http://agriprojournal.com
JOURNAL OF AGRICULTURAL PRODUCTION
ISSN: 2757-6620
PRENSIP
https://prensip.gen.tr

RESEARCH ARTICLE

Polystyrene Nanoplastics Affect the Expression of Genes Involved in Cellular Processes in *Arabidopsis thaliana* (L.)

Yonca Surgun-Acar

Çanakkale Onsekiz Mart University, Faculty of Agriculture, Department of Agricultural Biotechnology, Çanakkale/Türkiye

ARTICLE INFO

Article History
Received: 03.04.2026
Accepted: 04.05.2026
First Published: 08.05.2026

Keywords
Arabidopsis thaliana (L.)
Gene expression
Nanoplastics
Stress

ABSTRACT

This study examines how polystyrene nanoplastics (PS-NPs) influence the expression of genes associated with cell cycle and stress responses in *Arabidopsis thaliana* leaves. For this purpose, seedlings were exposed to PS-NPs at concentrations of 0, 10, 20, and 40 mg L^{-1} for seven days under hydroponic conditions. Transmission electron microscopy analysis revealed that PS-NPs were predominantly spherical in morphology. The expression levels of genes associated with the cell cycle (*CYCD3;1*), cell wall modification (*TCH4* and *KOR*), detoxification (*MATE1* and *MATE2*) and stress response (*HSP70* and *HSP90.1*) were determined by qRT-PCR. PS-NPs exposure led to significant downregulation of *CYCD3;1*, *TCH4*, *KOR*, *HSP70*, *HSP90.1*, and *MATE2* expression, while *MATE1* gene was upregulated. These findings demonstrate that PS-NPs affect specific molecular processes and mechanisms in plants.

Please cite this paper as follows:
Surgun-Acar, Y. (2026). Polystyrene nanoplastics affect the expression of genes involved in cellular processes in *Arabidopsis thaliana* (L.). *Journal of Agricultural Production*, *7*(2), 89-96. https://doi.org/10.56430/japro.1922714

1. Introduction

Global plastic production has increased dramatically over recent decades, reaching hundreds of million tons annually and contributing substantially to widespread environmental pollution (Geyer et al., 2017). It is estimated that only 9% of plastic waste is recycled, whereas approximately 12% is incinerated and the remaining 79% accumulates in landfills or natural environments (OECD, 2019). Over time, plastics released into the environment undergo physical, chemical, and biological degradation processes, resulting in the formation of particles of various sizes. Particles smaller than 5 mm are defined as microplastics (MPs), while those with dimensions below 100 nm are classified as nanoplastics (NPs). The relatively low density of polystyrene (PS) particles facilitates their dispersal by water currents, enabling them to reach distant environments and thereby contributing to the widespread distribution of plastic pollution (Klein et al., 2015). The annual inputs of MPs/NPs from sewage and biosolids applied to agricultural soils are estimated to potentially exceed the total amount present in the oceans (Wang et al., 2020). This high level of MPs/NPs accumulation poses a significant risk to plant growth, food quality, and long-term agricultural sustainability (Liu et al., 2026).

The primary pathways through which MPs/NPs enter crop plants include the apoplastic route (L. Li et al., 2019), endocytosis (Jiang et al., 2022), crack-entry mechanisms (L. Li

---

Correspondence
E-mail address: yoncasurgun@gmail.com

et al., 2020), and stomatal uptake in leaves (Sun et al., 2021), followed by transport to above-ground tissues via xylem-driven transpiration (Z. Li et al., 2020). In *Arabidopsis thaliana*, negatively charged NPs can potentially be taken up by root hairs within the maturation zone (Sun et al., 2020). Accumulating evidence indicates that exposure to MPs/NPs induces diverse physiological toxicities in plants, including reduced biomass, enhanced oxidative stress, inhibition of photosynthetic activity, impaired water and nutrient uptake, genotoxic damage, and delayed seed germination (Lima et al., 2023).

Although substantial evidence has demonstrated that MPs/NPs induce physiological and oxidative damage, the molecular mechanisms underlying plant responses, particularly to NPs, remain poorly characterized. Therefore, this study aimed to examine the impact of PS-NPs on the expression of selected genes involved in cell cycle (*CYCD3;1*; cyclin D-type protein), cell wall organization (*TCH4;* xyloglucan endotransglucosylase/hydrolase family protein and *KOR*; glycosyl hydrolase 9A1), transport (*MATE1*; multidrug and toxic compound extrusion efflux family protein1 and *MATE2*; multidrug and toxic compound extrusion efflux family protein2), and stress response (*HSP70*; heat shock protein 70 and *HSP90.1*; heat shock protein 90.1) in *A. thaliana* leaves.

