Transcriptomic Dissection of the AMF-*Solanum melongena* Interaction: Unveiling Molecular Secrets

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Abstract:

Fungus-based biofertilizers, in particular, have been shown to improve plant growth and health by providing essential nutrients and improving soil health. Arbuscular mycorrhizal fungi (AMF) form mutualistic symbiotic relationships with plants, including those in the Solanaceae family. They colonize the root systems of plants and aid in enhancing nutrient absorption efficiency, particularly in phosphorus-deficient soils. The present study was carried out to study the interaction between *Solanum melongena* L. with *Glomus macrocarpum* and *Funneliformis mosseae* (formely known as *Glomus mosseae*) at transcript level. In this study a total of 365 transcripts were upregulated (>1.5x) folds in *S. melongena* in response to both the fungi, while 44 transcripts were upregulated only in response to *G. macrocarpum* and 28 transcripts were upregulated only in response to *F. mosseae*. Similarly, 49 transcripts were downregulated less than -1.5 folds in response to both the fungi while 78 were downregulated only in response to the *G. macrocarpum* and 36 were downregulated only in response to *F. mosseae*.

KEGG pathway analysis of *S. melongena* treated with *G. macrocarpum* revealed carbon metabolism, cofactor biosynthesis and Endocytosis as the dominant metabolic pathway, while analysis of the *F. mosseae* treatment revealed Glycerophospholipid and Endocytosis metabolism as dominant metabolic pathways.

Key words : Arbuscular Mycorrhizal Fungi, Biofertilizer, *Funneliformis mossae*, *Glomus macrocarpum* and Transcriptomics, *Solanum melongena*,

Introduction

Plants play a significant role in our ecosystem and human survival, and agriculture is the cornerstone of global food security. Investigations into the environmentally-friendly and sustainable methods are needed to boost crop yields in order to meet the growing global demand for food.

In the recent years, studies on the role of microorganisms in plant growth and sustainable agriculture has increased. Fungus-based biofertilizers, in particular, have been shown to improve plant growth and health by providing essential nutrients and improving soil health. Particularly, the advantageous effects of arbuscular mycorrhizal fungi (AMF) on a variety of crops, such as cereals, legumes, and vegetables, have been extensively studied (Chen et al., 2018; Begum et al., 2019; Khan et al., 2022; Sui et al., 2022).

Most AMF species are members of the phylum Mucoromycota's sub-phylum Glomeromycotina. (Spatafora et al., 2016). This sub-phylum contains 25 species and four orders of AMF, namely Glomerales, Archaeosporales, Paraglomerales, and Diversisporales (Redecker et al., 2013). They use lipids and products from plant photosynthetic processes to complete their life cycle since they are obligatory biotrophs (Bago et al., 2000, Jiang et al., 2017).

Glomus macrocarpum and *Funneliformis mosseae* are both species of arbuscular mycorrhizal fungi (AMF) that form mutualistic symbiotic relationships with plants, including those in the Solanaceae family. They colonize the root systems of plants and aid in enhancing nutrient absorption efficiency, particularly in phosphorus-deficient soils (Aziz et al., 2011). These fungi develop structures in the root cells of plants called arbuscules, which expand the root system's surface area and enable a direct interchange of nutrients between the fungus and the plant. This causes the plant to absorb more nutrients, which improves plant development and productivity.

The vegetable crop brinjal (*Solanum melongena* L.), which is widely grown in tropical and subtropical regions, may be a potential candidate for the use of fungus-based biofertilizers. The impact of these biofertilizers on the proteins in brinjal is not well understood, though. More effective and environmentally friendly agricultural practices might come from a better understanding of the molecular mechanisms by which fungus-based biofertilizers interact with and alter the physiology of brinjal.

Systems biology is a cross-disciplinary area of research that brings together numerous fields, including biology, mathematics, computer science, and engineering, to comprehend complex biological systems. In order to develop a thorough understanding of biological processes, the system biology entails the integration of high-throughput experimental data with computer models.

Systems biology approaches have fundamentally changed how we understand the way plants grow and develop as well as the way they react to environmental stress. Plant systems biology is the study of the structure, function, and interactions of plant molecules and networks using high-throughput technologies. These technologies include genomics, transcriptomics, proteomics, and metabolomics. The system biology has become a potent tool for comprehending intricate biological processes in plants, and it is anticipated to be crucial in the advancement of sustainable agriculture

The purpose of the research is to employ the system biology to understand the mechanism via which the fungal biofertilizers affect the transcriptome of brinjal. The investigation would clarify the molecular mechanisms and pathways underpinning the effects of fungus-based biofertilizers on brinjal.

