

# From soil to shoot plant responses to polystyrene nanoplastics and relevance for sustainable food systems

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## ABSTRACT

Within the One Health framework, plants represent a critical interface between environmental contaminants and the food web. Among emerging pollutants, polystyrene nanoplastics (PS-NPs) are particularly concerning due to their small size, high surface reactivity, and ability to cross biological barriers. PS-NPs can be potentially internalized through roots or leaves, translocated to other organs, and, in some cases, accumulated in edible tissues, posing risks to food safety and human health. This review explores PS-NPs behavior in plants, focusing on uptake mechanisms, translocation pathways, accumulation sites, and physiological and molecular responses in different plant species, both model and crops. While wheat shows tolerance even at high PS-NPs concentrations, species like rice, lettuce, and garlic exhibit growth inhibition, oxidative stress, nutrient imbalances, and genotoxic effects. Transcriptomic studies confirm that PS-NPs alter gene expression linked to redox homeostasis, hormone signaling, and stress responses, though the specific pathways affected differ across species and conditions. Overall, plant species and PS-NPs concentration emerge as key factors determining phytotoxic outcomes. The detection of PS-NPs in edible plant parts highlights a tangible risk for humans. Standardized analytical methods, realistic scenarios, and the identification of molecular markers of tolerance are urgently needed to better assess and mitigate the impact of PS-NPs on agriculture and food safety within the One Health perspective.

## 1. Introduction

In the context of the One Health framework, which emphasizes the interconnection between the health of ecosystems, plants and animals, including humans, understanding the pathways through which environmental contaminants enter the food web is pivotal (Atlas,2013; Dangetal.,2022;Lebovetal.,2017;Morrisonetal.,2022;Saarimäkietal.,2023). Plants represent the primary node in the trophic network, acting as the first biological interface between environmental inputs and living organisms. As primary producers, they convert solar energy into chemical energy, synthesizing organic molecules from CO<sub>2</sub> and water, and serve as essential sources of nutrients for heterotrophic organisms (Balpardaetal.,2023;Pieterseetal.,2014). Any contaminant that interferes with plant growth, physiology, or metabolism can trigger cascading effects throughout ecosystems. These effects not only compromise plant productivity, central to food security, but also affect the safety of plant-derived food, raising important concerns for both

human and animal health. Among emerging contaminants, plastic particles have gained increasing attention due to their ubiquitous detection across a wide range of organisms, including humans. Recently, plastic particles have been found in human kidney, liver, and brain, with the highest concentration in brain tissue, despite the selective permeability of the blood–brain barrier. Moreover, their accumulation in these organs was observed significantly increased from 2016 to 2024, with particularly high levels in individuals diagnosed with dementia (Nihartetal.,2025). Because plants represent the main entry point of contaminants into terrestrial food webs, investigating how plastics interact with and are taken up by plants is essential to trace the origins of human exposure and to design effective mitigation strategies. As plastics degrade in the environment, they fragment into smaller particles: microplastics (MPs), ranging from 0.1 μm to 5 mm, and nanoplastics (NPs) smaller than 0.1 μm (FriasandNash,2019;Mohanaetal.,2021;Thompson,2015;Zianietal.,2023). Although both types are widespread pollutants, this review specifically focuses on NPs due to their distinctive physicochemical

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properties and potential biological impacts. Compared to MPs, NPs exhibit a significantly higher surface-area-to-volume ratio, greater surface reactivity, enhanced mobility in environmental matrices, and higher potential for uptake (Duetal.,2023). These characteristics increase their likelihood of interacting with biological systems and crossing cellular barriers. Unlike MPs, which often remain trapped in soils or adhere to root surfaces, NPs are highly mobile. They can easily migrate into groundwater and irrigation systems, facilitating their long-distance transport across terrestrial and aquatic ecosystems. Consequently, NPs can be taken up by crops and transferred through the food web (Azeemetal.,2023;Giorgettietal.,2020;Pérez-Reverónetal.,2023;Xu Y. et al., 2024;Zhouetal.,2023). NPs may penetrate plant tissues through the root epidermis or via stomatal openings, accumulate within cells, and translocate to other organs. This systemic distribution raises concerns about potential effects on plant function and their transfer to herbivores and humans through trophic interactions (Azeemetal.,2021; Jiangetal.,2022;Liuetal.,2022;Spanòetal.,2022;Sunetal.,2022,2021; Zhuetal.,2022). Therefore, assessing the mechanisms and factors behind that drive NPs entry, transport and accumulation in plants is crucial for One Health paradigm. This knowledge is important not only for assessing plant health and development, but also for evaluating risks to food safety and ecosystem integrity Fig. 1.

### 1.1. From NPs to PS-NPs

The behavior and toxicity of NPs in plants are strongly influenced by the polymer type. Different polymers such as polystyrene (PS), polyethylene (PE), polypropylene (PP), exhibit distinct physicochemical characteristics, including hydrophobicity, degradability, and surface chemistry, which determine their environmental persistence and biological interactions (Duetal.,2023;HasanandTarannum,2025;Wang J. et al., 2023). Despite this, NPs are often treated as a homogeneous group of environmental contaminants, with limited critical discussion in relation not only to particle size but also to polymer type. These differences lead to variability in uptake, mobility within plant tissues, and phytotoxic responses. Among the various polymers, polystyrene nanoplastics (PS-NPs) deserve special focus. PS is one of the most widely used yet least recyclable plastics, frequently detected in soils, marine environments, atmosphere, and often accumulates in landfills (Capricho et al., 2022; Wojnowska-Barylaetal.,2022). Its extensive use in agriculture and horticulture systems, through seedling trays, nursery containers, mulching films, and packaging enhances the likelihood of PS residues entering the environment, directly via agricultural practices or indirectly through waste mismanagement (Capricho et al., 2022; Maafa, 2021). PS-NPs are also among the most studied polymer types in NPs research (Caprichoetal.,2022;Hoetal.,2018;Maafa,2021;Marquezetal.,2023;Sa'aduandFarsang,2023;Wojnowska-Barylaetal.,2022). Their persistence and broad distribution make them particularly relevant for assessing the impacts of NPs on agricultural systems (Kimetal.,2019; Wojnowska-Barylaetal.,2022). However, as observed for other types of NPs, the effects of PS-NPs on plant growth, physiology, and metabolism are highly variable. Plant responses are influenced by multiple interacting factors, including the physicochemical properties of the plastic particles (such as size, surface charge, concentration, and exposure duration) as well as plant-related traits, such as plant species or variety, developmental stage, and concurrent exposure to other environmental stressors (Gongetal.,2021;Wang Y. et al., 2022; Wang F.etal.,2022;Xu L. et al., 2024; Xu Y. et al., 2024;Zhang L. et al., 2024) Fig. 2.

### 1.2. Objectives of this review

This review aims to elucidate the mechanism underlying PS-NPs internalization in plants and to identify the key factors influencing their uptake and translocation. Particular attention is given to species-specific variability in tolerance and susceptibility, with considerations regarding potential risks to food security and food safety. The analysis

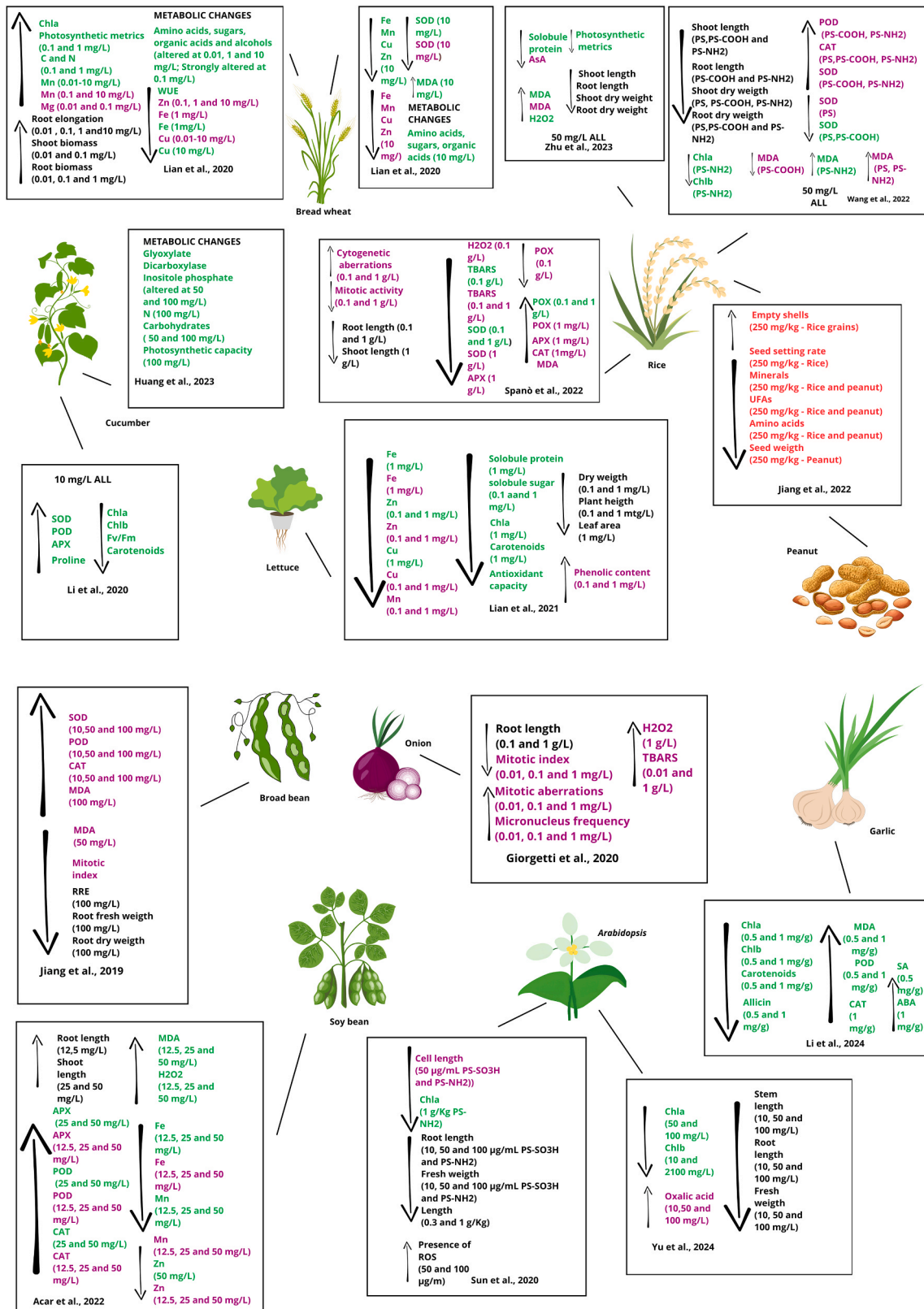
also addresses which of these variables most strongly modulate plant responses to PS-NPs exposure. Furthermore, the review explores whether common physiological or metabolic response patterns can be identified across studies, potentially serving as baseline markers of NPs-induced stress in plants and as targets for future genetic improvement strategies aimed at enhancing stress resilience. Finally, major knowledge gaps and methodological challenges are outlined, emphasizing the urgent need for standardized experimental protocols, environmentally realistic exposure scenarios, and a deeper molecular understanding of PS-NPs interactions within agroecosystems and trophic net.

