHCO_3$. The organic layer was dried with anhydrous Na_2SO_4, filtered, and concentrated to dryness. According to TLC and LC-MS analyses, the resulting residue contained the diacetylated tyrosol (M=222) and two new compounds with molecular masses of 442 and 458, respectively. Since the molecular mass of acetyl moiety is 43 g/mol the acetylation of the unknown metabolite (M=439) did not occur and, presumably, a rearrangement in its structure took place. Because all these efforts in Hungary have failed to characterize this new metabolite in depth we are currently looking for collaborating partners in the US to reveal the chemical structure of this metabolite.

4. In another study, *A. nidulans* was cultured in a medium supplemented with 1 % glucose, 2 % maltose and 1 % mycological peptone. For initial analyses in maltose-supplemented cultures, small-scale cultivation was performed, and TLC, LC-MS chromatograms as well as the MS spectra revealed a new peak presumably related to the metabolite with a relative molecular mass of 459. Large scale cultivation allowed us to isolate and purify the new metabolite in good yields. Extraction of mycelia by ethyl acetate and sonication and, following that, purification on standard silica gel chromatography with hexane ethyl acetate 9:1 gradient elution was performed. Although the isolation of the metabolite was confirmed by LC-MS measurement the presence of impurities indicated clearly the need for further HPLC purification. Interestingly, the peak of 481.58 m/z ($[M+Na]^+$) was present as two isomers and this presumption was supported by ^1H and ^{13}C and COSY NMR spectra. Preparative HPLC purification was made on reversed-phase C_{18} (100 ×2,10 mm 2,6 μm) column method using water-methanol (1:9) isocratic elution and UV detection. The separated fractions were submitted to NMR and HRMS measurements but decomposition of the molecules was observed. To avoid this problem, we eliminated the 0,1 % formic acid routinely used in the eluent of the HPLC method but no improvement was observed. Nevertheless, the data provided by LC-MS, ^1H and ^{13}C NMR spectra of the semi-pure compound

indicated that the new metabolite was most likely a secondary metabolite in the meroterpenoid family. Again, we are looking for international collaborating partners to identify and describe this apparently unstable metabolite.

5. We also collected and systematized literature data about mycotoxin secondary metabolites produced by *Aspergillus* species in reviews by Pfliegler et al. (2020), Ráduly et al. (2020) and in an editorial by Pócsi et al. (2020).

6. A novel CE-MS-based analytical technique was used to demonstrate that *F. verticillioides ΔFvatfA* produced drastically less FB1 and FB2 fumonisins (harmful mycotoxins affecting the liver, kidneys and the respiratory and nervous systems and also causing oesophageal and renal cancers) than the parental wild-type strain meanwhile the deletion of the *FvmnSOD* gene did not interfere with FB1 and FB2 fumonisin productions in *F. verticillioides* (Kecskeméti et al. 2019, Szabó et al. 2020a and 2020b, Leiter et al. 2021). Importantly, the expressions of selected biosynthetic genes (*fum1*, *fum8*) in the fumonisin biosynthetic gene cluster were repressed in the *ΔFvatfA* mutant. It is noteworthy that the regulatory function of FvAtfA on the fumonisin production of *F. verticillioides* was one of the key observations gained within this project, which has already generated significant international response and, hence, which will certainly initiate further research in this field in the near future.

7. In *F. verticillioides*, wild-type, *ΔFvatfA* deletion mutant and genetically complemented strains were cultivated using appropriate liquid culture medium (DG minimal medium for carotenoids under continuous illumination) to determine light-inducible carotenoid production. Remarkably, the *ΔFvatfA* mutant produced significantly lower amounts of carotenoids determined from lyophilized mycelial samples than the wild-type strain underlining the regulatory function of this bZIP-type transcription factor on the carotenoid biosynthesis in this important corn pathogenic fungus (Szabó et al. 2020a). This hypothesis was strongly supported by the observation that the expressions of selected biosynthetic genes (*carRA*, *carB*) in the carotenoid biosynthetic pathway were down-regulated in the *ΔFvatfA* strain.

8. The *F. verticillioides ΔFvatfA* strain produces a novel blue pigment instead of carotenoids (Szabó et al. 2020a). Unfortunately, the pigment could not be extracted by either water or any organic solvents tested and, therefore, mycelia will be digested by a suitable hydrolase mix to gain an access to the highly insoluble pigment.

9. In *F. verticillioides*, wild-type, *ΔFvatfA* deletion mutant and genetically complemented strains were cultivated in Bell's medium optimized for bikaverin (a red pigment with antimicrobial and anticancer activities) production. Interestingly, although the *ΔFvatfA* strain produced approximately ten times more bikaverin than the wild-type or the genetically complemented strains the expression of *bik1*, encoding the polyketide synthase key enzyme in bikaverin biosynthesis, was not up-regulated by the deletion of *FvatfA* (Szabó et al. 2020a). This result, which is likely to attract the attention of industrial experts interested in the large-scale production of this pigment, indicated that no further up-regulation of *bik1* was possible in the Bell's medium optimized for bikaverin production. Instead, building blocks of other down-regulated pigments (*e.g.* carotenoids) and secondary metabolites (*e.g.* fumonisins) were likely channeled towards bikaverin production under these culture conditions (Szabó et al. 2020a).