2. Materials and Methods

2.1. Morphology of PS-NPs

Carboxylated polystyrene nanoplastics (PS-NPs) with a diameter of 20–30 nm were commercially obtained from Thermo Fisher Scientific (Cat. No: F8787). The stock suspension contained 2% (w/v) solids and had a density of 1.05 g cm^{-3}; the excitation/emission wavelengths were specified as 505/515 nm. Morphological characterization of the PS-NPs was conducted using transmission electron microscopy (TEM; JEM-1400 Plus, Japan).

2.2. Plant Growth and Treatments

Arabidopsis thaliana (L.) ecotype *Columbia-0* was used as the plant material in this study. Seedlings were grown under hydroponic conditions using Hoagland solution (Hoagland & Arnon, 1938). Following a five-week growth period, seedlings were subjected to PS-NPs at final concentrations of 0, 10, 20, and 40 mg L^{-1} for a duration of seven days (Surgun-Acar, 2022). To obtain a homogeneous suspension, the PS-NPs stock solution was sonicated at low power for 3 min before use. Three independent glass hydroponic tanks were used for each treatment. During the exposure period, plants were maintained in a controlled-environment growth chamber at 22±2ºC under a 16 h light/8 h dark regime. The hydroponic solution was supplied with constant aeration and renewed at two-day intervals. At the end of the treatment period, leaf tissues were harvested, rapidly frozen in liquid nitrogen, and stored at -80ºC until gene expression analyses.

2.3. Gene Expression Analysis

Approximately 0.1 g of leaf material from control and treated plants was used for total RNA extraction using the Plant RNA Mini Prep Kit (Zymo Research, USA). RNA concentration and purity were assessed by UV spectrophotometry and agarose gel electrophoresis, followed by DNase I treatment to eliminate residual genomic DNA. First-strand cDNA was generated from 1 µg of total RNA using the cDNA Synthesis Kit (Thermo Fisher Scientific, Germany) in accordance with the supplier's protocol. The expression levels of *CYCD3;1* (*At4g34160*), *TCH4* (*At5g57560*), *KOR* (*At5g49720*), *MATE1* (*At2g04050*), *MATE2* (*At2g05070*), *HSP70* (*At3g12580*), and *HSP90.1* (*At5g52640*) genes were analyzed by quantitative reverse transcription PCR (qRT-PCR). Optimal annealing temperatures for each primer pair were determined experimentally, and primer details are summarized in Table 1. qRT-PCR reactions were performed using a StepOnePlus™ Real-Time PCR System (Thermo Fisher Scientific, Germany) with the 2X AMPIGENE qPCR Green Mix Hi-ROX Kit (Enzo Life Sciences, USA). Each reaction contained 5 µL of 2X AMPIGENE qPCR Green Mix Hi-ROX, 4 µL of diluted cDNA (1:10), 0.4 µL each of forward and reverse primers, and 0.2 µL of ddH$_2$O. The thermal cycling program consisted of an initial denaturation step at 95ºC for 10 min, followed by 40 cycles of 15 s at 95ºC, 30 s at 57ºC, and 1 min at 72ºC. The specificity of the amplified products was confirmed by melting curve analysis. Relative transcript abundance of the target genes was determined using the $2^{-\Delta\Delta Ct}$ method (Livak & Schmittgen, 2001), with *TUB2* (*At5g62690*; internal control) gene used as the reference gene.

2.4. Statistical Analysis

For each treatment, qRT-PCR analyses were conducted using three biological replicates and three technical replicates. Statistical evaluation of the data was performed using one-way analysis of variance (ANOVA), followed by Duncan's multiple range test to assess differences among treatments. Results were considered statistically significant at $p<0.05$ and are presented as mean±standard error (SE).

Table 1. Locus numbers, descriptions, and primer sequences of the genes used in the study.