## 2. Mechanisms of PS-NPs uptake, translocation, and accumulation in plants and dependence on PS-NPs features

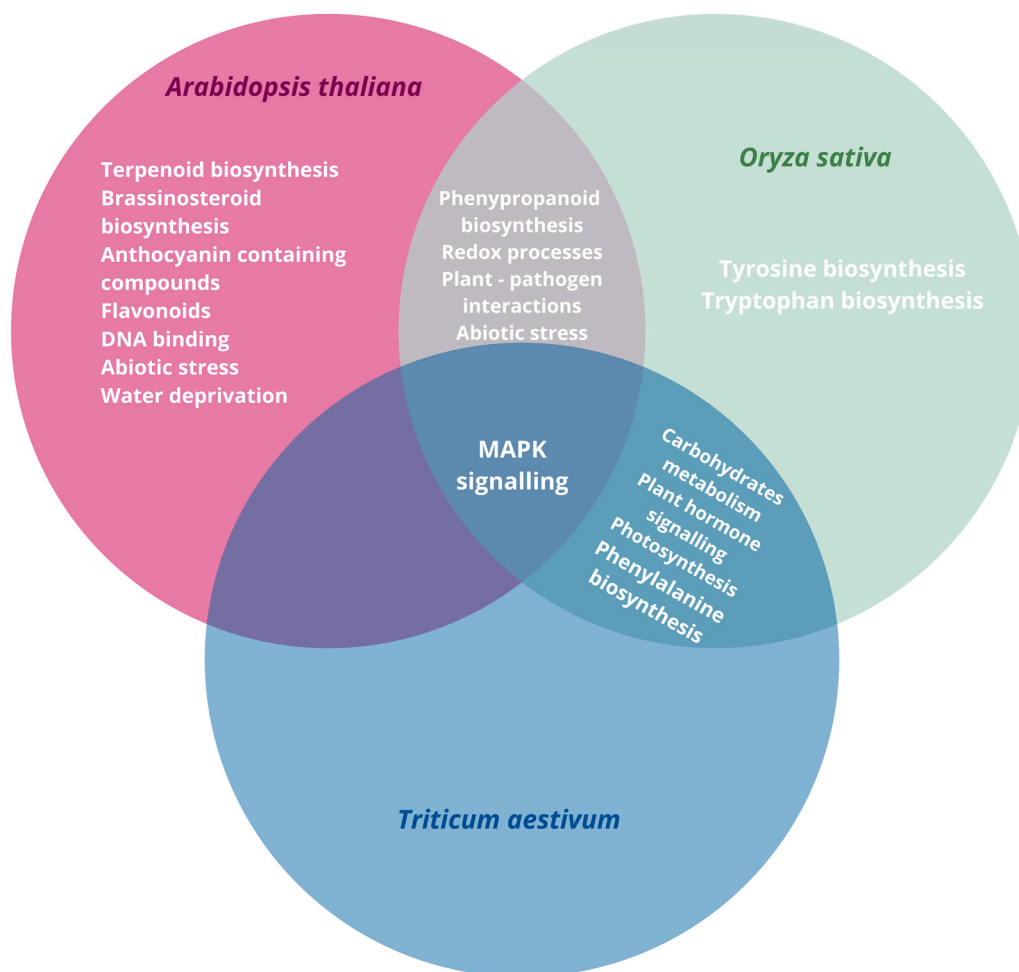
Recently, researchers focused on the possible routes of PS-NPs uptake, translocation, and accumulation sites within plants (Kumaretal., 2021). Plants can absorb PS-NPs through both their roots and aerial structures; indeed, PS-NPs can be dispersed in both the soil and atmosphere. Once internalized, they can move within the plant, reaching all plants organs (Wang et al., 2022a). While the precise pathways and dynamics of their uptake and distribution are still being explored, factors such as particle size, surface charge, and chemical composition are considered critical in influencing their interaction with plant tissues and absorption efficiency (Gaoetal.,2023;Liuetal.,2023;Yuetal.,2024a).

### 2.1. Root-to-shoot translocation and accumulation

PS-NPs are reported to predominantly enter plants as soil-borne particles, utilizing down-to-up transportation, from roots to leaves, and potentially reaching edible parts (Maityetal.,2022;Mateos-Cárdenasetal.,2021). Presently, two main mechanisms have been described to mediate the entry of PS-NPs into plants via the roots: through the solution imbibing root cell walls (apoplastic route) or crossing root cell plasma-membrane and further moving from one cell to another via cytoplasmic connections (symplastic route) (Agarwaletal.,2023). In the apoplastic route, PS-NPs uptake is facilitated by water flow absorbed by roots. Zhou et al. (2023) reported the presence of PS-NPs aggregates at the junctions between lateral and principal roots in lettuce, proposing these sites as potential entry points. Damage to the tegmental root cell walls due to wounds mechanically induced or caused by soil micro-organisms or animals was suggested to facilitate PS-NPs entrance via this pathway. The sharp surfaces of PS-NPs themselves may also induce cell wall wounds, enabling penetration (Zhouetal.,2023). Mineral nutrients also can cross tegmental and cortex tissues of root by the apoplastic route which is normally blocked in the endoderm by the Casparian band. PS-NPs uptake seems to bypass this barrier by the referred "crack-entry mode" supported by observations of discontinuities or breaks in the Casparian strip, due to the sharp surface of the PS-NPs. Recent studies suggest that this mechanism may be more common at sites of secondary root initiation, or at the tip roots where the Casparian strip barrier function may be less effective, allowing PS-NPs to cross the endoderm and to reach vascular tissues (Huaetal.,2023;Yangetal.,2023). In the symplastic route, the interaction of PS-NPs with plasma-membranes, ion channels, and aquaporins potentially interfering with endocytosis and the uptake of other substances which can impair plant growth (Tripathietal.,2017). In this route, the formation of vesicles seems to be pivotal for PS-NPs uptake in plant cells. Bandmann et al. (2012) confirmed that endocytosis plays a key role for PS-NPs uptake in Tobacco Bright Yellow-2 cells. Under confocal microscopy, bright fluorescence signals were observed after the addition of 20 and 40 nm fluorescence-labeled NPs, distributed throughout the cytoplasm regardless of size (Bandmannetal.,2012). This mechanism has been proposed as a potential pathway for the internalization of PS-NPs in root cells. However, the specific endocytosis processes involved in PS-NPs uptake and transport remain under investigation, and little has been proven up to now (Huaetal.,2023). Regardless of the route, PS-NPs can



**Fig. 1.** PS-PNs diverse dose-correlated effects on major crops and *Arabidopsis*. The figure summarizes the various effects PS-NPs exert on plants. Effects are reported in regards of the PS-NPs concentration. The highlights in black stand for phenotypic variations imposed by PS-NPs application, whereas green and purple highlights represent physiological and metabolic variations in shoots and roots, respectively. Variations of grain quality parameters are reported in red. All results displayed in the figure derive from studies referenced in this review. Only the effects induced by PS-NPs are included in the figure, although some of the studies in this review also included larger particles or other polymers. (RRE stands for Relative Root Elongation; chl a and b stand for chlorophyll a and b respectively; TBARS stand for thiobarbituric acid reactive-substances). (Image created with canva.com).