Materials and Methods

Study site and Sampling

The study was conducted at botanical garden, department of botany, Banaras Hindu University, Varanasi, India located at 25° 16' 4.3608" N and 82° 59' 25.7784" E with an altitude of 81 metres above the sea level.

Inoculation of *Solanum melongena* L. plants

For the purpose, pot culture experiment was set up. Control and both the treatments were set up in triplicates. Pure culture of Funneliformis mosseae and Glomus macrocarpum was obtained by monoculturing both these isolates of AMF. For biofertilizer experiment brinjal seeds disinfected with 1% sodium hypochloride was placed on sterilized sand-soil substrate(1:1v/v) in 200 ml disposable plastic containers. The germination set up were kept in B.O.D incubator at 25□ under white fluorescent tubes (Photoperiod 12 hr) and watered whenever required to keep the soil mixture moist. After one month, germinated seedlings of S.melongena were transferred in 8 x 7.6 inch clay pots containing sterilized sand-soil substrate(1:1 v/v) with 10g each of both the inoculants. Uninoculated(control) plants were also maintained. AMF colonisation was ascertained by advanced microscopy.

Transcriptomics studies was done for the inoculations.

Results

The paired-end libraries of the transcripts of *Solanum melongena* L. plant treated without or with arbuscular mycorrhizal fungi, *Glomus macrocarpum* and *Funneliformis mosseae* were sequenced on the Illumina HiSeq platform.

Figure 1. Sample Correlation Matrix of the transcriptome libraries

The paired-end libraries of the transcripts of *Solanum melongena* L. plant treated without or with arbuscular mycorrhizal fungi, *G. macrocarpum* and *F. mosseae* were sequenced on the Illumina HiSeq platform. The control samples i.e., *S. melongena* L. plant not treated with the AMF had mean number of 21722156.5 reads (78.81%) with 109050 fragments per kilobase per million mapped reads (FPKM) value greater than or equal to 1.0. Similarly, BHUSJ2 sample i.e., *S. melongena* L. plant treated with *Glomus macrocarpum* had mean number of 2150827 reads (80.65%) with 57733 FPKM value $\geq$ 1.0 and BHUSJ3 sample i.e., *S. melongena* plant treated with *Funneliformis mossae* had mean number of 25187514 reads (81.52%) with 95655 FPKM value $\geq$ 1.0.

The sample correlation matrix of the transcriptome libraries revealed that BHUSJ3 sample was closer to the control samples as compared to the BHUSJ2 samples (Figure 2). The

observation implies that the *Glomus macrocarpum* had more pronounced effect on the transcriptomics of the *S. melongena* than that of the *Funneliformis mossae*.

The volcano plots and MA plots of the differentially expressed genes (DEGs) of the libraries are shown in the figure 3. Comparisons of the control library with BHUSJ2 i.e., genes of *S. melongena* when treated with the *Glomus macrocarpum*, revealed nearly 56897 DEGs, of which 33136 were statistically significant (Figure 3a). Out of the differentially expressed genes included 7608 upregulated transcripts and 25528 downregulated transcripts. of the upregulated transcripts 2685 genes were upregulated more than 1.5 folds while among the downregulated transcripts, 1285 genes were downregulated below -1.5 folds. Similarly, the comparisons of the control library with BHUSJ3 library i.e., genes of *S. melongena* when treated with the *Funneliformis mossae*, revealed nearly 51495 DEGs, of which 11599 were statistically significant (Figure 3b).

Out of the differentially expressed genes included 4314 upregulated transcripts and 7285 downregulated transcripts. Of the upregulated proteins, 1695 transcripts were upregulated to more than 1.5 folds while among the downregulated transcripts, 575 transcripts were downregulated below -1.5 folds. A total of 365 transcripts were upregulated more than 1.5 folds in *S. melongena* in response to both the fungi, *Glomus macrocarpum* and *Funneliformis mosseae*, while 44 transcripts were upregulated only in response to *G. macrocarpum* and 28 transcripts were upregulated only in response to *F. mosseae* (Figure 4a). Similarly, 49 transcripts were downregulated less than -1.5 folds in response to both the fungi while 78 were downregulated only in response to the *G. macrocarpum* and 36 were downregulated only in response to *F. mosseae* (Figure 4b).

a). Control Versus BHUSJ2   b). Control Versus BHUSJ3

Figure 2. MA and Volcano plots of the differentially expressing libraries

a). Upregulated transcript
b). Downregulated Transcript

Figure 3. Upregulated and Downregulated transcripts of BHUSSJ2 and BHUSSJ3 in relation to the control samples.

