PHOTOSYNTHETICA
International Journal for Photosynthesis Research

DOI 10.32615/ps.2021.049 PHOTOSYNTHETICA 59 (4): 570-586, 2021

REVIEW

Insights into nanoparticle-induced changes in plant photosynthesis

M. GHORBANPOUR*,+, A. MOVAHEDI*, M. HATAMI*, K. KARIMAN**, F. BOVAND***,
and M.A. SHAHID#,+

Department of Medicinal Plants, Faculty of Agriculture and Natural Resources, Arak University,
*38156-8-8349 Arak, Iran**
*UWA School of Agriculture and Environment, The University of Western Australia, Perth, WA, 6009, Australia***
*Departments of Agronomy, Islamic Azad University, Arak Branch, Arak, Iran****
Department of Agriculture, Nutrition and Food Systems, University of New Hampshire, Durham NH 03824, USA#

Abstract

Photosynthesis can be affected by nanoparticles (NPs) both negatively (*e.g.*, through decreasing the chlorophyll content and electron transport rate, damages to chloroplast components, *etc.*) or positively (*e.g.*, *via* enhancing chlorophyll content, the activity of Rubisco enzyme, the performance of PSII, and CO_2 harvesting, as well as broadening the chloroplast photoabsorption spectrum). Enhanced photosynthetic efficiency could be a possible impact of NPs on photosynthetic organisms of major economic and ecological significance (*e.g.*, crops and algae), which warrants an in-depth understanding of NPs interactions with chloroplast and its structural components (*e.g.*, thylakoid membranes), signaling molecules, and pathways involved in photosynthesis. In this review, we comprehensively explore the potential effects of NPs on photosynthesis in different photosynthetic organisms (terrestrial plants, aquatic plants, and algae), and highlight research limitations and possible practical implications.

Keywords: chlorophyll; chloroplast; nanoparticles; photosynthesis.

Introduction

Nanus is a Greek word that means ‘dwarf’ and it is the base of the term ‘nano’ (Johal and Johnson 2018, Baker *et al.* 2019). When we divide a meter into 100 billion parts (10^{-9}), we encounter a new scale, which is referred to as nanoscale (El Naschie 2006). Nanotechnology is a technology that uses nanoscale in at least one dimension (Gogotsi 2006), and it has applications in various industries, such as medicine, agriculture, environment, pharmaceutical, and food industries (Gade *et al.* 2010, Hatami and Ghorbanpour 2014, Singh *et al.* 2017, Tian *et al.* 2018, Fahimirad *et al.* 2019, Hatami *et al.* 2019a, Rahayu *et al.* 2020, Sharifi-Rad *et al.* 2021). Nanoparticles (NPs) are important because of their physical, chemical, and magnetic properties as well as being cheap, safe, and clean (El Naschie 2006, Gade *et al.* 2010, Johal and Johnson 2018). ‘Dimension’ is one of the main properties of the NPs, however, some NPs have no dimensions such as quantum dots and carbon dots. The dimensional NPs could possess one dimension (nanowires), two dimensions (nanofilms), or three dimensions (metal NPs) (Baker *et al.* 2019). There are three types of NPs depending on their origin: (*1*) natural NPs, originated from volcano eruptions,

Highlights

- Photosynthesis can be affected by nanoparticles (NPs) both positively and negatively
- NPs augment plant light-harvesting ability in a dose-dependent manner
- NPs-promoted photosynthetic efficiency may arise from the upregulation of key enzymes

Received 1 July 2021
Accepted 12 October 2021

+Corresponding authors
e-mail: m-ghorbanpour@araku.ac.ir
Muhammad.shahid@unh.edu

Abbreviations: CdS – carbon quantum dots; CeO_2 – cerium oxide; Chl – chlorophyll; MWCNT – multi-walled carbon nanotube; NPs – nanoparticles; SWCNT – single-walled carbon nanotube; TiO_2 – titanium dioxide.
Conflict of interest: The authors declare that they have no conflict of interest.

(*2*) incidental NPs, produced by human activities unintentionally, and (*3*) engineered NPs, produced to be used in different industries, agriculture, *etc*. (Večeřová *et al*. 2016). All these NPs can affect plants, mainly through their interactions with key cell organelles such as chloroplasts and mitochondria (Pagano *et al*. 2018). Quantum dots and NPs are wildly used in agriculture.