**Fig. 2.** Venn diagram illustrating the metabolic and signalling pathways transcriptionally modulated in *Arabidopsis thaliana*, *Oryza sativa* and *Triticum aestivum* following PS-NPs exposure. Species-specific and shared responses were derived from published RNA-sequencing studies. The central dark blue overlap (MAPK signalling) identifies the core pathway consistently affected across all three species. The grey and light blue overlapping areas indicate responses shared exclusively between *Arabidopsis thaliana* and *Oryza sativa* (grey) and between *Oryza sativa* and *Triticum aestivum* (light blue), respectively. Outer non-overlapping sectors represent species-specific transcriptional responses.

reach vascular tissues and be transported to aerial organs via the transpiration stream. This has been demonstrated in several plant species. [Li L. et al. \(2020\)](#) showed PS-NPs beads movement from the substrate to the root stele and subsequently from root-to-shoot in *T. aestivum* and *L. sativa*. The authors stated that plastic particles enter the epidermal tissue of wheat roots following the stimulation of the pericycle activity associated with lateral root emergence. Once emerged, lateral roots cause discontinuities in the root epithelium, thereby facilitating the entry of NPs and their transfer into the xylem, from where they can migrate to the aerial section of the plant ([Li L. et al., 2020](#)). Validation of PS-NPs uptake and translocation in wheat was further confirmed by using 3D laser confocal scanning microscopy (LCSM) and scanning electron microscopy (SEM). The 3D LCSM imaging revealed the uptake of PS-NPs by root tips, and SEM observations confirmed their presence in both root and shoot xylem. This substantiates the potential down-top transportation of PS-NPs from roots to leaves through the xylem pathway, with implications for potential grain contamination ([Lianetal., 2020b](#)). A recent study from [Spanò et al. \(2022\)](#) underscores the early absorption and translocation of PS-NPs in rice seedlings, detectable in cytoplasm and vacuoles, either as single particles or aggregates, mainly localized in the cells of the cortical parenchyma and in some xylem vessels ([Spanòetal.,2022](#)). [Li L. et al., 2020](#) reported the presence of PS beads along the entire root cap and in the lateral root apical meristem of wheat and lettuce, suggesting that the interactions with the root cap

mucilage facilitate their penetration through the epidermal layers. This highlights the risk associated with the capacity of PS-NPs to interact with organic matter, which could modify the capacity of PS to interact with organisms. Indeed, scanning SEM further revealed PS beads in the epidermis, stem, and vascular tissue of secondary wheat roots ([Azeemetal.,2021;Li L. et al., 2020](#)).

## 2.2. Shoot to root translocation and accumulation

Given their atmospheric dispersion, PS-NPs can also be absorbed through aerial plant parts. [Sun et al. \(2022\)](#) demonstrated that PS-NPs can be transported from leaves to other organs in maize ([Sunetal., 2022](#)). Studies on lettuce provided insights into PS-NPs uptake through stomata, highlighting significant PS-NPs aggregation in root tissues when the foliage was exposed, indicating the plant phloem's ability to transport PS-NPs ([Lian et al., 2021](#)). Moreover, [Ilyas et al. \(2024\)](#) studied the effects of PS-NPs foliar application on four leafy vegetables (*Brassica rapa var. chinensis*, *B. rapa var. parachinensis*, *Amaranthus viridis*, and *Allium tuberosum*). Authors reported that PS-NPs tended to accumulate within the epidermal layers and cuticles of the plants, mainly around stomata. They also underlying that leaf structure, especially trichomes, strongly affects particle retention ([Ilyasetal.,2024](#)).

### 2.3. Influence of physicochemical properties on PS-NPs uptake and accumulation

The uptake and accumulation of PS-NPs in plants are strongly influenced by their physicochemical characteristics, particularly particle size and surface charge. PS-NPs have been detected across various plant tissues and organs, including roots, stems, leaves, flowers, and fruits, raising concerns about their potential entry into the food chain (Li C. et al., 2021; Saha et al., 2024). In watercress (*Lepidium sativum*), an edible herb, PS-NPs have been detected in various plant structures, including the tegumentary tissues of roots and shoots, the xylem and floem and the parenchymatic cells. Notably, accumulation occurs even at environmentally realistic exposure levels (as low as  $10 \mu\text{g L}^{-1}$ ), indicating a high capacity of plants to retain PS-NPs (Saha et al., 2024). Particle size appears to be a key determinant of uptake efficiency and translocation, though evidence remains somewhat contradictory. Several studies have demonstrated enhanced internalization of smaller particles: PS-NPs ranging from 20 to 80 nm were more efficiently absorbed and translocated than larger ( $\geq 100$  nm) particles in tobacco cells, rice seedlings, and other species (Azeem et al., 2021; Wu et al., 2021). In tobacco cultured cells, PS-NPs ranged from 20 to 40 nm, were taken up and directed towards vacuoles (Bandmann et al., 2012). On the contrary, 100 nm particles were not found in the vacuoles, probably because particles larger than 100 nm cannot follow the endocytosis pathways due to the too small dimension of endocytic vesicles (Ketelaar et al., 2008). In rice seedlings, a stronger fluorescence intensity was observed when fluorescent 80 nm PS-NPs were used rather than with fluorescent  $1 \mu\text{m}$  PS-NPs (Liu et al., 2022; Saha et al., 2024). This is consistent with the size limitations of endocytic vesicles, which likely restrict the entry of larger particles (Ketelaar et al., 2008). However, other reports observed that particles up to 200 nm can still penetrate plant tissues, suggesting that alternative, size-independent mechanisms, such as apoplastic transport, may also operate (Hua et al., 2023). In Arabidopsis, particles until 200 nm could enter tissues (Hua et al., 2023) and rice roots seemed to be able to internalize both nano and micro sized PS particles too (Hua et al., 2023; Liu et al., 2023). Moreover, Conti et al. also detected MPs in fruits purchased in local markets, using SEM-EDX analysis, with apples and carrots showing the highest contamination levels (OliveriConti et al., 2020). However, since PS-NPs tend to aggregate, some MPs detected in plants may originate from smaller NPs aggregating intracellularly. The potential capability of PS-NPs to form micro-sized clusters strongly complicates the interpretation of size-dependent uptake, as aggregates might mimic the presence of MPs in plant tissues (Chen et al., 2023; Prade et al., 2023). Surface charge further modulates PS-NPs-plant interactions. Studies on Arabidopsis demonstrated that negatively charged particles (e.g., PS-O<sub>3</sub>H) are generally internalized more efficiently than positively charged ones (PS-NH<sub>2</sub>), which tend to adhere to the rhizodermis and induce secretion of organic exudates promoting particle aggregation (Sun et al., 2020). Similarly, in maize, PS-NH<sub>2</sub> particles aggregated on leaf surfaces, while negatively charged particles penetrated tissues at a higher rate (Sun et al., 2021). Together, these findings indicate that both particle size and surface charge critically determine the pathways and extent of PS-NPs internalization, although inconsistencies across species and experimental conditions highlight the need for standardized approaches to disentangle these interacting effects.

### 3. Physiological and metabolic alterations induced by PS-NPs

PS-NPs have emerged as relevant environmental contaminants capable of entering plant tissues, perturbing metabolism, and altering key physiological processes (Motealle et al., 2024; Xu et al., 2025). The magnitude and direction of these effects are affected by nanoparticle properties, such as size, charge, and concentration, as well as by plant species and duration of the exposure (Kumaret al., 2021); (Gao et al., 2023; Liu et al., 2023; Yu et al., 2024a). The following sections summarize the biological processes most affected by PS-NPs, integrating evidence from

crops (cereals, vegetables, legumes), and the model plant *Arabidopsis thaliana*.

#### 3.1. Growth and development

Across a wide range of plants, from crops to model ones, several evidence underlines that PS-NPs modulate growth and developmental parameters suggesting that size, charge, and concentration of PS-NPs are relevant parameters for determining a certain effect. In bread wheat (*Triticum aestivum* L.), exposure to 100 nm PS-NPs in the range between 0.01 and 10 mg/L enhanced biomass accumulation particularly in roots, the elongation of which was increased in all the treatment, while root biomass increased when PS-NPs were present until 1 mg/L. On the other hand, shoot biomass increased only at 0.01 and 0.1 mg/L (Lian et al., 2020a). Although performed with MPs instead of NPs, another study indicates that exposure to high concentrations of PS (30–50 g/L) significantly reduced plant biomass (Riaz et al., 2025). Another cereal studied for PS-NPs effects was rice (*Oryza sativa* L.). Rice plants exposed to 50 nm PS-NPs at 0.1, 0.5, and 1 g/L showed progressive inhibition of seedling growth, with root elongation markedly reduced even at the lowest used PS-NPs concentration (0.1 g/L) (Spanò et al., 2022). In their whole, these results suggest a putative hormetic effect of PS-NPs, in which low nanoparticles concentration may stimulate metabolic or hormonal pathways before inhibitory effects might dominate when the PS-NPs concentration reaches a toxic threshold. Particle surface charge further shaped developmental outcomes as demonstrated in rice by Wang et al. (2022b). Indeed, neutral (PS), negatively charged (PS-COOH), and positively charged (PS-NH<sub>2</sub>) 50 nm particles at a concentration of 50 mg/L all reduced root and shoot growth, albeit to varying degrees, with PS-NH<sub>2</sub> causing the most pronounced inhibition (Wang et al., 2022b). This pattern indicates that electrostatic interactions between PS-NPs and the negatively charged root cell wall are relevant to the effects of PS-NPs, with cationic PS-NH<sub>2</sub> particles adhering more strongly and causing greater mechanical and biochemical disruption. In another study on rice, it was demonstrated that smaller, positively charged 50 mg/L PS microparticles critically determine the toxic effects. PS powders at 3–5 % (w/w) drastically reduced plant height, biomass, and root length more than fibers or beads, revealing that the irregular morphology of the powders amplifies physical interference with plant tissues. Interestingly, Hussain et al. (2025) observed a milder response in citrus rootstocks compared to wheat. At 1 % solids 20 nm PS-NPs mainly impaired the total root length and root surface area, while inducing an increase in root diameters. On the other hand, exposure to 1 % solid 50 nm PS-NPs reduced the number of root forks without significant biomass loss (Hussain et al., 2025). These data suggest a species-specific threshold of sensitivity and a size-specific effect. Overall, these findings demonstrate that PS-NPs affect plant development by impairing biomass accumulation, root elongation, and mitotic activity, primarily in concentration, size, and charge-dependent manner. Differences in sensitivity among species are also evident, as is the fact that, among the developmental processes regulating plant growth, PS-NPs clearly affect cell cycle progression. Future studies should clarify whether these responses are primarily triggered by oxidative imbalance, hormonal perturbation, failure in cell-cycle regulation, or other mechanisms, as current evidence does not distinguish among these overlapping pathways.