Gene Ontology and KEGG Pathway analysis of the BHUSJ2 and BHUSJ3 samples

The gene ontology analysis by the DAVID software revealed identified 101 different statistically significant "molecular functions" in the differentially expressed genes with the p value less than 0.05. The analysis revealed that the genes belonging to the protein binding dominated the transcript abundance in the BHUSJ2 sample representing the effect of *Glomus macrocarpum* on *S. melongena* with 19% of the genes involved followed by the ATP binding and metal binding activity with the involvement of 11.5 % and 9.3 % of the genes. The analysis of "cellular components" in which the genes were located revealed that the transcript of the membrane, chloroplast and cytoplasm dominated the differentially expressed genes with count 966 (19.2%), 941 (18.67%) and 914 (18.13%) respectively. Similarly, the "biological process" analysis revealed that the differentially expressed transcripts were dominated by the transcript involved in the embryo development leading to breaking the seed dormancy, protein phosphorylation, and salinity responsive transcripts with transcript count 145 (2.93%), 143 (2.89%) and 114 (2.3%) respectively. Pathway KEGG analysis of the DEGs revealed that the top three pathways in which these transcripts were involved included

carbon metabolism (76 transcripts - 9.5%), biosynthesis of cofactors (71 transcripts – 8.86%), and Endocytosis (56 transcripts – 7%) (Figure 8)

Figure 4: GO annotation representing Top 10 terms in the 'Molecular Function' category of Differential expressing transcripts of Control Versus BHUSJ2 Samples

Figure 5: GO annotation representing Top 10 terms in the 'Cellular Component' category of Differential expressing transcripts of Control Versus BHUSJ2 Samples

Figure 6: GO annotation representing Top 10 terms in the 'Biological Process' category
of Differential expressing transcripts of Control Versus BHUSJ2 Samples

The gene ontology analysis of BHUSJ3 sample representing the effect of *Funneliformis mosseae* on *S. melongena* revealed that the genes belonging to the function of "protein binding" dominated the DEGs with count = 640 (20.50%) followed by the ATP binding and metal ion binding with count = 410 (13.14%) and 313 (10.02 %) respectively. The analysis of "cellular components" in which the genes were located revealed that the transcript of the membrane, chloroplast and cytoplasm dominated the differentially expressed genes with count 691 (22.14 %), 620 (19.87 %) and 591 (18.94 %) respectively. Similarly, the "biological process" analysis revealed that the differentially expressed transcripts were dominated by the transcript involved in the protein phosphorylation, response to abscisic acid and drought-responsive transcripts with transcript counts 119 (3.81 %), 116 (3.72 %) and 112 (3.6%) respectively. Pathway KEGG analysis of the DEGs revealed that the Glycerophospholipid and Endocytosis metabolism were the dominant metabolic pathway with 34 transcripts (9%) each (Figure 12).

Figure 7: Figure of KEGG analysis representing pathway information related to transcript of Differential expressing transcripts of Control Versus BHUSJ2 Samples

Figure 8: GO annotation representing Top 10 terms in the 'Molecular Function' category of Differential expressing transcripts of Control Versus BHUSJ3

Figure 9: GO annotation representing Top 10 terms in the 'Cellular Component' category of Differential expressing transcripts of Control Versus BHUSJ3

Figure 10: GO annotation representing Top 10 terms in the 'Biological Process' category of Differential expressing transcripts of Control Versus BHUSJ3

Figure 11: KEGG analysis representing pathway information related to Differential expressing transcripts of Control Versus BHUSJ3.