According to Das *et al*. (2017), plants harvest almost 100 TW (terawatts) of solar energy annually, which is ten times higher than human consumption. Since NPs have the potential to increase the solar energy harvest by plants, nanotechnology may revolutionize agriculture in the future. Nanotechnology has been used to produce genetically manipulated (GM) products (El Naschie 2006, Večeřová *et al*. 2016). Nanotechnology has also been used as a tool for sustainable productivity and protection of food/feed crops (Baker *et al*. 2019). Nanotechnology can make agricultural production better or worse by affecting the photosynthetic activities of plants (Djanaguiraman *et al*. 2018, Tombuloglu *et al*. 2019). The nature and magnitude of the impacts of NPs on photosynthesis depend on concentration, size, surface charge as well as the physicochemical properties of NPs, size of cell wall pores, plant species, and also the culture bed (Pagano *et al*. 2018, Tighe-Neira *et al*. 2018, Tan *et al*. 2019, Verma *et al*. 2019, Falco *et al*. 2020). Furthermore, the duration of the exposure between NPs and plant tissues may also be important. For example, *Chlamydomonas reinhardtii* (a single-cell green alga) cultures that were treated with TiO_2 NPs for 8 h did not differ significantly in comparison with the untreated controls, whereas 12-h exposure stimulated their growth (Chen *et al*. 2012).

The size of NPs is another factor associated with their effects on plants. Small TiO_2 NPs (50 nm) had a significant positive effect on the chlorophyll (Chl) content of okra (*Abelmoschus esculentus*) plants, while the larger TiO_2 NPs (68 nm) inhibited photosynthesis (Ogunkunle *et al*. 2020). When NPs are absorbed through the plasma membrane, they attach to proteins forming a complex called protein corona, which enters the neighboring cells *via* plasmodesmata channels (Hatami *et al*. 2016). Although NPs are in nanoscale, they must be small enough to pass through different barriers, such as cell walls, cell membrane, Casparian strip, cuticle, *etc*. (Večeřová *et al*. 2016, Tombuloglu *et al*. 2019). For example, NPs should be between 5–20 nm to be able to penetrate the cell wall pores (Hatami *et al*. 2016, Večeřová *et al*. 2016).

Nanoparticles can affect different processes of photosynthesis, or even in different parts of chloroplasts. In other words, NPs may affect the morphology of photosynthetic structures, contents of photosynthetic pigments, *etc*. (Tan *et al*. 2019). For example, NPs can increase the photosynthetic rate by enhancing the activity of Rubisco (Hussain *et al*. 2019, Kataria *et al*. 2019). Nanoparticles can also alter the performance of PSII and CO_2 harvesting (Falco *et al*. 2020). Some NPs may decrease the absorption of sunlight by decreasing the Chl contents of plants (Tao *et al*. 2015). As photosynthetic rate depends on the Chl contents of plants, decreased Chl contents can negatively affect the photosynthetic rate (Wang *et al*. 2018).

Some NPs can change the wavelength domains of photosynthesis. For example, carbon dots (CDs) nanocapsules absorb wavelengths between 200–700 nm, which can increase the light harvest and also electron transport chain performance in PSII, and ultimately promote photosynthesis (Chandra *et al*. 2014, Verma *et al*. 2019, Xu *et al*. 2020). Interestingly, NPs may also act as a shadow, preventing light harvesting in plants, which is referred to as the ‘shading effect’. As a result, plants start producing more Chl to harvest more light, however, they usually cannot afford it, leading to a decrease in photosynthesis (Middepogu *et al*. 2018). Hence, plants can be affected by NPs in different ways. Due to the significance of photosynthesis for plants and human life, it is vital to investigate NPs–plant interactions and their impact on photosynthesis. In this review, we mechanistically explore the effects of different NPs on photosynthesis and photosynthetic pigments in a broad range of photosynthetic organisms.

Engineered nanoparticles

Engineered NPs can change diverse metabolic pathways in plants including transpiration, gas exchange, biosynthesis and composition of pigments (*e.g.*, Chl), and expression of photosynthesis-related genes (Tan *et al*. 2019). Here, we categorize engineered NPs into three main groups including (*1*) nanocarbons, which are made of carbon, (*2*) metal NPs, which include different kinds of metals and metal oxide compounds, and (*3*) magnetic NPs, which are metal NPs with magnetic properties.