10. Because *F. verticillioides* FvAtfA seems to have a crucially important role in the regulation of the biosynthesis of both pigments and mycotoxins, we wrote a review paper summarizing the versatile physiological functions of fungal Atf1 (*Schizosaccharomyces pombe*) – AtfA (*A. nidulans*) - FvAtfA (*F. verticillioides*) orthologs in the vegetative growth, sexual and asexual developments, stress response, secondary metabolite production, and virulence both in human pathogenic and plant pathogenic fungi (Leiter et al. 2021).

11. A paper about the interaction of two other important bZIP-type transcription factors, NapA and RsmA in *A. nidulans* has also been published recently by our team (Bákány et al. 2021). We found that NapA coordinated sterigmatocystin production *via* regulating reactive intracellular species levels meanwhile RsmA modulated mycotoxin production independently of the redox status of the cells.

(ii) Transcriptomics studies, construction of fungal stress database

1. Genome-wide transcriptional changes in *A. nidulans* strains (a control strain and an oxidative stress sensitive *ΔatfA* mutant) induced by nine different stress conditions {menadione sodium bisulfite, *tert*-butyl hydroperoxide, diamide, low concentration (5 mM) H_2O_2, high concentration (75 mM) H_2O_2, NaCl, amphotericin B, Congo Red, $CdCl_2$} were evaluated to reveal the general environmental stress response gene set showing unidirectional expressional changes under various types of stress. Altogether, 1642 co-up-regulated and 3916 co-down-regulated genes were

identified in the control strain. Deletion of the *atfA* gene markedly altered the co-regulated gene sets primarily by changing the reference transcriptome; not by changing the stress responsiveness of genes. The functional characterization of AtfA-dependent co-regulated genes demonstrated the involvement of AtfA in the regulation of both vegetative growth and conidiogenesis in untreated cultures. Our data also suggested that the diverse effects of *atfA* gene deletion on the transcriptome were the consequence of the altered transcription of several phosphorelay signal transduction system genes (Antal et al. 2019). Previously, oxidative stress (menadione sodium bisulfite, *tert*-butyl hydroperoxide, diamide) induced stress-specific modulation of the AtfA-dependent signaling networks had also been described and discussed in details by Orosz et al. (2017). Further on-going discussions aim at the transcriptional changes recorded on the secondary metabolite gene clusters of the fungus under various environmental stress conditions.

2. $CdCl_2$ exposure experiments suggested that the stress response of the control and the *ΔatfA* mutant strains were surprisingly different. Therefore, we repeated this experiment and studied the genome-wide transcriptional changes by high throughput RNA sequencing to obtain more accurate datasets. Transcriptional activities in the case of 12 genes were also recorded by RT-qPCR in both strains and in both treated and untreated cultures. The Pearson's correlation coefficient between the RNAseq and RT-qPCR data were 0.77. Both the control and *ΔatfA* strains showed up-regulation of the *crpA* Cu^{2+}/Cd^{2+} pump gene and AN7729 predicted to encode a putative bis(glutathionato)-cadmium transporter, and transcriptional changes associated with elevated intracellular Cys availability leading to the efficient adaptation to Cd^{2+}. Although the deletion of *atfA* did not alter the cadmium tolerance of the fungus the cadmium stress response of the mutant differed from that of a reference strain. Promoter and transcriptional analyses of the "Phospho-relay response regulator" genes suggested that the AtfA-dependent regulation of these genes could be relevant in this phenomenon. Most likely the regulatory network of *A. nidulans* has a high flexibility allowing the fungus to adapt efficiently to stress both in the presence and absence of this important transcription factor. Cadmium stress had minor effect on the transcription of "Secondary metabolite cluster" genes. A few clusters, however, showed up-regulation (inp cluster) or down-regulation (microperfuranone cluster, AN1242 cluster) (Emri et al. 2021).

3. In another work of Gila et al. (2022) we studied the genome-wide transcriptional changes of *A. nidulans* cultivated on glucose, lactose, or arabinogalactan, as well as under carbon-starved conditions. We determined both carbon-stress specific changes (weak or no carbon source vs. glucose) and carbon-source-specific changes (one type of culture vs. all other cultures) demonstrating that the highest number of downregulated clusters was observed on glucose but there also were clusters (Microperfuranone cluster, Pkh cluster, and AN3273 cluster) that showed upregulation relative to all the other cultures under this condition. Sterigmatocystin biosynthetic cluster was upregulated in the three carbon-stressed cultures, and the formation of this mycotoxin was also demonstrated in these cultures with TLC (Gila et al. 2022).