DEAD-box helicases in the transcriptomes

Among the transcripts involved in the tolerance to salinity stress, DEAD-box helicase motif are known to play significant roles. DEAD-box ATP-dependent RNA helicase 16 (TRINITY_DN6185_c0_g1_i9 and TRINITY_DN2471_c0_g1_i1), helicase 18 (TRINITY_DN15662_c0_g1_i3 and TRINITY_DN20762_c0_g1_i6), and helicase 20 (TRINITY_DN19824_c0_g1_i34) (EC 3.6.4.13) were upregulated to 7.8, 9 and 5.5 folds respectively in *S. melongena* upon association with *G. macrocarpum* and 7.7, 9.7 and 6.9 folds upon association with *F. mosseae*. Another DEAD-box ATP-dependent RNA helicase 18 protein which is also known as, BRI1-KD-interacting protein 115 (BIP115) with Trinity Id TRINITY_DN15662_c0_g1_i5 was upregulated to 2.7x in response to *G. mossae*. Helicases, DEAD-box ATP-dependent RNA helicase 5 (TRINITY_DN22150_c0_g1_i7), helicase 10 (TRINITY_DN26429_c0_g1_i4), helicase 17 (TRINITY_DN8171_c0_g1_i8), helicase 32 (TRINITY_DN48781_c0_g1_i1), helicase 35 (TRINITY_DN1888_c0_g1_i5), helicase 52C (TRINITY_DN1065_c3_g1_i5) and helicase 58, chloroplastic (TRINITY_DN37178_c0_g1_i3) were upregulated to 1.7, 9.9, 2.1, 8.4, 2.7, 3.5, and 8.4

folds respectively in the case of *S. melogena* and *G. macrocarpum* association only. On the other hand, DEAD-box ATP-dependent RNA helicase 22 (TRINITY_DN13923_c0_g1_i1), helicase 36 (TRINITY_DN17609_c4_g1_i5), and helicase 40 (TRINITY_DN14283_c1_g1_i1) were upreguated to 9, 9, and 10.6 folds respectively upon *S. melogena* and *G. macrocarpum* association only . The DEAD-box ATP-dependent RNA helicase 50 (TRINITY_DN37563_c0_g1_i5) was upregulated upon *S. melogena* and *G. macrocarpum* association to 7.9 folds however, another variant of the helicase 50 (TRINITY_DN39418_c0_g1_i3) was decreased to 2 folds in the case of *S. melogena* and *F. mossae* association

The modulation of the DEAD box helicases during salinity stress has been correlated with the changes in the superoxide dismutase (Chen, 2016). The levels of superoxide dismutase [Cu-Zn] 2 (EC 1.15.1.1) (TRINITY_DN19272 c1 g1 i4) was upregulated to 9.7x in *S. melongena* in association with *G. macrocarpum* and 7.991x with *F. mosseae* .

Table 1: List of significantly modulated DEAD-box ATP-dependent RNA helicases and superoxide dismutase of *Solanum melongena* in association with either *F. mossae* or *G. macrocarpum*

Trinity Id	Name	*G. macrocarpum*	*F. mossae*
RINITY_DN19824_c0_g1_i34	DEAD-box ATP-dependent RNA helicase 20	6.844	5.540
RINITY_DN6185_c0_g1_i9	DEAD-box ATP-dependent RNA helicase 16	7.786	
RINITY_DN2471_c0_g1_i1	DEAD-box ATP-dependent RNA helicase 16		7.638
RINITY_DN15662_c0_g1_i3	DEAD-box ATP-dependent RNA helicase 18	9.647	
RINITY_DN15662_c0_g1_i5	DEAD-box ATP-dependent RNA helicase 18 (BRI1-KD-interacting protein 115) (BIP115)	2.664	
RINITY_DN20762_c0_g1_i6	DEAD-box ATP-dependent RNA helicase 18		9.061
RINITY_DN22150_c0_g1_i7	DEAD-box ATP-dependent RNA helicase 5	1.696	
RINITY_DN26429_c0_g1_i4	DEAD-box ATP-dependent RNA helicase 10	9.932	
RINITY_DN8171_c0_g1_i8	DEAD-box ATP-dependent RNA helicase 17	2.059	
RINITY_DN48781_c0_g1_i1	DEAD-box ATP-dependent RNA helicase 32	8.363	
RINITY_DN1888_c0_g1_i5	DEAD-box ATP-dependent RNA helicase 35	2.657	
RINITY_DN1065_c3_g1_i5	DEAD-box ATP-dependent RNA helicase 52C	3.517	
RINITY_DN37178_c0_g1_i3	DEAD-box ATP-dependent RNA helicase 58 chloroplastic	8.399	
RINITY_DN13923_c0_g1_i1	DEAD-box ATP-dependent RNA helicase 22		9.121
RINITY_DN17609_c4_g1_i5	DEAD-box ATP-dependent RNA helicase 36		8.911
RINITY_DN14283_c1_g1_i1	DEAD-box ATP-dependent RNA helicase 40		10.534
RINITY_DN37563_c0_g1_i5	DEAD-box ATP-dependent RNA helicase 50		7.964