The entry and interaction pathways of NPs in plants through roots and leaves

To deeply understand the nature of NPs–plant interactions, it is necessary to characterize the entry, uptake, translocation, accumulation, biotransformation, and fate of NPs within plant cells, tissues, and organelles. Entry and translocation of NPs can occur through root to shoot (down–top) or shoot to root (top–down) routes, an important feature that makes both foliar and soil applications feasible in agroecosystems. The entry (Fig. 1*A*) and interaction pathways of NPs in plants through leaves (Fig. 1*B*) and roots (Fig. 1*C*), and their long-distance transport *via* xylem and phloem (Fig. 1*D*), as well as their possible routes of cellular uptake (Fig. 1*E*) were schematically illustrated in Fig. 1. When applied to the foliage, NPs penetrate leaves through cuticles, stomatal openings, hydathodes, lenticels, trichomes, and wounds. NPs may undergo long-distance transport *via* the vascular systems, such as xylem and phloem conductive tissues, after entering the leaf apoplast through the aforementioned routes. When exposed to plant roots, NPs can penetrate *via* root tip, root hairs, lateral roots, rhizodermis, and rupture. As shown, when NPs are available either in culture medium or soil matrix, they can be transferred *via* both symplastic and apoplastic pathways to penetrate the root epidermis, pass through the cortex, and finally translocate and distribute to the aerial parts of plants including stems and leaves *via* the xylem and

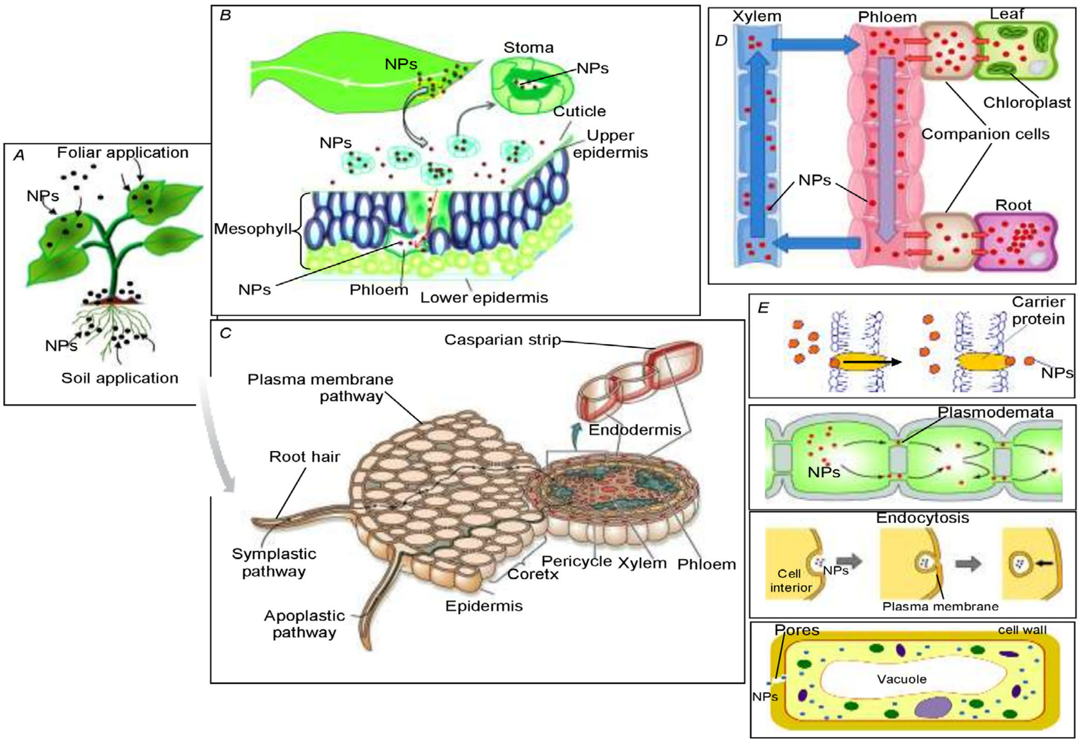


Fig. 1. The entry (*A*) and interaction pathways of nanoparticles (NPs) in plants through roots and leaves (*B* and *C*). Long-distance NPs transport *via* xylem and phloem (*D*). Probable routes of cellular uptake of the NPs in the plant cell (*E*).