Gene name	**Locus ID**	**Description**	**Primer sequence (5′- 3′)**	**Reference**
CYCD3;1	*At4g34160*	Cyclin D-type protein	F-TCGTTGAACAGTCCAAGCTG R-TGCAAAATCGGCTTCTTCTT	Surgun and Bürün (2015)
TCH4	*At5g57560*	Xyloglucan endotransglucosylase/ hydrolase family protein	F-CAAGAACATGGAGTCTCTAGGCAC R-GTGAAAGGAGCTTTAGACCAATCG	Surgun and Bürün (2015)
KOR	*At5g49720*	Glycosyl hydrolase 9A1	F-GTCCAACGGAGCAGAAGAAG R-TTGGCAATTTCCCAGATTTC	Surgun and Bürün (2015)
MATE1	*At2g04050*	Multidrug and toxic compound extrusion (MATE) efflux family protein	F-CGTTTCCGGGTTCAGTATTT R-CAGGGTCTTGACCGAGAGAG	Kasajima and Fujiwara (2007)
MATE2	*At2g05070*	Multidrug and toxic compound extrusion (MATE) efflux family protein	F-TGTCTCCGGTTTCAGCATTA R-TGTTAGAGGAAATTGCGGAGT	Kasajima and Fujiwara (2007)
HSP70	*At3g12580*	Heat shock protein 70	F-GGAAAGTTCGAGCTCAGTGG R-ACCTTCCCTTGTCGTTTGTG	Surgun et al. (2016)
HSP90.1	*At5g52640*	Heat shock protein 90-1	F-AAACGCTCTCGAAGTTCCAA R-TGAGCTCACGGAGGAAGATT	Surgun et al. (2016)
TUB2	*At5g62690*	Internal control	F-ATCCGTGAAGAGTACCCAGAT R-AAGAACCATGCACTCATCAGC	Surgun-Acar (2026)

3. Results

Transmission electron microscopy analysis revealed that PS-NPs predominantly exhibited a smooth, spherical morphology; however, the NPs were not uniformly dispersed and showed a marked tendency toward agglomeration (Figure 1).

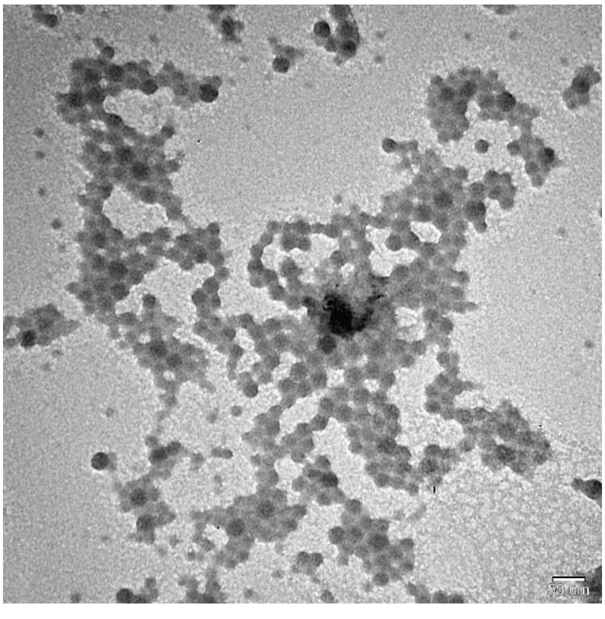

Figure 1. Transmission electron microscopy (TEM) images of PS-NPs. Scale bar: 50 nm.

Following a seven-day exposure period, PS-NPs treatments at concentrations of 10, 20, and 40 mg L^{-1} resulted in a 2.49-, 3.04-, and 2.12-fold decrease, respectively, in *CYCD3;1* expression compared with the control (Figure 2A). The mRNA level of the *TCH4* gene in leaf tissue was downregulated by 2.28-fold and 1.25-fold following application of 20 and 40 mg L^{-1} PS-NPs, respectively (Figure 2B). Exposure to 10 mg L^{-1} PS-NPs led to a more pronounced 2.23-fold reduction in the transcript level of the *KOR* gene, whereas treatments with 20 and 40 mg L^{-1} PS-NPs caused similar decreases (1.65- and 1.55-fold, respectively) (Figure 2C).