Trinity Id	Name	G. macrocarpum	F. mossae
RINITY_DN39418_c0_g1_i3	DEAD-box ATP-dependent RNA helicase 50	-2.004	
RINITY_DN36611_c0_g1_i1	DEAD-box ATP-dependent RNA helicase 3, chloroplastic (Protein EMBRYO DEFECTIVE 1138)	-2.023	
RINITY_DN5165_c0_g1_i4	DEAD-box ATP-dependent RNA helicase 6	-1.633	
RINITY_DN5165_c0_g1_i1	DEAD-box ATP-dependent RNA helicase 8	-1.605	
RINITY_DN17915_c0_g1_i2	DEAD-box ATP-dependent RNA helicase 21	-2.293	
RINITY_DN22733_c0_g1_i6	DEAD-box ATP-dependent RNA helicase 24	-1.738	
RINITY_DN1272_c0_g2_i1	DEAD-box ATP-dependent RNA helicase 37	-2.145	
RINITY_DN1065_c3_g1_i7	DEAD-box ATP-dependent RNA helicase 11		-2.008
RINITY_DN26075_c0_g1_i1	DEAD-box ATP-dependent RNA helicase 42 (RCF1) (REGULATOR OF CBF GENE EXPRESSION 1)		-1.794
RINITY_DN4309_c0_g1_i3	DEAD-box ATP-dependent RNA helicase 56 (UAP56 homolog B)		-3.430
TRINITY_DN19272_c1_g1_i4	Superoxide dismutase [Cu-Zn] 2 (EC 1.15.1.1)	9.730	7.991
TRINITY_DN2333_c0_g1_i4	Receptor-like cytoplasmic kinase 176 (OsRLCK176) (EC 2.7.11.1)	4.310	2.412
TRINITY_DN20147_c0_g1_i2	Calmodulin-binding receptor-like cytoplasmic kinase 1 (EC 2.7.11.1)	4.016	
TRINITY_DN4521_c0_g1_i13	Serine/threonine-protein kinase PBL34 (EC 2.7.11.1) (PBS1-like protein 34) (Receptor-like cytoplasmic kinase PBL34)	2.994	
TRINITY_DN4374_c0_g1_i12	Serine/threonine-protein kinase PBL36 (EC 2.7.11.1) (PBS1-like protein 36) (Receptor-like cytoplasmic kinase PBL36)	1.890	
TRINITY_DN7927_c0_g1_i5	Glutathione S-transferase (EC 2.5.1.18) (25 kDa auxin-binding protein) (GST class-phi)		-1.576
TRINITY_DN6516_c0_g1_i19	Glutathione S-transferase T1 (AtGSTT1) (EC 2.5.1.18) (GST class-theta member 1)		9.048

Trinity Id	Name	G. macrocarpum	F. mossae
	(Glutathione S-transferase 10)		
TRINITY_DN6516_c0_g1_i21	Glutathione S-transferase T1 (AtGSTT1) (EC 2.5.1.18) (GST class-theta member 1) (Glutathione S-transferase 10)	9.102	
TRINITY_DN19508_c0_g1_i3	Glutathione S-transferase U9 (AtGSTU9) (EC 2.5.1.18) (GST class-tau member 9) (Glutathione S-transferase 14)		2.498
TRINITY_DN4653_c0_g1_i5	Glutathione S-transferase U17 (AtGSTU17) (EC 2.5.1.18) (GST class-tau member 17) (Glutathione S-transferase 30) (Protein EARLY RESPONSIVE TO DEHYDRATION 9)	2.133	
TRINITY_DN22883_c0_g1_i1	Glutathione S-transferase Z1 (AtGSTZ1) (EC 2.5.1.18) (GST class-zeta member 1) (Glutathione S-transferase 18) (Maleylacetone isomerase) (MAI) (EC 5.2.1.-)		1.856

Conclusion

Arbuscular mycorrhizal fungi have important role in the agriculture sector. The fungi associate with the roots of plants to form vesicles, arbuscules, and hyphae in roots, and also spores and hyphae in the rhizosphere. The fungi is known to confer a lot of advantage to the host plant in return of shelter including the ability to tolerate stress. The egg plant when treated with two different species of Glomus. viz G. mossae and G. macrocarpum, the two AMF species were found to differentially contribute to the stress tolerance to Solanum melanogena. The findings suggest more studies under salinity stress to gain more insight into the process.