phloem vessels. The absorbed NPs *via* the foliage could be redistributed to other plant organs such as roots through the phloem. There are several routs for NPs to enter the symplastic pathway such as endocytosis (Etxeberria *et al.* 2006), pore formation (Serag *et al.* 2011, Wong *et al.* 2016), carrier proteins (Rico *et al.* 2011, Schwab *et al.* 2015), plasmodesmata (Zhai *et al.* 2014) and ion channels (Perez-de-Luque 2017). Several factors affect the plant uptake of NPs such as physicochemical characteristics of NPs, plant species type, plant growth/physiological stage, root exudates, soil properties (pH, organic matter, salt ions, and microflora), *etc.*

Nanocarbons

Carbon dots (CDs) are one type of nanocarbons, which function as electron donors and acceptors, so they can influence electron transportation positively (Wang *et al.* 2018, Xu *et al.* 2020). In PSI, Fe-S proteins act as the carriers of electrons. Wang *et al.* (2018) declared that CDs can attach to these proteins and accelerate electron transport (Wang *et al.* 2018). Exposure to > 0.02 mg(CDs) mL^{-1} led to a positive impact on the growth of mung bean sprouts, which could be attributed to enhanced electron transport (Wang *et al.* 2018). Carbon dots can also affect Chl contents, photosynthesis, and the Rubico activities of plants (Wang *et al.* 2018). Spraying 3,900 mg L^{-1} of CDs nanocapsules significantly increased the photosynthetic rate of *Lactuca sativa* (Xu *et al.* 2020). The Chl pigments in *Lablab purpureus* plants were shown to absorb more light *via* increasing the concentration of carbon NPs, and application of 1.2–2.5 mg mL^{-1} of carbon NPs led to the maximum light absorption (Swapna *et al.* 2019). Carbon dots may also influence plants negatively. For example, the application of CDs decreased the activities of photosynthetic enzymes in *Arabidopsis thaliana* (Chen *et al.* 2018). Carbon nanotubes (CNTs) increased the number of stomata, electron transport rate, and ultimately the photosynthetic rate in rice (Joshi *et al.* 2020). These CNTs caused an increase in Chl content and leaf surface area of tobacco (Mahto *et al.* 2019).

Single-walled carbon nanotubes (SWCNTs) and multi-walled carbon nanotubes (MWCNTs) are two kinds of CNTs that can positively affect plant metabolism and photosynthesis (Ghorbanpour and Hadian 2015, Hatami *et al.* 2017, Samadi *et al.* 2020, 2021). The SWCNTs absorb a wide range of light, including ultraviolet, visible light, and infrared, which can promote photosynthesis (Giraldo *et al.* 2014, Wang *et al.* 2020). The electron transport from PSII to PSI can also be improved by SWCNTs (Gong and Zhao 2018). The photosynthetic activities were tripled in *Arabidopsis thaliana* plants subjected to SWCNTs (Giraldo *et al.* 2014). Similar effects have been documented for MWCNTs. Rice plants exposed to MWCNTs (70, 80, and 90 mg mL^{-1}) had increased total Chl contents (Joshi *et al.* 2020). Likewise, MWCNTs application at concentrations of 0.1, 0.25, and 0.5 g L^{-1}, caused an increase in the Chl concentration of amaranth plants (Jia *et al.* 2019). MWCNTs application (> 50 mg L^{-1}) was shown to increase light absorption, along with photosynthetic rate and function in *Arabidopsis thaliana* (Fan *et al.* 2018). Adverse effects have also been established in plants subjected to MWCNTs. Application of MWCNTs at 100 mg L^{-1} had no significant effect on carrot seedlings, whereas a higher concentration (200 mg L^{-1}) led to a 10% reduction in the growth of the seedlings (Park and Ahn 2016).