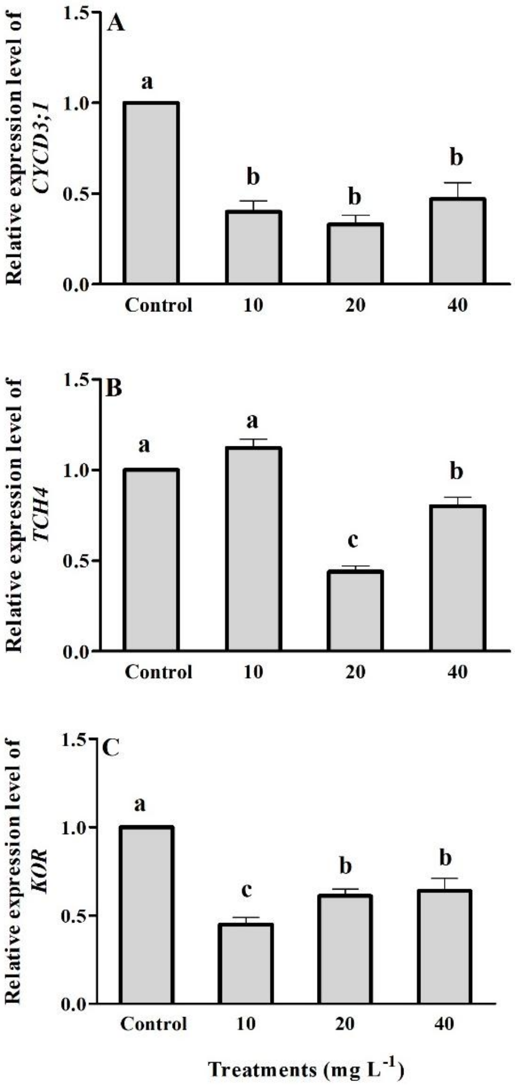

Figure 2. Effects of seven-day PS-NPs treatment at different concentrations on the expression of (A) *CYCD3;1*, (B) *TCH4*, and (C) *KOR* genes in *Arabidopsis* leaf tissue. Data are presented as mean±SE (n=3). Bars with different letters indicate significant differences at p<0.05.

Under PS-NPs conditions, the expression of multidrug and toxic compound extrusion (MATE) efflux family genes in *Arabidopsis* leaves was differentially regulated (Figure 3). The expression level of *MATE1* increased across all PS-NP concentrations, with more pronounced induction observed in the leaves of seedlings exposed to 20 and 40 mg L^{-1} PS-NPs (Figure 3A). In contrast, *MATE2* transcript levels were reduced following PS-NPs application, showing 3.66-, 1.88-, and 2.61-fold decreases at 10, 20, and 40 mg L^{-1}, respectively, relative to the control (Figure 3B).

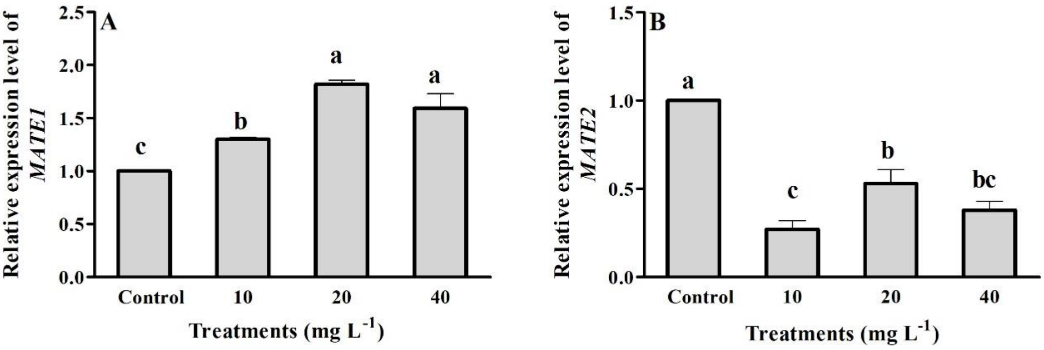

Figure 3. Effects of seven-day PS-NPs treatment at different concentrations on the expression of (A) *MATE1* and (B) *MATE2* genes in *Arabidopsis* leaf tissue. Data are presented as mean±SE (n=3). Bars with different letters indicate significant differences at p<0.05.

HSP70 and *HSP90.1* genes exhibited similar expression patterns in the leaves of *Arabidopsis* seedlings following PS-NPs applications (Figure 4). At 10 mg L^{-1}, PS-NPs caused an 8.22-fold reduction in *HSP70* expression in leaf tissue, whereas concentrations of 20 and 40 mg L^{-1} resulted in decreases of 1.86- and 2.40-fold, respectively (Figure 4A). Similarly, 10 mg L^{-1} PS-NPs markedly downregulated *HSP90.1* expression, with a 6.53-fold decrease. At higher concentrations (20 and 40 mg L^{-1}), reductions in *HSP90.1* mRNA levels were 1.56- and 2.56-fold, respectively (Figure 4B).

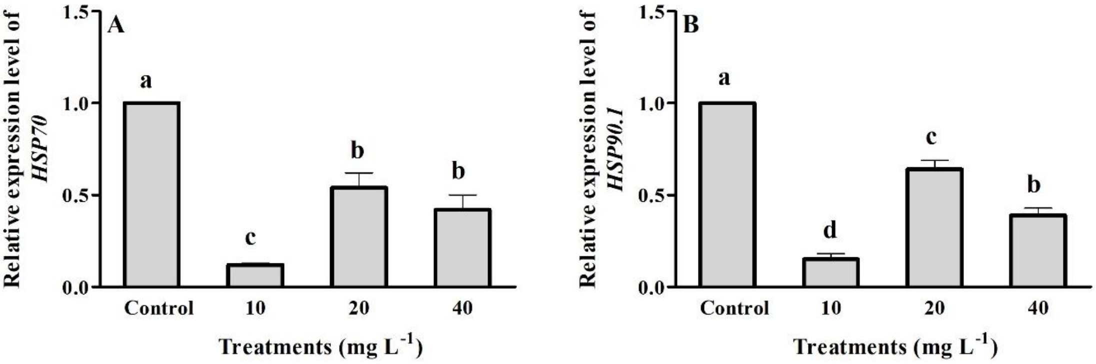

Figure 4. Effects of seven-day PS-NPs treatment at different concentrations on the expression of (A) *HSP70* and (B) *HSP90.1* genes in *Arabidopsis* leaf tissue. Data are presented as mean±SE (n=3). Bars with different letters indicate significant differences at $p<0.05$.