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We do not have any conflict of interest to declare.

References:

Ahanger, M. A., Tyagi, S. R., Wani, M. R., Ahmad, P. (2014). "Drought tolerance: role of organic osmolytes, growth regulators, and mineral nutrients," in Physiological mechanisms and adaptation strategies in plants under changing environment, vol. 1 . Eds. Ahmad, P., Wani, MR (New York, NY: Springer), 25–55. doi: 10.1007/978-1-4614-8591-9_2

AZIZ, I & AYOOB, M & JITE, P. (2011). Response of Solanum melongena L. to Inoculation with Arbuscular Mycorrhizal Fungi under Low and High Phosphate Condition. Notulae Scientia Biologicae. 3. 10.15835/nsb.3.3.6106.

Begum N, Qin C, Ahanger MA, Raza S, Khan MI, Ashraf M, Ahmed M, Zhang L. Role of Arbuscular Mycorrhizal Fungi in Plant Growth Regulation: Implications in Abiotic Stress Tolerance. Front. Plant Sci., 2019. 10. https://doi.org/10.3389/fpls.2019.01068

Birhane, E., Sterck, F., Fetene, M., Bongers, F., Kuyper, T. (2012). Arbuscular mycorrhizal fungi enhance photosynthesis, water use efficiency, and growth of frankincense seedlings under pulsed water availability conditions. Oecologia 169, 895–904. doi: 10.1007/s00442-012-2258-3

Chen, J., Wan, S., Liu, H., Fan, S., Zhang, Y., Wang, W., Xia, M., Yuan, R., Deng, F. and Shen, F. (2016). Overexpression of an Apocynum venetum DEAD-Box Helicase Gene (AvDH1) in Cotton Confers Salinity Tolerance and Increases Yield in a Saline Field. Front Plant Science, 6, 1227. doi: 10.3389/fpls.2015.01227.

Chen M, Arato M, Borghi L, Nouri E, Reinhardt D. Beneficial Services of Arbuscular Mycorrhizal Fungi - From Ecology to Application. Front Plant Sci. 2018 Sep 4;9:1270. doi: 10.3389/fpls.2018.01270.

Fall, A.F.; Nakabonge, G.; Ssekandi, J.; Founoune-Mboup, H.; Apori, S.O.; Ndiaye, A.; Badji, A.; Ngom, K. Roles of Arbuscular Mycorrhizal Fungi on Soil Fertility: Contribution in the Improvement of Physical, Chemical, and Biological Properties of the Soil. Front. Fungal Biol. 2022, 3, 723892.

Gong, Z., Dong, C.H., Lee, H., Zhu, J., Xiong, L., Gong, D., et al., (2005) A DEAD box RNA helicase is essential for mRNA export and important for development and stress responses in Arabidopsis. The Plant cell, 17, 256-267. doi:10.1105/tpc.104.027557.

Guan, Q., Wu, J., Zhang, Y., Jiang, C., Liu, R., Chai, C., et al., (2013) A DEAD box RNA helicase is critical for pre-mRNA splicing, cold-responsive gene regulation, and cold tolerance in Arabidopsis. The Plant cell, 25, 342-356. doi: 10.1105/tpc.112.108340.

Kant, P., Kant, S., Gordon, M., Shaked, R. and Barak, S. (2007). STRESS RESPONSE SUPPRESSOR1 and STRESS RESPONSE SUPPRESSOR2, two DEAD-box RNA helicases that attenuate Arabidopsis responses to multiple abiotic stresses. Plant Physiology, 145(3), 814– 30. doi:10.1104/pp.107.099895.

Khan Y, Shah S, Hui T. The Roles of Arbuscular Mycorrhizal Fungi in Influencing Plant Nutrients, Photosynthesis, and Metabolites of Cereal Crops—A Review. Agronomy. 2022; 12(9):2191. https://doi.org/10.3390/agronomy12092191.

Kim, M. J., Kim, H. J., Pak, J. H., Cho, H. S., Choi, H. K., Jung, H. W., Lee, D. H. and Chung, Y. S. (2017). Overexpression of AtSZF2 from Arabidopsis showed enhanced tolerance to salt stress in soybean. Plant Breeding and Biotechnology, 5(1), 1–15. doi:10.9787/PBB.2017.5.1.1.