#### 3.2. Photosynthesis and energy metabolism

Photosynthesis is one of the most sensitive physiological targets of stress, as it integrates physical and chemical processes. Being responsible for energy production, plant autotrophy, and redox homeostasis, its impairment triggers a cascade of effects on a plethora of metabolic processes involved in plant development and productivity (Ashraf and Harris, 2013).

It has been suggested that PS-NPs affect photosynthesis. In cereals,

bread wheat exposed to 100 nm PS-NPs (0.01–1 mg/L) showed moderate stimulation of chlorophyll content and photosynthetic rate. At 0.1 and 1 mg/L PS-NPs, bread wheat also displayed increased C and N content, in agreement with the stimulation of shoot and root growth observed in the same study (Lianetal.,2020a). In rice, the influence of surface charge on photosynthetic regulation, was clear: positively charged PS-NH<sub>2</sub> induced severe losses in chlorophyll a and b, while PS-COOH had milder effects (Wangetal.,2022b). Cucumber exposed to 10 mg/L 100 nm PS-NPs exhibited significant decreases in chlorophylls and carotenoids, coupled with the downregulation of genes associated with pigment biosynthesis and with a reduction of the photosynthetic index Fv/Fm. The authors suggested that benzene rings produced by PS degradation interfered with pigment metabolism (LiZ. etal.,2020). In cucumber, 100 mg/L PS-NPs also led to photosynthetic inhibition (Huangetal.,2023). Lettuce displayed strong pigment loss already at 1 mg/L PS-NPs, consistently with reduced biomass accumulation (Lianetal.,2021). In garlic, both chlorophyll and carotenoid contents declined progressively with increasing PS-NPs concentrations from 0.5 to 1 mg/g (LiG. etal.,2024). In *Arabidopsis thaliana*, PS-NH<sub>2</sub> nanoparticles reduced chlorophyll accumulation at 1 g/Kg concentration (Sunetal.,2020). Recent evidence supports these trends but adds mechanistic depth. Zhu et al. (2023) found that in rice seedlings, in addition to reducing chlorophyll content and affecting photosynthetic parameters, 5 μm PS-NH<sub>2</sub> also impaired photosynthetic lighting, light collection in photosystem I, and the gene expression of photosynthesis-antenna protein (Zhuetal.,2023). These effects collectively influenced the light-harvesting complex, thereby impairing light energy absorption and light reaction process. A similar effect was also evident with 50 nm PS-NH<sub>2</sub>. Intriguingly, co-treatment with phenanthrene mitigated these inhibitory effects by stimulating antioxidant activity and reducing chloroplast oxidative damage, highlighting a complex response dependent on particle charge and the presence of co-contaminants (Zhuetal., 2023). Similarly, Riaz et al. (2025) confirmed that higher PS concentrations severely reduced wheat chlorophyll content and photosynthetic rate, especially when powder-shaped particles were used; while bead-shaped PS induced a minor effect at least in gas exchange (Riazetal.,2025). Hussain et al. (2025) noted that PS-NPs at concentrations affecting photosynthesis in other species, did not affect its efficiency nor transpiration rate and stomatal conductance in citrus, suggesting species-dependent tolerance thresholds and possible compensatory upregulation of photoprotective mechanisms (Hussainetal.,2025). PS-MPs and NPs similarly affected photosynthesis (Riazetal.,2025;Zhuetal.,2023) thus suggesting that, based on the currently available literature, the impairment of chloroplast function is not dependent on PS particle size or charge.

### 3.3. Microelement uptake and nutrient transport

Metal micronutrients and essential elements are critical for enzymatic and photosynthetic functions. Several studies demonstrate that PS-NPs disturb their uptake and distribution (Hussainetal.,2025;Jiangetal.,2022;Lianetal.,2020a). In bread wheat, PS-NPs up to 10 mg/L strongly affected the micronutrient content. For instance, Zn and Cu suffered a strong decrease in plant roots exposed to PS-NPs concentration between 0.1 and 10 mg/L while in shoots the decrease was only evident with the highest PS-NPs. Fe was decreased similarly in roots and shoots but only when wheat was exposed to 1 mg/L PS-NPs. On the contrary, Mn and Mg absorption increased at 0.1 and 10 mg/L and 0.01 and 0.1 mg/L, respectively in roots and to 0.01–10 mg/L in shoots (Lianetal.,2020a). In lettuce, 1 mg/L PS-NPs markedly lowered Fe levels in leaves and roots, while Zn content declined at 0.1 mg/L. Cu and Mn in roots were reduced at both PS-NPs concentrations while in leaves, Cu only decreased at the highest concentration, demonstrating a systemic disturbance of micronutrient homeostasis (Lianetal.,2021). In rice and peanuts, high PS-NPs levels (250 mg kg<sup>-1</sup>) not only impaired seed filling but also reduced amino acids and mineral nutrients in grains (Jiangetal.,

2022). Comparable patterns were observed under other polymeric nanoparticles such as polymethyl methacrylate (130 nm), which decreased the content of Fe, Zn, Cu, Mn, Ca, Mg, K, P, and B in various plants (Ekner-Grzybetal.,2022;Yildiztugayetal.,2022). A general reduction in mineral uptake could be the consequence of the aggregation of PS-NPs in the rhizosphere that could hinder the free diffusion of ions in soil solution by chelating them or increasing their adhesion to soil particles; but PS-NPs could also determine physical barriers for apoplastic transport systems. Complementing previously described results, Hussain et al. (2025) found a different effect of PS-NPs on mineral uptake in citrus roots, since 20 nm PS-NPs strongly affected only Zn, Mg and Mn accumulation, decreasing their concentration in roots; while 50 nm PS-NPs mainly decreased Ca and Mn content in roots (Hussainetal.,2025). According to these data, PS-NPs of different sizes affected the uptake of specific nutrients in citrus, in contrast to the more general systemic disturbances reported in other species (Ekner-Grzybetal.,2022;Hussainetal.,2025;Jiangetal.,2022;Lianetal.,2020a). Differences in root architecture and, perhaps even more importantly, variations in the organic matter present in the rhizosphere of different species could influence the interaction between PS-NPs and the macro- and micronutrients available in the soil (Hussainetal.,2025;Ryzenkoetal.,2025;Yueetal.,2023). Indeed, nanoparticle size and charge might influence the ability of PS-NPs to chelate micronutrients or bind root exudates, potentially modifying nutrient bioavailability and, probably, the root capacity to uptake minerals from the soil solution (Azeemetal., 2021;Hussainetal.,2025). Therefore, the observed nutrient depletion could not merely be due to a general uptake inhibition but also to complex surface interactions at the soil–root interface.

### 3.4. Oxidative stress and antioxidant response

Reactive oxygen species (ROS) generation and modulation of antioxidant defense represent key mechanisms of stress responses. Several studies report that PS-NPs induce oxidative stress manifested by increased levels of H<sub>2</sub>O<sub>2</sub>, superoxide anion, and lipid peroxidation products such as malondialdehyde (MDA) (Lianetal.,2020b,2021;Li C. et al., 2021;LiG. etal.,2024;LiZ. etal.,2020;Spanoetal.,2022;Sunetal., 2020;Surgun-Acar,2022;Wangetal.,2022b).

In bread wheat, co-contamination with 10 mg/L PS-NPs and Cd reduced oxidative markers in comparison with the exposure to Cd-only, without increasing the activity of antioxidant enzymes. This suggests that PS-NPs may alleviate Cd toxicity probably by limiting metal uptake. However, treatment with 10 mg/L PS-NPs alone increased MDA content in leaves and decreased SOD in both roots and shoots (Lianetal.,2020b). Rice seedlings exhibited strong systemic oxidative stress after root exposure to 50 nm PS-NPs at 0.1–1 g L<sup>-1</sup>, with an altered spatial localization of ROS accumulation in both roots and shoots tissues. Histochemical analyses revealed that H<sub>2</sub>O<sub>2</sub> and lipid peroxidation were differently distributed between tissues. Indeed, in treated samples, rhizodermis, exodermis and sclerenchyma were strongly displaying H<sub>2</sub>O<sub>2</sub> signal compared to controls (Spanoetal.,2022). In shoots, PS-NPs treatment resulted in H<sub>2</sub>O<sub>2</sub> localization mainly in the vascular bundles and surrounding mesophyll cells, while epidermal tissues were weakly H<sub>2</sub>O<sub>2</sub> reactive compared to controls. The activities of antioxidant enzymes increased but were insufficient to fully mitigate oxidative imbalance (Spanoetal.,2022). Positively charged 50 mg/L PS-NH<sub>2</sub> particles also induce an intense oxidative damage in rice, elevating MDA levels in both roots and shoots, whereas negatively charged PS-COOH particles had milder or opposite effects. Additionally, both neutrally, positively and negatively charged plastic particles promote peroxidase (POD) and catalase (CAT) activities in roots and decrease superoxide dismutase (SOD) activity in shoots, while neutral PS particles reduce SOD in both roots and shoots (Wangetal.,2022b). Cucumber exposed to 100 nm 10 mg/L PS-NPs displayed significant enhancement of SOD, POD and ascorbate peroxidase (APX) gene expression, indicating a clear activation of antioxidant defense which efficiently controlled oxidative stress,