4. Discussion

The presence of MPs/NPs can stimulate reactive oxygen species (ROS) production, causing oxidative damage at the cellular level and compromising genetic integrity (Giorgetti et al., 2020). Plants mitigate these detrimental effects through multiple defense mechanisms, such as transcriptional regulation of stress-adaptive genes (Hu et al., 2024). In line with this, we investigated the impact of PS-NPs on the molecular regulation of genes associated with growth, detoxification, and stress responses.

In *A. thaliana*, *CYCD3;1* (cyclin D-type protein) is predominantly expressed in proliferative tissues and functions as a key regulator of G1-to-S phase transition in the cell cycle. Constitutive overexpression of *CYCD3;1* enhances mitotic cycling while suppressing endoreduplication leading to pronounced alterations in leaf architecture (Dewitte et al., 2003). PS-NPs caused a significant downregulation of *CYCD3;1* expression in leaves compared with the control. Maity et al. (2020) reported that 100 nm PS-MPs at varying concentrations induced cytotoxic effects in *Allium cepa*, as indicated by reduced mitotic activity and downregulation of *cdc2*, a cyclin-dependent kinase essential for cell cycle regulation. Furthermore, MPs/NPs of different sizes and polymer types significantly reduced leaf area and other growth parameters in *Lactuca sativa* (Lian et al., 2021) and *Glycine max* (B. Li et al., 2021). These findings suggest that PS-NPs–induced stress, potentially mediated via metabolic or oxidative signaling pathways, may disrupt cell cycle checkpoints and reduce proliferative activity, thereby influencing leaf growth and development.

Plant cell walls serve as the primary barrier against harmful substances and exhibit considerable plasticity, enabling adaptive restructuring in response to environmental stresses (Houston et al., 2016). The primary cell wall is largely composed of cellulose, hemicellulose, and pectin. In dicot species such as *A. thaliana*, xyloglucan represents the predominant hemicellulosic polysaccharide (Fry, 1989). The incorporation and remodeling of newly synthesized xyloglucan are mediated by members of the XTH (xyloglucan endotransglucosylase/hydrolase) family, which includes enzymes with transglucosylase (XET) and hydrolase (XEH) activities that regulate cell wall restructuring (Rose et al., 2002; Thompson & Fry, 2001). *TCH4* (also referred to as *XTH22*) encodes an XET enzyme and is highly responsive to environmental changes, exhibiting rapid transcriptional activation under mechanical and thermal stress conditions as well as following auxin and brassinosteroid application (Xu et al., 1996). In the cell wall, endoglucanases (E.C.3.2.1.4) can hydrolyze the β-1,4 linkages of cellulose chains, and the membrane-bound endoglucanase Korrigan (KOR) has been demonstrated to be essential for the formation of a structured, cellulose–hemicellulose network (Maloney et al., 2011). In this study, PS-NPs led to downregulation of both *TCH4* and *KOR* gene expression levels. The concurrent reduction of these genes across PS-NPs concentrations points to the possibility that both the flexibility and structural integrity of the cell wall may be compromised, potentially restricting tissue expansion and overall leaf growth. Chen et al. (2025) showed that under europium-doped PS-NPs stress, the reduction in xyloglucan via XTH is accompanied by an increase in other hemicellulosic polysaccharides, likely reinforcing the cell wall and restricting root elongation in *Oryza sativa*. This structural adjustment acts as an adaptive mechanism limiting NPs toxicity and internalization.

Members of the multidrug and toxic compound extrusion (MATE) protein family (also called Detoxification Efflux Carriers, DTXs) function as efflux transporters that facilitate the transport of a broad spectrum of substrates, including organic acids, phytohormones, and secondary metabolites. In plants, these transporters are also associated with detoxification processes and heavy metal tolerance, and they participate in the regulation of stress and defense responses (Takanashi et al., 2014). In *A. thaliana*, *MATE1* and *MATE2* encode plasma membrane–localized detoxification proteins that play a role in the removal of various toxic compounds, including heavy metals (Upadhyay et al., 2019). In the present study, PS-NPs induced differential regulation of *MATE* transporter genes in leaves. This contrasting response suggests a possible functional divergence within the MATE transporter family. Previous studies have reported that the expression levels of the *MATE* transporter genes *AtDTX1* and *AtDTX3* significantly increased in the leaves of *A. thaliana* exposed to boron and manganese stress, respectively (Kasajima & Fujiwara, 2007; Surgun-Acar & Zemheri-Navruz, 2022).