Li, D., Liu, H., Zhang, H., Wang, X. and Song, F. (2008) OsBIRH1, a DEAD-box RNA helicase with functions in modulating defence responses against pathogen infection and oxidative stress. Journal of experimental botany, 59: 2133-2146.

Linder, P. and Jankowsky, E. (2011) From unwinding to clamping - the DEAD boxRNA helicase family. Nature reviews. Molecular cell biology, 12: 505-516. doi: 10.1038/nrm3154.

Neha and Kharb P (2022). Psp68, A Dead Box Helicase Confers Salinity Tolerance in Transgenic Pigeon Pea. Int.J.Curr.Microbiol.App.Sci (2019) 8(4): 309-324.

Pandey T, Chhetri G, Chinta R, Kumar B, Singh DB, Tripathi T, Singh AK. Functional classification and biochemical characterization of a novel rho class glutathione S-transferase in Synechocystis PCC 6803, FEBS Open Bio, 5, 2015, 1-7, https://doi.org/10.1016/j.fob.2014.11.006.

Pasbani B, Salimi A, Aliasgharzad N, Hajiboland R, (2020). Colonization with arbuscular mycorrhizal fungi mitigates cold stress through improvement of antioxidant defense and accumulation of protecting molecules in eggplants, Scientia Horticulturae, 272, 109575, ISSN 0304-4238, https://doi.org/10.1016/j.scienta.2020.109575.

Pozo MaJ, Azcón-Aguilar C, Dumas-Gaudot E, Barea JM (1999) β-1,3-Glucanase activities in tomato roots inoculated with arbuscular mycorrhizal fungi and/or Phytophthora parasitica and their possible involvement in bioprotection. Plant Sci 141: 149-157

Rodriguez, R. J., Henson, J., Van Volkenburgh, E., Hoy, M., Wright, L., Beckwith, F., et al. (2008). Stress tolerance in plants via habitat-adapted symbiosis. Int. Soc. Microb. Ecol. 2, 404–416. doi: 10.1038/ismej.2007.106

Salam, E. A., Alatar, A., El-Sheikh, M. A. (2017). Inoculation with arbuscular mycorrhizal fungi alleviates harmful effects of drought stress on damask rose. Saudi J. Biol. Sci. 25 (8), 1772–1780. doi: 10.1016/j.sjbs.2017.10.015.

Shehab M, Iovene M, Ciancio A, Colagiero M, Finetti-sialer M (2022) Transcriptome analysis provides novel insights into salt stress response in two egyptian rice varieties with different tolerance levels. Rice Sci 29(6):499–502. https://doi.org/10.1016/j.rsci.2022.09.001

Shivakumara, T. N., Sreevathsa, R., Dash, P. K., Sheshshayee, M. S., Papolu, P. K., Rao, U., Tuteja, N. and UdayaKumar, M. (2017). Overexpression of Pea DNA Helicase 45 (PDH45) imparts tolerance to multiple abiotic stresses in chili (Capsicum annuum L.). Scientific Reports, 7(1), 1-12. doi:10.1038/s41598- 017-02589-0.

Song Y, Chen D, Lu K, Sun Z, Zeng R (2015) Enhanced tomato disease resistance primed by arbuscular mycorrhizal fungus. Front Plant Sci.

Sui X, Guan K, Chen Y, Xue R, Li A. A Legume Host Benefits More from Arbuscular Mycorrhizal Fungi Than a Grass Host in the Presence of a Root Hemiparasitic Plant. Microorganisms. 2022 Feb 15;10(2):440. doi: 10.3390/microorganisms10020440.

Tuteja, N. and Tuteja, R. (2004a) Prokaryotic and eukaryotic DNA helicases. Essential molecular motor proteins for cellular machinery. European journal of biochemistry / FEBS, 271, 1835-1848.

Tuteja, N. and Tuteja, R. (2004b) Unraveling DNA helicases. Motif, structure, mechanism and function. European journal of biochemistry / FEBS, 271, 1849-1863

Zeng DD, Qin R, Li M, Alamin M, Jin XL, Liu Y, Shi CH. The ferredoxin-dependent glutamate synthase (OsFd-GOGAT) participates in leaf senescence and the nitrogen

remobilization in rice. Mol Genet Genomics. 2017 Apr;292(2):385-395. doi: 10.1007/s00438-016-1275-z.