since MDA or H<sub>2</sub>O<sub>2</sub> resembled control-like levels (LiZ. et al., 2020). In the same study, however, it was shown that PS-MPs of 300 nm, 500 nm, and 700 nm, similarly induced hyperexpression of antioxidant genes, but oxidative stress markers were higher than controls in this case. Thus, PS-MPs might still be inducing the inactivation of antioxidant defenses at a molecular level, but this is too weak, leading cucumber plants to fail to counteract oxidative stress in an efficient manner. The same species showed increased proline accumulation, an osmo-protectant that can also be a hallmark of oxidative stress adaptation (LiZ. et al., 2021). In lettuce, PS-NPs treatment led to a marked reduction in the total antioxidant capacity, that seemed to be the cause of the occurrence of a redox imbalance (Lianetal., 2021). Garlic exposed to PS-NPs (0.05–1 mg/g) exhibited significant rises in MDA and POD activities, while CAT activity only increased at the highest concentration of PS-NPs, thus suggesting a PS-NPs dose dependent increase in ROS generation (LiG. et al., 2024). Similarly, in soybean, exposure to 12–50 mg/L PS-NPs resulted in elevated MDA, APX, POD and CAT in leaves; surprisingly these antioxidant enzymes reduced their activity in roots (Surgun-Acar, 2022). The model plant *Arabidopsis thaliana* displayed a comparable pattern, with PS-NH<sub>2</sub> nanoparticles inducing higher H<sub>2</sub>O<sub>2</sub> accumulation in comparison to PS-SO<sub>3</sub>H at both 50 and 100 µg/mL (Sunetal., 2020). Following exposure to PS-MPs, a significant MDA increase coupled with salicylic acid accumulation was seen in dicots (lettuce and carrot), whereas monocots (wheat and barley) remained largely unaffected, confirming that oxidative stress intensity is modulated by plant taxonomic traits (Zantisetal., 2023). Despite species-dependent differences in sensitivity to PS-induced damage, an increase in MDA and ROS has been reported to be triggered by both nano- and micro-sized PS particles. The concentration of PS seemed to be a pivotal aspect for the induction of specific responses: Riaz et al. (2025) reported different responses when wheat plants were exposed to different concentration of PS-MPs powder, since lower concentration only induced an increase in CAT and MDA, while higher concentration also induced an increase in SOD and POD, without increase in MDA (Riazetal., 2025). This suggested that a more efficient antioxidant response was activated when wheat was exposed to higher concentration of PS. Again, the shape of the microparticles was a relevant aspect for their effects, since particle with irregular shapes were more effective in inducing oxidative stress responses than spheric or regular shapes (Riazetal., 2025). Taken together, these findings confirm that PS-NPs disrupt cellular redox homeostasis, eliciting strong but often insufficient antioxidant responses that fail to fully counteract oxidative stress in some species, while do not induce high oxidative stress in others, reinforcing the concept of the species-dependent-related effects of PS-NPs. On the contrary, bigger PS particles, on the macro scale, generally induce oxidative stress regardless of the plant species.

### 3.5. Primary and secondary metabolism

PS-NPs induce broad metabolic rearrangements, affecting both primary and secondary metabolism. These alterations include changes in carbohydrates, amino acids, and lipid metabolism as well as in the synthesis of key bioactive compounds as described here in detail. In bread wheat, metabolic profiling after 100 nm 0.01–10 mg/L PS-NPs revealed substantial rearrangements in energy-related pathways and amino acids metabolism, indicating a reprogramming of carbon and nitrogen fluxes. Particularly, metabolic alterations involved sugars, organic acids and alcohols metabolism (Lianetal., 2020a). In rice, 50 nm PS-NPs reduced grain quality and nutritional value, lowering amino acids, unsaturated fatty acid, and mineral content. At higher concentrations (250 mg/Kg) the frequency of rice empty grains increased, suggesting that PS-NPs interfere with nutrient allocation during seed development (Jiangetal., 2022). Studies on cucumbers showed pronounced changes in carbohydrates and sugar metabolism after 100 nm PS-NPs exposition. In this plant 100 mg/L PS-NPs disrupted nitrogen and carbohydrate metabolism, impairing energy homeostasis, while

lower concentrations (up to 50 mg/L) slightly enhanced carbohydrate turnover, even if glyoxylate decarboxylase and inositol phosphate metabolisms were profoundly altered by both 50 and 100 mg/L PS-NPs (Huangetal., 2023). Recent studies reinforce these metabolic findings in other species. Hussain et al. (2025) reported that in citrus rootstocks, PS-NPs disrupted the balance of soluble sugars and amino acids, particularly reducing sucrose and glutamine while increasing proline, suggesting metabolic reallocation to mitigate nanoparticle-induced stress (Hussainetal., 2025). Research investigating the impact of NPs on secondary metabolism is still relatively more limited. In garlic, PS-NPs (0.05–1 mg g<sup>-1</sup>) drastically reduced allicin accumulation, a key organosulfur compound responsible for garlic's antioxidant and antimicrobial properties (LiG. et al., 2024). Such inhibition indicates that PS-NPs can alter secondary metabolic routes related to plant defense with cascade effects on plant nutritional quality. These observations support a broader view that PS-NPs provoke metabolic reprogramming, with shifts toward stress-related and antioxidant metabolites, which, with the other alteration induced by PS-NPs, may have varying repercussions on productivity and on the bromatological properties of plant edible tissues and organs.

### 3.6. Cytotoxicity and genotoxicity

Cytotoxic and genotoxic manifestations provide direct evidence of cellular stress induced by PS-NPs. In several species, these effects are linked to disturbed mitotic processes and chromosomal damage. In onion (*Allium cepa*), one of the most widely used genotoxicity models, 50 nm PS-NPs (0.01–1 g/L) caused a reduction in the mitotic index and the appearance of micronuclei and mitotic aberrations, indicating chromosomal instability and impaired cell division (Giorgettietal., 2020). Broad bean (*Vicia faba*) exhibited a similar pattern: 100 nm PS-NPs (100 mg/L) significantly decreased the mitotic index (Jiangetal., 2019). In rice, PS-NPs altered root cellular ultrastructure and induced strong cytogenetic aberrations, at 0.1 and 1 g/L, reducing mitotic activity only at 1 g/L concentration. These abnormalities likely result from physical obstruction of the mitotic apparatus or interference with DNA replication (Spanò et al., 2022). Collectively, these studies highlight that PS-NPs can compromise cell division fidelity and genome stability, causing cytogenetic damage across diverse taxa, even if with different efficiency. The consistency of mitotic inhibition and DNA damage across monocots and dicots indicates a conserved cellular stress pathway, modulated primarily by particle charge, dimension, and probably shape.

### 3.7. Aquaporin-mediated uptake and hormonal crosstalk

Recent findings highlight the pivotal role of aquaporins and hormonal crosstalk in mediating plant responses to PS-NPs. Aquaporins, membrane channel proteins responsible for water transport, also contribute to plant defense by restricting the entry of harmful molecules, including NPs (Maityetal., 2022). Moreover, certain aquaporins facilitate H<sub>2</sub>O<sub>2</sub> diffusion across membranes, thereby helping maintain redox homeostasis under stress (Wangetal., 2020). In Tartary buckwheat (*Fagopyrum tataricum*), PS-NPs (100 nm, 100 mg/L) enter root cells via transmembrane routes, accompanied by an increase in ROS accumulation and the overexpression of specific aquaporin genes such as *FtPIP2;8 (FT01Gene33590.t1)*. Co-localization and molecular docking analyses revealed that FtPIP2;8 directly interacts with PS-NPs, suggesting that this water-channel protein functions as a molecular gateway modulating nanoparticles uptake and stress signaling (Houetal., 2025). Consistent results were obtained in crown daisy (*Chrysanthemum coronarium*), where aquaporin inhibitors such as glycerol significantly reduced PS-NPs internalization, and reverted all the effects of PS-NPs toxicity such as oxidative stress, and reduction in chlorophyll content and biomass. This finding indicates that aquaporin-mediated water transport strongly influences PS-NPs absorption. Moreover, PS-NPs altered enzymes of tricarboxylic acid cycle and ion transport (notably Fe and Ca),

linking aquaporin regulation to both metabolic and nutrient homeostasis (Gaoetal.,2025). At the biochemical level, PS-NPs-dependent oxidative stress activates hormonal signaling networks involving abscisic acid (ABA) and salicylic acid (SA). In different cell cultures of crop species (wheat, barley, carrot, tomato), PS-NPs increased SA and phenolic compounds while decreasing ABA (Adamczyketal.,2023). This behavior suggests that NPs-induced stress shifts signaling from ABA-dependent drought-type responses toward SA-mediated antioxidant defenses (Adamczyketal.,2023). Taken together, these findings suggest that PS-NPs uptake and toxicity are governed by a complex network of mechanisms involving aquaporin-mediated transmembrane transport and ROS-hormone regulatory feedback, ultimately shaping plant tolerance and physiological adaptation.

#### 4. Omics-guided insights into plants responses and mitigation strategies under PS-NPs stress

##### 4.1. Omics approaches to unravel plant responses to NPs and MPs stress

Omics technologies, including transcriptomics, proteomics, metabolomics, and their integrative applications, have become indispensable tools for deciphering how plants perceive, transduce, and respond to PS-NPs and PS-MPs exposure across multiple biological scales (Arifetal., 2025;Gongetal.,2021;Lianetal.,2020a;Qietal.,2018;WangC. et al.,2023).