Heat shock proteins (HSPs) represent a key component of the plant stress-response system, contributing to the maintenance of protein homeostasis under adverse conditions. Among these proteins, HSP70 functions in the refolding and trafficking of misfolded proteins and can also regulate the activity of heat shock transcription factors (HSFs) (Kim & Schoffl, 2002). HSP90 proteins facilitate protein folding and sorting, thereby maintaining cellular stability by mitigating the effects of mutations under stress (Queitsch et al., 2002). Our results showed decreased expression of *HSP70* and *HSP90.1* in leaves under NPs-induced stress, potentially impairing cellular defense mechanisms and disrupting protein regulation. In a study conducted on barley, it was found that members of three different *HSP* gene families (*HSP70*, *HSP90*, and *HSP100*) exhibited differential and tissue-specific expression under normal conditions as well as various stress conditions, including heat, heavy metal, drought, and salinity stress (Chaudhary et al., 2019).

5. Conclusion

Overall, this study demonstrates that PS-NPs modulate key molecular processes in *Arabidopsis thaliana* leaves. The decrease in *CYCD3;1* could limit cell proliferation, while changes in *TCH4* and *KOR* may alter cell wall properties. Differential regulation of *MATE* transporter genes suggests potential impacts on detoxification processes, and reduced expression of *HSP70* and *HSP90.1* indicates effects on cellular stress responses. These findings provide a useful starting point for future investigations into the molecular mechanisms underlying PS-NPs–induced stress in plants.

Compliance with Ethical Standards

This study does not require ethical committee approval.

Conflict of Interest

The author declares that there is no conflict of interest related to this article.

Disclosure of Generative AI Use

ChatGPT (OpenAI) was used for language editing and grammar refinement.

References

Chaudhary, R., Baranwal, V. K., Kumar, R., Sircar, D., & Chauhan, H. (2019). Genome-wide identification and expression analysis of *Hsp70*, *Hsp90*, and *Hsp100* heat shock protein genes in barley under stress conditions and reproductive development. *Functional & Integrative Genomics*, *19*(6), 1007-1022. https://doi.org/10.1007/s10142-019-00695-y

Chen, C., Liu, J., Xing, C., Wu, X. L., Zhu, E., Rao, Y., Lin, Y., Yan, J., Cai, M., Zhang, H., & Luo, Y. (2025). From stress to defense: Spatial confinement of nanoplastics in rice root cell walls via pectin matrix remodeling. *Journal of Hazardous Materials*, *498*, 139887. https://doi.org/10.1016/j.jhazmat.2025.139887

Dewitte, W., Riou-Khamlichi, C., Scofield, S., Healy, J. S., Jacqmard, A., Kilby, N. J., & Murray, J. A. (2003). Altered cell cycle distribution, hyperplasia, and inhibited differentiation in Arabidopsis caused by the D-type cyclin CYCD3. *The Plant Cell*, *15*(1), 79-92. https://doi.org/10.1105/tpc.004838

Fry, S. C. (1989). Cellulases, hemicelluloses and auxin-stimulated growth: A possible relationship. *Physiologia Plantarum*, *75*(4), 532-536. https://doi.org/10.1111/j.1399-3054.1989.tb05620.x

Geyer, R., Jambeck, J. R., & Law, K. L. (2017). Production, use, and fate of all plastics ever made. *Science Advances*, *3*(7), e1700782. https://doi.org/10.1126/sciadv.1700782

Giorgetti, L., Spanò, C., Muccifora, S., Bottega, S., Barbieri, F., Bellani, L., & Castiglione, M. R. (2020). Exploring the interaction between polystyrene nanoplastics and *Allium cepa* during germination: Internalization in root cells, induction of toxicity and oxidative stress. *Plant Physiology and Biochemistry*, *149*, 170-177. https://doi.org/10.1016/j.plaphy.2020.02.014

Hoagland, D. R., & Arnon, D. I. (1938). *The water culture method for growing plants without soil*. Circular California Agricultural Experiment Station.