4. We also studied the effect of tyrosol on the global transcriptomic changes in *A. nidulans. A. nidulans* FGSC A4 strain was maintained on *Aspergillus* minimal medium (AMM) at 37 °C for 6 days. For RNA extraction, AMM broths (50 ml in 250 ml flasks) were inoculated with 1×10^6 conidia and were incubated at 24 °C with 3.7 Hz shaking frequency. Following 48 h incubation time, the mycelia were harvested and inoculated in fresh AMM medium for 5 h at 24 ºC. Then AMM medium was supplemented with a final concentration of 35 mM tyrosol and mycelia were collected 1 h following tyrosol exposure and stored at -70°C until use. Total RNA was isolated from control and tyrosol treated cultures in three biological replicates. RNA sequencing was carried out at the Genomic Medicine and Bioinformatics Core Facility, Department of Biochemistry and Molecular Biology, Faculty of Medicine, University of Debrecen. The FungiFun package was used to test the enrichment of genes related to FunCat and KEGG pathway categories in tyrosol-responsive genes in *A. nidulans*. Significant shared GO (gene ontology) terms were also determined with AspGD Gene Ontology Term Finder. Only hits with an adjusted p value of < 0.05 were taken into consideration during the evaluation process. The tyrosol treatment resulted in 2250 and 2199 differentially expressed genes with at least a 2-fold increase or decrease in expression. Genes involved in ergosterol biosynthesis, sulphate assimilation, ribosome biogenesis and RNA metabolic process showed downregulation, while genes related to autophagy, lactose utilization, and secondary metabolites biosynthesis as well as several lipase genes were upregulated. Tyrosol treatment also increased the transcription of the glutathione synthase gene (AN12476), several glutathione S-transferase genes (*gstA*, *gstB*, *gst3*, AN5831) and a putative ATPase-coupled glutathione S-conjugate transmembrane transporter (AN7729) gene. These transcriptional changes were accompanied with increased intracellular

glutathione content and elevated specific glutathione S-transferase activities of the cultures and suggest the glutathione dependent detoxification of tyrosol. A manuscript on these novel transcriptome data is under preparation.

5. We optimized unstressed and stress exposed cultures of the wild-type, and the *ΔFvatfA* and *ΔFvmnSOD* deletion mutant strains of *F. verticillioides* (Szabó et al. 2020b) prior to performing the planned large-scale total RNAseq-based transcriptomics studies. Shaken cultures were stress treated at 41 h (wild type and *ΔFvatfA* strains) and 47 h (*ΔFvmnSOD* strain) incubation times after inoculation with various concentrations of menadione sodium bisulfite (MSB). Dry cell mass of the cultures was determined after 24 h of stress treatment and growth inhibition values were calculated. Our goal was to find the MSB concentration which inhibited the growth of cultures approximately by 20-25 %. We also started to examine the response of *F. verticillioides* (FGSC 7600) wild-type, *ΔFvmnSOD* and *ΔFvatfA* deletion mutants to oxidative stress induced by MSB at the transcriptomic level. The experiments have been performed and the transcriptomic data are now under evaluation and discussion.

6. Similar culture optimizations were also done with the *A. nidulans* control and *ΔmnSOD* mutant strains. In this case, 16 h submerged cultures were treated with different concentrations of MSB for 30 min. Dry cell mass of the cultures was measured after 24 h of stress treatment and the optimal MSB concentration (0.12 mM) was selected for the *ΔmnSOD* mutant. We also started similar MSB inhibition optimization experiments with the orthologous *ΔmnSOD* mutant of *Aspergillus fumigatus* for RNAseq analysis. Comparative transcriptomics studies of *F. verticillioides*, *A. fumigatus* and *A. nidulans mnSOD* gene deletion strains will hopefully provide us with new pieces of information on the role of this antioxidant enzyme in a plant pathogenic, an opportunistic human pathogenic as well as in a saprophytic model fungus. We would like to gain a deeper insight in the global transcriptional effects of these gene deletions and MSB-induced oxidative stress on the expressions of the well-known and still function-unknown secondary metabolite gene clusters of these filamentous fungi. The transcriptomic responses of the control and *ΔmnSOD* mutant strains of *A. nidulans*, *F. fumigatus* and *F. verticillioides* liquid cultures to oxidative stress elicited by MSB have been studied at the transcriptomic level by RNAseq technique. We have started to analyze the gene expression data especially focusing on the expression patterns of function-unknown secondary metabolite gene clusters.

7. To support future omics-techniques based fungal stress biology and fungal evolutionary biology studies planned to be performed in our laboratory, we constructed the Fungal Stress Database (Orosz et al. 2018), which have been used successfully to estimate the physiological effects of stress gene losses and duplications on the environmental stress tolerance of various *Aspergillus* spp. (Emri et al. 2018). Furthermore, we connected the remarkable Cd^{2+} tolerance of *Aspergillus fumigatus* to the presence of the PcaA cadmium pump in this opportunistic human pathogen (Kurucz et al. 2018). The construction and applicability of fungal stress databases was presented by István Pócsi at The Third International Symposium on Fungal Stress – ISFUS-2019, São José dos Campos, Brazil (Alder-Rangel et al. 2020).

Papers published within the frame of this project:

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Tamás Emri (2019) Study on the stress responses of *Aspergillus* species, Hungarian Academy of Sciences, defended

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Erzsébet Vassné Orosz (2018) Oxidative stress response of *Aspergillus* spp., University of Debrecen, Debrecen, defended

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