These approaches provide a holistic framework for capturing dynamic interactions among genes, proteins, and metabolites, thereby uncovering adaptive mechanisms often overlooked by single-omics studies (Wang et al., 2025; Xu L. et al., 2024). PS-NPs and PS-MPs impose a complex and multifactorial stress on plants, modulating gene expression, protein turnover, metabolite accumulation, and epigenetic regulation, processes that collectively influence growth, development, and physiological resilience (Larueetal.,2021;Lianetal.,2022;Rilligand-Lehmann,2020). Transcriptomic studies consistently demonstrated that PS-NPs exposure triggers tissue- and species-specific differential gene expression, strongly influenced by particle size, surface charge, concentration, exposure duration, and plant genotype (Sunetal.,2020; Wangetal.,2022a;Yuetal.,2024b). In *Arabidopsis thaliana*, PS-NH<sub>2</sub> nanoparticles upregulate genes associated with anthocyanin and flavonoid biosynthesis, ROS detoxification, peroxidase activity, and general stress adaptation, whereas PS-SO<sub>3</sub>H exposure induces transcriptional patterns indicative of water deficit and abiotic stress, accompanied by the downregulation of DNA-binding and pathogen-response genes (Sunetal.,2020). Similarly, in *Oryza sativa*, PS-COOH exposure predominantly affected ion transport, phenylpropanoid metabolism, and photosynthetic processes in shoots, while PS-NH<sub>2</sub> mainly altered macromolecular synthesis and ROS-related pathways in roots (Luetal., 2023;Renetal.,2021;Wangetal.,2022a,2022b). Weighted gene co-expression network analysis (WGCNA) further highlighted rapid perception of PS-NPs-induced abiotic stress, shifts in biomass allocation, and modulation of phenylpropanoid and photosynthetic pathways (Xu, 2024). In wheat, transcriptomic analyses revealed a similar trend, with root tissues exhibiting more extensive gene downregulation than shoots under 100 nm PS-NPs exposure, particularly in pathways related to photosynthesis, phytohormone signalling, energy metabolism, and plant-pathogen interactions (Lianetal.,2022,2020a). Polystyrene particles ≤ 100 nm were associated with elevated ROS accumulation, reduced starch and soluble sugar contents, and disrupted amino acid metabolism, which collectively compromised plant defense responses and grain quality in rice (Miaoetal.,2025). These findings emphasized that NPs size, surface functionalization, and aggregation behaviour critically determine plant transcriptomic outcomes, shaping ROS homeostasis, secondary metabolite biosynthesis, and stress adaptation mechanisms (Sunetal.,2020;Wangetal.,2022a;Yuetal.,2024b). Proteomic analyses complement transcriptomic data by revealing changes in protein abundance, structure, and post-translational modifications under PS-NPs and PS-MPs stress. Reported alterations include the

modulation of antioxidant enzymes (SOD, CAT, POD, APX), ion transporters, photosynthetic proteins, and phosphorylation patterns essential for signal transduction (Huangetal.,2023;Xu,2024). Similarly, exposure studies in *Torreya grandis* demonstrated that PS-NPs affect the translation of proteins associated with ion transmembrane transport and transporter activity (Yuetal.,2022). In various crops, including rice, pea, cucumber, and wheat, PS-NPs and MPs exposure has been shown to either suppress or enhance protein synthesis depending on particle size and concentration, highlighting the size-dependent duality of PS-NPs toxicity (Kimetal.,2022;Lianetal.,2022;LiZ. et al.,2021;Maetal.,2022; Wuetal.,2020). Metabolomic analyses reveal the functional consequences of transcriptional and proteomic modulation, highlighting alterations in amino acid, carbohydrate, lipid, phenolic, and terpenoid metabolism across multiple species (Huangetal.,2023;Matichetal., 2019). In *Arabidopsis*, *Stevia rebaudiana*, and wheat, PS-NPs exposure perturbed glycolysis, the pentose phosphate pathway, the tricarboxylic acid cycle, and galactose metabolism, while stimulating phenylpropanoid, flavonoid, and carotenoid biosynthesis as part of a compensatory defense response (Comanetal.,2023;Lianetal.,2020a; Sunetal.,2020). In broccoli, radish, and dandelion, PS-NPs and MPs enhanced the accumulation of antioxidant secondary metabolites, including flavonoids, anthocyanins, and polyphenols, helping to mitigate oxidative stress and preserve cellular integrity (GaoM. et al.,2022; Lópezetal.,2022). Metabolic reprogramming appears to be highly size-dependent, with smaller particles often exerting greater toxicity through the downregulation of carbohydrate and lipid metabolism and impairment of nutrient assimilation (Wuetal.,2021;ZhangY. et al.,2024). Epigenetic modifications, including DNA methylation, histone remodelling, and RNA-mediated regulation, further shaped plant adaptive responses to NPs stress (Pomaetal.,2023;Thiebautetal.,2019;Wangetal., 2015). In both monocots (wheat, barley) and dicots (carrot, tomato), PS-NPs exposure has been linked to increased DNA methylation levels, correlating with enhanced antioxidant enzyme activity (Adamczyketal., 2023). DNA methylation and histone dynamics likely coordinate organ-specific transcriptional plasticity and metabolic reprogramming under PS-NPs stress, although mechanistic understanding remains limited. The integration of transcriptomic, proteomic, and metabolomic data offers a multidimensional perspective on plant adaptation to PS-NPs, revealing intricate crosstalk among stress perception, ROS signalling, secondary metabolism, and energy allocation (Xu,2024). For example, *Populus euramericana* exposed to PS-NPs exhibited coordinated upregulation of flavonoid biosynthetic genes alongside corresponding metabolite accumulation, linking transcriptional regulation to functional biochemical outcomes (XuL. et al.,2024). Likewise, a multi-omics study in *Taxus mairei* elucidated the regulatory mechanisms underlying nanoparticle-induced stress, providing valuable insights for the development of *Taxus* species with enhanced environmental adaptability. Integrated physiological, transcriptomic, and metabolomic analyses revealed that PS-NPs exposure significantly disrupted energy metabolism through the modulation of *FRK* gene expression (Wang et al., 2025).

Collectively, omics-based investigations underscored the profound impact of PS-NPs and MPs on plant systems, with responses modulated by particle size, surface chemistry, and exposure conditions. Transcriptomic, proteomic, metabolomic, and epigenomic analyses revealed both conserved and organ-specific stress responses involving ROS management, hormone signalling, secondary metabolite biosynthesis, and nutrient transport. The integration of these datasets provides a high-resolution, mechanistic framework for understanding plant adaptation to plastic-induced stress, thereby informing strategies to mitigate PS-NPs risks in agroecosystems and advancing the One Health paradigm, which links environmental contamination, plant physiology, and food security.

#### 4.2. Molecular and hormonal strategies to limit nanoplastic accumulation in plants

To mitigate the environmental pressures caused by NPs, one potential strategy involves preventing their accumulation in plants by blocking their root uptake from the soil, either through the application of specific biomolecules or by targeting key transporters (Gao et al., 2023; Li Z. et al., 2021). In this regard, a recent study demonstrated that treatment with the plant hormone strigolactone suppresses PS-NPs accumulation and enhances maize tolerance by modulating the expression of genes associated with MAPK cascades, hormone signaling, and plant–pathogen interaction pathways (Li Q. et al., 2024). Similarly, in tomatoes, the exogenous application of brassinosteroids significantly reduced PS-NPs accumulation in edible tissues (Gao et al., 2023). Brassinosteroids are known to regulate key physiological processes, including growth, development, metabolism, signal transduction, stomatal regulation, and plant responses to abiotic and biotic stresses, in more than 100 plant species, including wheat (Divietal., 2016; Liangetal., 2024; Peresetal., 2019; ZulloandAdam, 2002). Another promising strategy to mitigate NPs absorption in plants is the application of exogenous melatonin. In *Triticum aestivum*, melatonin treatment reduced both root uptake and shoot translocation of NPs, primarily through the modulation of aquaporin gene expression. Specifically, melatonin altered the expression of *TIP2-9*, *PIP2*, *PIP3*, and *PIP1.2* in leaves, and *TIP2-9*, *PIP1-5*, *PIP2*, and *PIP1.2* in roots (Lietal., 2021). The melatonin-induced upregulation of specific aquaporins not only enhances redox balance but also mitigates NPs-induced impairments in carbohydrate metabolism, collectively improving plant tolerance to nanomaterial toxicity (Li S. et al., 2021). Aquaporin modulation in response to NPs exposure has also been observed in tomato and rice (Gao et al., 2023; Zhou et al., 2021). In tomato, Gao et al. (2023) reported upregulation of aquaporins, specifically of *TIP2-1*, *TIP2-2*, *PIP2-6*, *PIP2-8*, *PIP2-9*, *SIP2-1*, and *NIP1-2* following NPs exposure, likely due to channel obstruction by NPs. Interestingly, exogenous brassinosteroid application reversed this induction, reducing NPs uptake and alleviating toxicity in edible plants through the activation of antioxidant defense pathways. These findings contrast with observations in wheat, where NPs exposure induces an expression increase of *TIP2-9*, *PIP2*, *PIP3*, *PIP1.2* in leaves and of *TIP2-9*, *PIP1-5*, *PIP2*, *PIP1.2* in roots. However, in this case, the increase of aquaporin gene expression determined a reduction of NPs accumulation (Li S. et al., 2021). The application of bioactive molecules such as brassinosteroids, strigolactones, and melatonin therefore represents a viable strategy to enhance plant growth and stress tolerance under NPs exposure. However, further research is needed to evaluate their feasibility in intensive agricultural systems, to understand long-term effects, and to optimize their use across different crop species. Possible strategies to improve stress tolerance to NPs are breeding programs focused on the production of new crops with elevated amounts of endogenous bioactive compounds. Beyond these hormonal and membrane-mediated mechanisms, recent transcriptomic studies have highlighted the pivotal role of transcription factors (TFs) families in coordinating plant defense networks under NPs stress. A multi-omics study in rice revealed that PS-NPs exposure triggers spatiotemporal modulation of TFs families, including WRKY, MYB, and AP2/ERF (Xu, 2024). OsWRKY24 and OsWRKY53, key regulators of plant–pathogen interaction and defense signaling, were significantly upregulated, suggesting that PS-NPs elicit transcriptional programs like those activated by biotic and oxidative stress (Xu, 2024). These findings underscore the central role of WRKY-mediated transcriptional reprogramming in enhancing stress tolerance and maintaining redox and metabolic homeostasis under NPs exposure. Importantly, such TFs could serve as early molecular indicators in risk assessment, as their expression could be monitored via qPCR before physiological damage becomes apparent. The involvement of other TFs families such as NAC, and bZIP under PS-MPs or PS-NPs stress remains underexplored and warrants further investigation. Another molecular mechanism influencing NPs uptake from the soil