Graphene NPs are another important type of carbon-based NPs that have agricultural applications (Ghorbanpour *et al*. 2018, Hatami *et al*. 2019b). *Capsicum annuum* plants exposed to graphene nanosheets showed an elevated photosynthetic rate (Younes *et al.* 2019). Also, 0.4 mg L^{-1} of graphene oxide (GO) NPs decreased the Chl content of pea plants (Chen *et al.* 2019). GO NPs can also decrease light absorption in plants (Nogueira *et al.* 2015). Fullerenols (C60) NPs are another type of nanocarbon material, which were demonstrated to increase the Chl content in wheat (Wang *et al.* 2016). Approximately, half of the global photosynthesis occurs in aquatic ecosystems, hence, it is crucial to investigate the effects of different NPs on photosynthetic organisms inhabiting these ecosystems (Zhang *et al.* 2017). Carbon dots (CDs) were demonstrated to promote the productivity of microalgal species including *Haematococcus pluvialis* (5, 10 mg mL^{-1}) and *Chlorella* sp. KR-1 (5 mg mL^{-1}), whereas a higher CDs concentration (50 mg mL^{-1}) decreased the growth rate of *Chlorella vulgaris* (Choi *et al.* 2020). Graphene oxide NPs, at 1 mg L^{-1}, were shown to adversely affect the growth of the freshwater plant *Lemna minor* (Hu *et al.* 2018). The Chl content decreased in the microalga *Raphidocelis subcapitata* exposed to GO NPs (Nogueira *et al*. 2015). Upon exposure to C60 NPs, Chl *a* and Chl *b* contents decreased in *Lemna gibba* (2 mg L^{-1}) and *Scenedesmus obliquus* (> 0.18 mg L^{-1}) (Santos *et al.* 2013, Tao *et al*. 2015).

Metal/metal oxide nanoparticles

Although most metal NPs may harm plants, some metal oxide NPs can improve the production of chemical energy in photosynthetic systems. Some metal-based NPs, such as CuO, ZnO, and Ag NPs, may disrupt Chl biosynthesis, however, some other NPs, *e.g.*, TiO_2 and Au NPs, were shown to increase the Chl content in several plant species (Večeřová *et al.* 2016). Metal NPs can also increase the Chl content of plants, helping them absorb more energy and consequently enhance their photosynthesis (Wang *et al*. 2018, Kataria *et al*. 2019).

Titanium dioxide nanoparticles (TiO_2 NPs)

TiO_2 NPs possess a high capability in increasing light absorption (especially UV light), photosynthesis, electron transport, and also protecting Chl molecules (Park and Ahn 2016, Morelli *et al*. 2018, Mahto *et al.* 2019, Faraji and Sepehri 2020). However, TiO_2 NPs may affect various plants differently (Hatami *et al*. 2014). For example, TiO_2 NPs can disrupt electron transport to PSII and their effect depends on the application/uptake type and also the plant species (Conway *et al*. 2015). Yang *et al.* (2007) evaluated the effects of TiO_2 NPs (0.25%) on the oxygen evolution of spinach leaves and found that exposure to TiO_2 NPs and their bulk significantly enhanced the oxygen-evolving rate. However, the oxygen evolution was restrained in plants grown under N-deficient conditions. Moreover, the oxygen-evolving rate in plants exposed to TiO_2 NPs was much higher than bulk TiO_2-treated and untreated controls under such conditions, representing that application of TiO_2 NPs may intensely ameliorate the adverse impacts of N-deficiency on the oxygen evolution of plants. Increased oxygen-evolution rate in leaves following exposure to TiO_2 NPs was attributed to the improved light absorption and photochemical reaction activity (Yang *et al*. 2007), which is consistent with enhancement of chlorophyll synthesis and sensitization of TiO_2 NPs in chloroplasts (Gao *et al.* 2006). Both TiO_2 NPs and bulk TiO_2 may enhance plastid pigments of chloroplasts to absorb and transfer light energy and excite electrons, causing water photolysis (Hong *et al*. 2005).

Generally, the application of Ti not only improved soybean photosynthesis by increasing leaf area and leaf chlorophyll contents, but also increased shade tolerance and yield of soybean under maize–soybean relay strip intercropping conditions (Hussain *et al.* 2021). However, TiO_2 NPs might have positive structural and biochemical effects on some crops, whereas they could harm other plant/algae species (Tighe-Neira *et al*. 2018). Furthermore, the positive effects of TiO_2 NPs on plants are more pronounced as compared to the bulk TiO_2, which is attributed to their size differences (Cox *et al*. 2016). Table 1 presents the effects of TiO_2 NPs on photosynthesis machinery in different plant/algal species.