Houston, K., Tucker, M. R., Chowdhury, J., Shirley, N., & Little, A. (2016). The plant cell wall: A complex and dynamic structure as revealed by the responses of genes under stress conditions. *Frontiers in Plant Science*, *7*, 984. https://doi.org/10.3389/fpls.2016.00984

Hu, M., Huang, Y., Liu, L., Ren, L., Li, C., Yang, R., & Zhang, Y. (2024). The effects of Micro/Nano-plastics exposure on plants and their toxic mechanisms: A review from multi-omics perspectives. *Journal of Hazardous Materials*, *465*, 133279. https://doi.org/10.1016/j.jhazmat.2023.133279

Jiang, M., Wang, B., Ye, R., Yu, N., Xie, Z., Hua, Y., Zhou, R., Tian, B., & Dai, S. (2022). Evidence and impacts of nanoplastic accumulation on crop grains. *Advanced Science*, *9*(33), 2202336. https://doi.org/10.1002/advs.202202336

Kasajima, I., & Fujiwara, T. (2007). Identification of novel *Arabidopsis thaliana* genes which are induced by high levels of boron. *Plant Biotechnoloy*, *24*, 355-360. https://doi.org/10.5511/plantbiotechnology.24.355

Kim, B. H., & Schoffl, F. (2002). Interaction between *Arabidopsis* heat shock transcription factor 1 and 70 kDa heat shock proteins. *Journal of Experimental Botany*, *53*(367), 371-375. https://doi.org/10.1093/jexbot/53.367.371

Klein, S., Worch, E., & Knepper, T. P. (2015). Occurrence and spatial distribution of microplastics in river shore sediments of the Rhine-Main in Germany. *Environmental Science & Technology*, *49*(10), 6070-6076. https://doi.org/10.1021/acs.est.5b00492

Li, L., Zhou, Q., Yin, N., Tu, C., & Luo, Y. (2019). Uptake and accumulation of microplastics in an edible plant. *Chinese Science Bulletin*, *64*(9), 928-934. https://doi.org/10.1360/n972018-00845

Li, L., Luo, Y., Li, R., Zhou, Q., Peijnenburg, W. J. G. M., Yin, N., Yang, J., Tu, C., & Zhang, Y. (2020). Effective uptake of submicrometre plastics by crop plants via a crack-entry mode. *Nature Sustainability*, *3*, 929-937. https://doi.org/10.1038/s41893-020-0567-9

Li, Z., Li, R., Li, Q., Zhou, J., & Wang, G. (2020). Physiological response of cucumber (*Cucumis sativus* L.) leaves to polystyrene nanoplastics pollution. *Chemosphere*, *255*, 127041. https://doi.org/10.1016/j.chemosphere.2020.127041

Li, B., Huang, S., Wang, H., Liu, M., Xue, S., Tang, D., Cheng, W., Fan, T., & Yang, X. (2021). Effects of plastic particles on germination and growth of soybean (*Glycine max*): A pot experiment under field condition. *Environmental Pollution*, *272*, 116418. https://doi.org/10.1016/j.envpol.2020.116418

Lian, J., Liu, W., Meng, L., Wu, J., Chao, L., Zeb, A., & Sun, Y. (2021). Foliar-applied polystyrene nanoplastics (PSNPs) reduce the growth and nutritional quality of lettuce (*Lactuca sativa* L.). *Environmental Pollution*, *280*, 116978. https://doi.org/10.1016/j.envpol.2021.116978

Lima, J. Z., Cassaro, R., Ogura, A. P., &Vianna, M. M. G. R. (2023). A systematic review of the effects of microplastics and nanoplastics on the soil-plant system. *Sustainable Production and Consumption*, *38*, 266-282. https://doi.org/10.1016/j.spc.2023.04.010

Liu, Y., Wu, X., Le, X., Cheng, H., Peng, Q., Wen, L., Hou, H., Hayat, K., Liu, W., & Yin, S. (2026). Multiomics insights into the ecotoxicological effects of soil microplastics on crop plants. *Journal of Agricultural and Food Chemistry*, *74*(7), 5832-5844. https://doi.org/10.1021/acs.jafc.5c11305

Livak, K. J., & Schmittgen, T. D. (2001). Analysis of relative gene expression data using real-time quantitative PCR and the $2^{-\Delta\Delta CT}$ method. *Methods*, *25*(4), 402-408. https://doi.org/10.1006/meth.2001.1262

Maity, S., Chatterjee, A., Guchhait, R., De, S., & Pramanick, K. (2020). Cytogenotoxic potential of a hazardous material, polystyrene microparticles on *Allium cepa* L. *Journal of Hazardous Materials*, *385*, 121560. https://doi.org/10.1016/j.jhazmat.2019.121560