involves the formation of NPs–metal complexes. Oppositely charged NPs and toxic metals (e.g., arsenic, cadmium) can form conjugates, creating transport vectors that enhance the bioavailability and mobility of these contaminants in plant tissues (Davranche et al., 2019; Domenech et al., 2021; Yu et al., 2019). It has been proposed that NPs entry into plants is facilitated through these complexes, which are transported via the same membrane systems used for heavy metal uptake (Lian et al., 2020b; Xu et al., 2023). These include well-characterized transporter gene families identified in multiple plant species, notably in model plants such as Arabidopsis and rice (Chien et al., 2022; Huang et al., 2022; Kumaretal., 2023; Mitani-Ueno et al., 2023; Singhetal., 2023; Tao and Lu, 2022; Yang et al., 2024). The identification of specific marker genes, proteins, and metabolites through omics approaches provides a mechanistic foundation for assessing plant responses to PS-NPs and for establishing molecular indicators of environmental risk. TFs such as WRKY24 and WRKY53, which are rapidly induced by PS-NPs in rice, could function as early warning biomarkers detectable via qPCR before phenotypic or physiological alterations occur (Xu, 2024). Similarly, shifts in antioxidant enzyme levels or flavonoid metabolite profiles could be used as biochemical markers in standardized toxicity assays. Beyond diagnostic applications, omics-driven insights inform mitigation strategies and risk management. For instance, transcriptomic evidence shows that exogenous application of bioactive molecules such as brassinosteroids, strigolactones, or melatonin can modulate aquaporin gene expression (e.g., PIP and TIP families), enhance redox balance and restrict PS-NPs uptake (Gao et al., 2023; Li S. et al., 2021). Identification of transporter genes mediating NPs entry, as well as TFs orchestrating stress adaptation, offers valuable targets for molecular breeding or gene-editing programs aimed at developing NPs-resilient crops.

#### 5. Gene-editing and transgenic approaches as emerging mitigation tools

Since plastic pollution has become a major global environmental issue, there is an increasing need to develop sustainable remediation strategies beyond physical and chemical approaches.

Among these, phytoremediation represents a cost-effective and eco-friendly alternative traditionally used to remove heavy metals and organic pollutants from soil and water (Waseemetal., 2024; Yuan et al., 2024). Experimental evidence supports the potential of aquatic and wetland plants for microplastic removal. For instance, *Eichhornia crassipes* shows a high adsorption capacity, mainly retaining fine plastic particles within its intercellular spaces, and demonstrates remarkable long-term tolerance to plastic exposure (Yuan et al., 2023). Similarly, roots in constructed wetlands facilitate the interception of microplastics in flowing water (Chen et al., 2021). In line with these observations, microplastics have been shown to adhere to *Lemna minor* and to seaweeds and macroalgae in intertidal zones, mainly through hydrophobic interactions and plant-secreted polysaccharides that stabilize plastics on plant surfaces (Rozman et al., 2022; Sundbæk et al., 2018). Overall, the ability of plants to capture and retain MPs and NPs reduces their mobility and ecological impact, suggesting that plant-based stabilization could represent a promising green strategy for mitigating plastic pollution (Yuan et al., 2024). However, the potential of plants for phytoremediation and phytodepuration of MPs and NPs remains largely unexplored. Further studies are required to identify the most suitable plant species for these applications, considering their physiological traits, growth habits, and interactions with different types of plastics. Factors such as root architecture, surface properties, exudate composition, and the ability to form beneficial rhizosphere associations are likely to influence plastic adsorption, uptake, translocation, accumulation, and stabilization in plant tissues. Likewise, the chemical composition, size, and surface charge of plastics may differentially affect these processes (Chen et al., 2025). In addition, the potential of intercropping systems should be carefully evaluated, as plant–plant interactions could enhance the overall efficiency of phytoremediation. Combining species

with complementary root systems, exudation profiles, or microbial associations may improve the interception and immobilization of MPs and NPs, offering new opportunities to optimize plant-based strategies for mitigating plastic pollution while promoting agricultural sustainability. Recent advances in gene-editing technologies are opening new perspectives for enhancing plastic remediation efficiency. CRISPR-based strategies have been proposed to engineer plants and microorganisms capable of transforming plastic polymers, highlighting the potential of biotechnology in mitigating plastic pollution (Palitetal.,2025). For instance, the modulation of heavy metal and xenobiotic transporters, including the ABC, NRAMP, and ZIP families, could minimize NPs internalization and facilitate their compartmentalization or efflux, thereby preserving cellular homeostasis. Indeed, previous evidence demonstrates that CRISPR/Cas9-mediated knockout of the cadmium uptake transporter OsNRAMP5 generates low-Cd rice lines without yield penalties, effectively enhancing tolerance to cadmium toxicity by limiting root uptake and grain accumulation (Luoetal.,2023).

However, despite the growing interest in these approaches, no experimental studies have yet demonstrated the use of genome-edited plants specifically engineered to degrade, immobilize, or improve the binding and uptake efficiency of MPs and NPs from soil environments. Current review articles acknowledge these approaches as conceptually promising, but they remain largely hypothetical and unexplored in practice (Bansaletal.,2024). These approaches can be strategically adapted not only to enhance plant detoxification, but also to increase plant tolerance and productivity under NPs exposure. In this context, CRISPR-based editing could target key redox and stress-response genes, such as *APX*, *SOD*, *CAT*, or *GPX*, to reinforce the antioxidant defense system that counteracts NP-induced oxidative stress. Indeed, in rice, CRISPR/Cas knock-out of the *NADPH oxidase OsRbohB* reduces ROS overaccumulation and improves performance under heat stress, demonstrating that tuning ROS production can enhance stress tolerance (Liuetal.,2025). Similarly, the CRISPR-based editing of multiple peroxidase and catalase genes influences reactive oxygen species homeostasis and stress tolerance in plants, providing further insights into the coordinated regulation of antioxidant defense systems (Zhangetal.,2019). In addition, the overexpression or CRISPR-mediated activation of genes encoding glutathione S-transferases, phytochelatin synthases, and heat shock proteins (HSPs), can be employed to enhance plant tolerance to MPs and NPs (Gao M. et al., 2022; Gao H. et al., 2022;Lietal.,2004;Selmaetal.,2019). Despite these promising developments, several research gaps remain critical for translating molecular insights into field applications. First, the molecular signaling pathways underlying NPs perception and cellular response in plants remain poorly characterized, particularly regarding receptor-mediated endocytosis, secondary messenger cascades, and the role of small RNAs in stress signaling. A deeper understanding of how NPs interact with plant plasma membranes, redox hubs, and hormonal pathways (e.g., ABA, SA, JA, ethylene) is essential to identify effective genetic targets for editing. Second, although CRISPR systems are highly efficient in model species, their application in crops with complex polyploid genomes, such as wheat, is more challenging. This is mainly due to the presence of multiple homologous gene copies that must be edited simultaneously to obtain a detectable phenotype, which increases the risk of off-target events. This genetic redundancy, together with variable transformation efficiency, reduces overall editing precision and effectiveness. Third, the integration of multi-omics and phenotyping approaches is needed to link molecular edits to physiological resilience, ensuring that enhanced tolerance does not compromise yield or quality traits. From a translational perspective, CRISPR-based genome engineering offers an interesting potential pathway toward developing pollution-resilient crops and sustainable agricultural systems. By combining gene-edited plants with engineered microbial consortia, it may be possible to create synergistic bio-based remediation platforms within the rhizosphere. Such “plant–microbe partnerships” could both immobilize or transform plastic particles and maintain soil health, promoting nutrient

cycling and water retention. Furthermore, crops endowed with enhanced antioxidant capacity and efficient NPs sequestration could sustain productivity in contaminated fields, contributing to food security in vulnerable regions where soil pollution increasingly threatens yield stability. In the longer term, the integration of CRISPR-edited traits into breeding pipelines could accelerate the development of climate- and pollution-resilient varieties while supporting the transition to low-input, circular, and regenerative agriculture.