Silver nanoparticles (Ag NPs)

Ag NPs are one of the most important NPs because of their antimicrobial properties and also their extensive use in care products, food industry, agriculture, building materials, *etc*. (Hatami and Ghorbanpour 2013, Qian *et al.* 2013, Hajian *et al*. 2022). Exposure to Ag NPs can lead to maximum absorption of visible light in certain plants (Wang *et al.* 2020). Ag NPs and $AgNO_3$ NPs are two main types of Ag NPs, both of which were shown to significantly reduce the photosynthetic performance, total chlorophyll, carotenoids, and total protein content and also increased the oxidative stress in cucumber (*Cucumis sativus*); the adverse effects were greater in plants treated with $AgNO_3$ NPs (Tripathi *et al.* 2017a). Likewise, exposure to 400 mg L^{-1} of Ag NPs or $AgNO_3$ NPs led to significant reductions in the Chl contents and growth parameters in *Brassica nigra*, however, Ag NPs were demonstrated to be more toxic than $AgNO_3$ NPs as revealed by monitoring the Ag accumulation as well as the lipid peroxidation and the H_2O_2 content of root and shoot tissues (Amooaghaie *et al*. 2018).

Ag NPs, in low concentrations, are useful for improving the biosynthesis of Chl and Chl fluorescence parameters in plants (Ghorbanpour and Hatami 2014,

Table 1. The effects of TiO_2 nanoparticles (NPs) on photosynthesis in different plant/algal species.

Plant/algal species	NPs concentration	NPs size	Growth medium	Effects	Reference
Zea mays	Not mentioned	Not mentioned	Not mentioned	Increased in photosynthetic pigments and light absorption	Park and Ahn (2016)
Zea mays	100 mg kg^{-1}	592 ± 7 nm	Soil	No effect on Chl *a*, Chl *b*, and carotenoids	Zhao *et al.* (2019)
Zea mays	Not mentioned	30.1–60 nm	Not mentioned	Decreased in leaves growth and transpiration rate	Mishra *et al.* (2014)
Dracocephalum moldavica	100 mg L^{-1}	Not mentioned	Hydroponic growth medium containing cocopit and perlit	Increased in Chl *a*, Chl *b*, and carotenoids	Gohari *et al.* (2020)
Mentha piperita	100 mg L^{-1}	Not mentioned	Not mentioned	Increased in essential oil contents	Samadi *et al.* (2014)
Abelmoschus esculentus (L.) Moench	800 mg kg^{-1}	50 nm	Loamy soil	Decreased in Chl *a*, Chl *b*, and total Chl content	Ogunkunle *et al.* (2020)
Mentha piperita L.	150 mg L^{-1}	< 21 nm	Pot, filled with homogenous mixture of soil and organic manure	Increased in Chl contents, photosynthetic rate, and Rubisco activity	Ahmad *et al.* (2018)
Petroselinum crispum	10,000; 20,000; 30,000; and 40,000 mg L^{-1}	83.7 nm	Murashige and Skoog medium	Increased in Chl content	Hu *et al.* (2020)
Spinacia oleracea	Not mentioned	Not mentioned	Not mentioned	Chl formation, increasing in Rubisco activity and photosynthesis	Kataria *et al.* (2019)
Spinacia oleracea	Not mentioned	Not mentioned	Not mentioned	Increasing Chl content and photosynthetic activities	Baker *et al.* (2019)
Spinacia oleracea	Not mentioned	5 nm	Experimental flower pot	Increasing net photosynthetic rate and accumulation of organic substances and Rubisco activity	Gao *et al.* (2008)
Spinacia oleracea	0.25%	5 nm	Not mentioned	Damaging chloroplast and decreasing photosynthesis	Missaoui *et al.* (2017)
Linum usitatissimum	Not mentioned	Not mentioned	Not mentioned	Increasing in Chl and carotenoid content	Kataria *et al.* (2019)
Lycopersicon esculentum	Not mentioned	Not mentioned	Not mentioned	Increasing photosynthesis	Kataria *et al.* (2019)
Lycopersicon esculentum	0.05, 0.1 g L^{-1}	16.04 nm	Nutrition pot inside heated solar greenhouse	Enhanced net photosynthetic rate	Qi *et al.* (2013)
Lycopersicon esculentum	0.2 g L^{-1}	16.04 nm	Nutrition pot inside heated solar greenhouse	Decreased in net photosynthetic rate	Qi *et al.* (2013)
Ulmus elongata	Not mentioned	Not mentioned	Not mentioned	Decreased in quantum function of PSII and electron transportation rate	Kataria *et al.* (2019)
Spirodella polyrrhiza	1, 5, 10 mg l^{-1}	8 nm	Glass aquaria, a specific culture medium	Decreased in total Chl content	Movafeghi *et al.* (2018)
Lactuca sativa	1, 10, and 100 mg L^{-1}	Not mentioned	Hydroponic	No significant effect on plastid pigments	Tan *et al.* (2019)
Clarkia unguiculata	100 mg L^{-1}	27 ± 4 nm	Soil	Disturbance in CO_2 absorption	Cox *et al.* (2016)
Chlorella vulgaris	Not mentioned	25 nm	Slightly modified OECD algal medium	Decreased in total Chl content	Dauda *et al.* (2017)
Chlorella vulgaris	50, 100, 150, and 200 ppm	Not mentioned	Not mentioned	Hinder the photosynthetic activities	Ghazaei and Shariati (2020)