Maloney, V. J., Samuels, A. L., & Mansfield, S. D. (2011). The endo-1, 4-β-glucanase *Korrigan* exhibits functional conservation between gymnosperms and angiosperms and is required for proper cell wall formation in gymnosperms. *New Phytologist*, *193*(4), 1076-1087. https://doi.org/10.1111/j.1469-8137.2011.03998.x

OECD. (2019). *Plastic use in 2019*. https://doi.org/10.1787/efff24eb-en

Queitsch, C., Sangster, T. A., & Lindquist, S. (2002). Hsp90 as a capacitor of phenotypic variation. *Nature*, *417*, 618-624. https://doi.org/10.1038/nature749

Rose, J., Braam, J., Fry, S. C., & Nishitani, K. (2002). The XTH family of enzymes involved in xyloglucan endotransglucosylation and endohydrolysis: Current perspectives and a new unifying nomenclature. *Plant and Cell Physiology*, *43*(12), 1421-1435. https://doi.org/10.1093/pcp/pcf171

Sun, H., Lei, C., Xu, J., & Li, R. (2021). Foliar uptake and leaf-to-root translocation of nanoplastics with different coating charge in maize plants. *Journal of Hazardous Material*, *416*, 125854. https://doi.org/10.1016/j.jhazmat.2021.125854

Sun, X. -D., Yuan, X. -Z., Jia, Y., Feng, L. -J., Zhu, F. -P., Dong, S. -S., Liu, J., Kong, X., Tian, H., Duan, J. -L., Ding, Z., Wang, S. -G., & Xing, B. (2020). Differentially charged nanoplastics demonstrate distinct accumulation in *Arabidopsis thaliana*. *Nature Nanotechnology*, *15*(9), 755-760. https://doi.org/10.1038/s41565-020-0707-4

Surgun, Y., & Bürün, B. (2015). Analysis of effects of 24-epibrassinolide and boron treatments on the expression of *CycD3; 1*, *TCH4* and *KOR* genes in *Arabidopsis thaliana* (L.) heynh seedlings using semi-quantitative

RT-PCR. *Journal of Applied Biological Sciences*, *9*(3), 59-65.

Surgun, Y., Çöl, B., & Bürün, B. (2016). Differential expression analysis of boron transporters and some stress-related genes in response to 24-epibrassinolide and boron by semi-quantitative RT-PCR in *Arabidopsis thaliana* (L.) Heynh. *Genetika*, *48*(2), 547-563. https://doi.org/10.2298/GENSR1602547S

Surgun-Acar, Y. (2022). Response of soybean (*Glycine max* L.) seedlings to polystyrene nanoplastics: Physiological, biochemical, and molecular perspectives. *Environmental Pollution*, *314*, 120262. https://doi.org/10.1016/j.envpol.2022.120262

Surgun-Acar, Y., & Zemheri-Navruz, F. (2022). Exogenous application of 24-epibrassinolide improves manganese tolerance in *Arabidopsis thaliana* L. via the modulation of antioxidant system. *Journal of Plant Growth Regulation*, *41*(2), 546-557. https://doi.org/10.1007/s00344-021-10320-7

Surgun-Acar, Y. (2026). The impact of polystyrene nanoplastics on lignin biosynthesis in *Arabidopsis thaliana* (L.). *Physiology and Molecular Biology of Plants*, *32*, 81-94. https://doi.org/10.1007/s12298-025-01698-9

Takanashi, K., Shitan, N., & Yazaki, K. (2014). The multidrug and toxic compound extrusion (MATE) family in plants. *Plant Biotechnology*, *31*(5), 417-430. https://doi.org/10.5511/plantbiotechnology.14.0904a

Thompson, J. E., & Fry, S. C. (2001). Restructuring of wall-bound xyloglucan by transglycosylation in living plant cells. *The Plant Journal*, *26*(1), 23-34. https://doi.org/10.1046/j.1365-313x.2001.01005.x

Upadhyay, N., Kar, D., Deepak Mahajan, B., Nanda, S., Rahiman, R., Panchakshari, N., Bhagavatula, L., & Datta, S. (2019). The multitasking abilities of MATE transporters in plants. *Journal of Experimental Botany*, *70*(18), 4643-4656. https://doi.org/10.1093/jxb/erz246

Wang, W., Ge, J., Yu, X., & Li, H. (2020). Environmental fate and impacts of microplastics in soil ecosystems: Progress and perspective. *Science of The Total Environment*, *708*, 134841. https://doi.org/10.1016/j.scitotenv.2019.134841

Xu, W., Campbell, P., Vargheese, A. K., & Braam, J. (1996). The Arabidopsis XET-related gene family: Environmental and hormonal regulation of expression. *The Plant Journal*, *9*(6), 879-889. https://doi.org/10.1046/j.1365-313X.1996.9060879.x