## 6. Concluding remarks and critical perspectives

While gene-editing and transgenic technologies offer promising opportunities to enhance plant tolerance and remediation capacity under NPs exposure, their effective implementation requires a solid understanding of the underlying biological mechanisms. In this context, a critical evaluation of current experimental evidence is essential to identify the physiological and molecular processes that determine plant sensitivity or resilience to PS-NPs. This review provides a comprehensive synthesis of the current knowledge on PS-NPs interactions with crop plants, focusing on their uptake, translocation, accumulation, physiological effects, and transcriptomic responses within the One Health framework, understanding how PS-NPs infiltrate plant systems and ultimately enter the food chain is crucial. However, the critical analysis of the available literature reveals that our understanding remains fragmentary and challenged by a high degree of experimental heterogeneity (Table 1). Despite increasing evidence that PS-NPs can be internalized by plant tissues and transported to edible parts, the precise mechanisms governing their uptake and distribution are still not fully elucidated. Many of the proposed pathways, such as endocytosis, apoplastic and symplastic routes, or crack-entry mechanisms, are supported by limited or indirect evidence, often obtained under artificial or non-standardized conditions. Additionally, few studies systematically compare the behavior of PS-NPs with different physicochemical characteristics (e.g., size, charge, surface chemistry) under environmentally realistic scenarios, limiting our ability to extrapolate findings to agricultural systems. Given the lack of data on realistic PS-NPs concentrations in soils, another major research gap lies in the poor standardization of experimental conditions across studies. Variations in methods, plant developmental stages, growth media, and PS-NPs concentrations hinder reproducibility and complicate the comparison of results across species and experimental settings. There is thus a pressing need for studies based on environmentally relevant concentrations and routes, including long-term field-based assessments particularly those based on standardized experimental systems in terms of concentrations, exposure times, analyzed parameters, and plant developmental stages, in order to identify whether a certain species is more tolerant to PS-NPs than others, in order to understand the mechanisms behind PS-NPs resilience. Although bread wheat has been reported to sustain growth and enhance photosynthesis by Lian et al. (2020), this is still not sufficient to understand if this species could really be the most resistant. Moreover, studies on durum wheat are still lacking; to date, only two investigations have examined the effect of plastic particles on this species, despite its global cultivation and major economic and nutritional importance (Sharma et al., 2025; Fontanini et al., 2025). A recent study reported that composts contaminated with microplastics, particularly polyvinyl chloride and polyethylene, reduced germination in durum wheat to about 60 %, while bread wheat maintained nearly full germination, highlighting the higher susceptibility of durum wheat to microplastic pollution (Sharma et al., 2025). Another very recent paper showed that although durum wheat seedlings can activate compensatory antioxidant and phenolic responses, exposure to nanoplastics, especially under heat stress, still caused moderate physiological alterations, indicating a measurable yet not extreme sensitivity of this crop to plastic pollution in warming conditions (Fontanini et al., 2025).

While plant responses to PS-NPs are highly variable and species-dependent, few attempts have been made to establish common

**Table 1**

Different species used as study objects and the various experimental conditions extracted from the referenced studies in this review for both PS-MPs and PS-NPs.

Plant species	Size (nm/ $\mu$ m)	Particle type	Concentration	Exposure duration	Growth medium	Reference
<i>Hordeum vulgare</i>	500 nm	PS-MPs (unmodified)	$10^3$ – $10^7$ particles/mL	21 days	Hydroponic	Zantis et al., (2023)
<i>Oryza sativa L.</i>	50 nm and 5 $\mu$ m	PS-NH <sub>2</sub> , positively charged	50 mg/L PS-NH <sub>2</sub> , 1 mg/L Phe	7 days	Culture sol., Petri dishes	Zhu et al., (2023)
	20–200 nm (85 % < 100 nm)	PS-NPs, unmodified	1 g/L	96 h	Petri dishes, deionized water	Spanò et al., (2022)
	50 nm	PS, PS-COOH, PS-NH <sub>2</sub> ; neg. and pos. charged	50 mg/L	7 days	Hydroponic nutrient sol.	Wang et al., (2022)
<i>Triticum aestivum L.</i>	80–91 nm	PS-NPs, fluorescent, slightly neg. (–3.21 mV)	50, 250 mg/kg	125–150 days	Soil (loamy), pots	Jiang et al., (2022)
	Avg 87.8 $\pm$ 8.6 nm (nominal 100 nm), hydrodynamic ~120–254 nm	PS-NPs, unmodified, dispersed in SDS	0.01–10 mg/L	21 days	25 % Hoagland solution	Lian et al., (2020a)
	5–25 $\mu$ m (powder, bead, fiber)	PS-MPs (negatively charged)	30–50 g/L	42 days	Soil (sandy loam, Haplic Calcisol)	Riaz et al., (2025)
	500 nm	PS-MPs (unmodified)	$10^3$ – $10^7$ particles/mL	21 days	Hydroponic	Zantis et al., (2023)
<i>Allium cepa</i>	100 nm	PS-NPs, not functionalized, negatively charged	10 mg/L	21 days	25 % Hoagland solution	Lian et al., (2020b)
	Nominal 50 nm (20–190 nm; 85 % < 100 nm)	Red PS-NPs, fluorescent	0.01–1 g/L	72 h	Distilled water (germination)	Giorgetti et al., (2020)
<i>Allium sativum L.</i>	75.1 $\pm$ 0.53 nm	PS-NPs, unmodified, spherical	0.05–1.0 mg/g soil	28 and 42 days	Soil + 20 % Hoagland sol.	Li G. et al., (2024)
<i>Chrysanthemum coronarium L.</i>	100 nm	PS-NPs fluorescent $\pm$ aquaporin inhibitors	10 mg/L	10 days	Hydroponic	Gao et al., (2025)
<i>Citrus ('US-942')</i>	20 nm, 50 nm	PS-NPs (green fluorescent)	1 % solid	15–30 days	Aeroponic culture	Hussain et al., (2025)
<i>Arabidopsis thaliana</i>	50, 100, 1000 nm	PS micro/nanoplastics, COOH, fluorescent	10–100 $\mu$ g/mL	21 days	Solid 1/4MS, sterile	Yu et al., 2024
	55 nm (PS-SO <sub>3</sub> H), 71.6 nm (PS-NH <sub>2</sub> ), 162.6 nm (PS-Pd)	PS-SO <sub>3</sub> H, PS-NH <sub>2</sub> , PS-COOH, PS-Pd	0.3, 1 g/Kg, 10–100 $\mu$ g/mL	7 weeks and 10 days	Soil, pot-based setup	Sun et al., (2020)
<i>Cucumis sativus L.</i>	50–100 nm	PS-NPs, negatively charged	50, 100 mg/L	3 weeks	Soil (potted, light incubator)	Huang et al., (2023)
	100–1000 nm	PS-NPs, unmodified	10 mg/L	21 days	Hoagland nutrient solution	Li et al., (2020)
<i>Daucus carota L.</i>	500 nm	PS-MPs (unmodified)	$10^3$ – $10^7$ particles/mL	7 days	Hydroponic	Zantis et al., (2023)
<i>Fagopyrum tataricum</i>	100 nm	PS-NPs (unmodified)	100 mg/L	0–2–4–6–8 days	Hydroponic	Hou et al., (2025)
<i>Glycine max L.</i>	20–30 nm (hydrodynamic ~122 nm)	PS-NPs, COOH-modified, neg. charged	12.5–50 mg/L	7 days	25 % Hoagland solution	Surgun-Acar, (2022)
<i>Lactuca sativa L.</i>	Avg 93.6 nm (hydrodynamic 113–135 nm)	PS-NPs, neg. charged (SDS-stabilized)	0.1, 1 mg/L	21 days	Soil (1/3 natural + 2/3 potting)	Lian et al., (2021)
	500 nm	PS-MPs (unmodified)	$10^3$ – $10^7$ particles/mL	21 days	Hydroponic	Zantis et al., (2023)
<i>Vicia faba</i>	100 nm and 5 $\mu$ m	PS-MPs, fluorescent	10–100 mg/L	48 h	Distilled water, Petri dishes	Jiang et al., (2019)
<i>Multi-species (wheat, barley, carrot, tomato)</i>	< 100 nm	PS-NPs (unmodified)	0.1–10 mg/L	3–7 days	Cell culture (in vitro)	Adamczyk et al., (2023)

response markers or predictive toxicity models. Alterations of the photosynthetic and sugar metabolic pathways are recurrently observed in some of the studied species, although the only common alteration induced by PS-NPs in all the analyzed species is probably an impairment in mineral nutrition. Transcriptomic analyses showing an increase in the expression of genes related to specialized/ secondary metabolites give interesting information on the possibility that these metabolites are involved in PS-NPs tolerance. The relation between strigolactons or brassinosteroids and PS-NPs tolerance is another issue of promising potential application in agriculture. However, too few studies have been made to verify the hypothesis arising from these first evidence. Moreover, the molecular bases of this tolerance remain poorly understood and require further investigation. Identifying conserved stress-response pathways and candidate genes conferring tolerance represents a promising research avenue, potentially informing future breeding strategies or phytotechnologies for contaminated systems. Importantly, transcriptomic analyses have begun to shed light on the molecular mechanisms triggered by PS-NPs, revealing modulation of genes involved in redox homeostasis, hormone signaling, and cell wall stability. However,

transcriptomic responses vary considerably depending on particle type, size, and plant species, and often lack functional validation. Integration of omics data with plant behavior and phenotypic analysis is needed to build a more coherent picture of NPs-induced plant stress responses. Such multidisciplinary approach is also pivotal for identifying robust biomarkers of exposure and effect as well as metabolic pathways capable to reduce PS-NPs toxicity in term of plant productivity but also, and probably more relevant, in term of first vehicle allowing plastic to enter in trophic networks. Finally, while several studies report the accumulation of PS-NPs in edible tissues, including grains, fruits, and leafy vegetables, the extent to which these particles retain bioactivity, and their potential transfer and transformation within the human body, remain open questions. This constitutes a critical knowledge gap with direct implications for food safety and human health. In conclusion, this review provides a comprehensive overview of the present knowledge of NPs effects on higher plants. However, while current research confirms that PS-NPs can affect plants at multiple levels, from root uptake to shoot gene expression, the field is still in its infancy. Progress will depend on the implementation of standardized protocols, multidisciplinary

approaches, and cross-species comparisons to generate a reliable risk assessment framework. Only through such efforts can we move toward a more accurate understanding of NPs behavior in agroecosystems and its implications for sustainable food production and global health.

### CRedit authorship contribution statement

**Benedetta Pizziconi:** Writing – original draft, Conceptualization. **Giuliana Bruno:** Writing – original draft. **Samuela Palombieri:** Writing – review & editing, Conceptualization. **Francesco Sestili:** Writing – review & editing, Funding acquisition. **Sara Cimini:** Writing – review & editing, Conceptualization. **Laura De Gara:** Writing – review & editing, Funding acquisition, Conceptualization.

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### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Data availability

No data was used for the research described in the article.

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