Chlorella ellipsoidea	0.1 µg L^{-1}	< 21 nm	Algal medium	Increased in Chl *a*, Chl *b*, and total Chl contents	Matouke *et al.* (2018)
Chlorella pyrenoidosa	20 mg L^{-1}	12.0 ± 3.5 nm	Erlenmeyer flasks	Increased in Chl *a* content	Middepogu *et al.* (2018)
Dunaliella salina	50, 100, 150, and 200 ppm	Not mentioned	Johnson modified medium	Decreased in Chl content and photosynthesis efficiency	Ghazaei and Shariati (2020)
Dunaliella tertiolecta	50,100, 150, and 200 ppm	Not mentioned	Johnson modified medium	Decreased in Chl content and photosynthesis efficiency	Ghazaei and Shariati (2020)
Dunaliella tertiolecta	0.1–10 mg l^{-1}	25 nm	Algal medium	No effect on photosynthetic pigments	Morelli *et al.* (2018)

Sami *et al.* 2020). Exposure to Ag NPs at 20, 40, and 60 mg L^{-1} led to increased Chl contents in *Zea mays* and *Phaseolus vulgaris*, while higher concentrations (80 and 100 mg L^{-1}) led to adverse effects on the Chl content (Salama 2012). Rubisco activities increased in tobacco plants treated with Ag NPs and $AgNO_3$ NPs (25, 50, and 76 µM) (Tkalec *et al.* 2017). Similarly, Ag NPs increased the Chl contents in carrots (Park and Ahn 2016). Likewise, a dose-dependent effect was observed in *Brassica juncea* plants exposed to Ag NPs, *i.e.*, 25, 50, and 100 mg L^{-1} of Ag NPs, increased the Chl contents and PSII efficiency, whereas these parameters decreased by higher Ag NPs concentrations of 200 and 400 mg L^{-1} (Sharma *et al.* 2012). Ag NPs also increased the Chl and carotenoid contents in *Pelargonium zonale* (Kataria *et al.* 2019). Moreover, exposure to Ag NPs increased the Chl content and quantum efficiency in *Brassica juncea* (Torrent *et al.* 2020). Treatment with 25–50 mg L^{-1} of Ag NPs enhanced the number of shoots per explant, shoot height, and Chl content in micropropagation of vanilla plants in temporary submerged systems (Spinoso-Castillo *et al.* 2017).

Ag NPs can also affect photosynthesis negatively. Here, we briefly mention several examples of negative Ag NPs–plant interactions. A high concentration of Ag and Ag^+ NPs (0.5 and 3 mg L^{-1}) decreased the Chl contents in *A. thaliana* (Qian *et al.* 2013). The negative effects of Ag^+ are generally more than Ag NPs (Qian *et al.* 2013). Exposure to 1,000 and 3,000 µM of Ag NPs decreased growth parameters, photosynthetic pigments, and Chl fluorescence in *Pisum sativum* (Tripathi *et al.* 2017b). Ag NPs caused an overproduction of reactive oxygen species (ROS) in the leaves of cucumber plants, leading to decreased photosynthetic activities (Wang *et al.* 2020). ROS directly damage chloroplasts in stressed plants (Tripathi *et al.* 2017c). The acceptor site of PSI in the chloroplast has been found as a major source of free radicals (ROS), which are responsible for the oxidative damage-induced reduction in photosynthetic activity and destruction of photosystems as well as improper regulation of PSI electron transport in wheat seedlings exposed to AgNPs (at 5 mM) (Rastogi *et al.* 2019b). Ag NPs reduced the rate of electron transport chain, CO_2 absorption, and the photochemical efficiency of PSII, while causing an increase in the nonphotochemical quenching in *Vicia faba* plants (Falco *et al.* 2020). Application of Ag NPs led to decreased transpiration in *Cucurbita pepo* (Mishra *et al.* 2014). The concentrations of Chl *a* and Chl *b* decreased in Brazilian waterweed (*Egeria densa*) upon exposure to Ag NPs (Winkelmann *et al.* 2017). Treatments with Ag NPs (20–50 mg L^{-1}) harmed mung plants and decreased their total Chl contents (Mahto *et al.* 2019). Application of Ag NPs (10–15 nm) at high concentrations (> 500 mg L^{-1}) significantly decreased the Chl contents in tomato plants (Pagano *et al.* 2018). In rice, Ag NPs (0.2, 0.5, and 1 mg L^{-1}) decreased the total Chl and carotenoid contents (Nair and Chung 2014). A decrease in maximum electron transport rate was observed in *Vicia faba* plants subjected to Ag NPs (Falco *et al.* 2020). Inhibition of photosynthetic pathways was observed in *A. thaliana* plants treated with 0.5 and 1 mg L^{-1} of Ag NPs (Cox *et al.* 2016). Both Ag and $AgNO_3$ NPs were demonstrated to have a negative impact on Chl *a*, Chl *b*, and carotenoid contents in tobacco seedlings, however, the magnitude of the negative effects was greater in plants subjected to $AgNO_3$ NPs (Peharec Štefanić *et al.* 2018). Likewise, both Ag and $AgNO_3$ NPs significantly decreased the Chl content and photosynthesis in *Cucumis sativus* (Tripathi *et al.* 2017a).

Generally, Ag NPs that are coated with PVP, PEG or citrate, display reduced phytotoxicity (Torrent *et al.* 2020). Exposure of Ag NPs-citrate (Ag NPs coated with citrate) had no significant effect on Chl contents of *Physcomitrella patens*, whereas Ag NPs-PVP [coated with poly(N-vinyl-2-pyrrolidone)] increased the Chl *a* content in these plants (Liang *et al.* 2018). However, Chl *a* and Chl *b* contents of these plants significantly reduced upon exposure to Ag NPs without surface coating (Liang *et al.* 2018). Although both Ag NPs and Ag NPs-PVP decreased the transpiration rate and stomatal conductance in *Lactuca sativa*, the negative effects of Ag NPs-PVP were lesser than that of the uncoated Ag NPs. Similar to terrestrial plants, Ag NPs may cause negative or positive effects on aquatic plants and algae. Application of Ag NPs decreased the Chl content and PSII function of the marine diatom *Skeletonema costatum* (Tighe-Neira *et al.* 2018). A low concentration of Ag NPs (0.05 mg L^{-1}) increased the Chl *a* content, whereas a higher Ag NPs concentration (5 mg L^{-1}) decreased the Chl contents in *S. costatum* (Huang *et al.* 2016). Treatment with Ag NPs, at 40–50 mg L^{-1}, reduced the electron transportation from Q_A to Q_B in PSII in the green alga *Chlamydomonas* (Nam *et al.* 2018). Application of both Ag and $AgNO_3$ NPs led to a negative effect on the photosynthesis efficiency of *Euglena gracilis* (freshwater single-celled alga) (Li *et al.* 2015). Ag NPs (10 µg L^{-1}) also decreased the total Chl content in the green eukaryotic microalga *Chlorella vulgaris* (Tayemeh *et al.* 2020). Ag NPs (1–10 mg L^{-1}) increased the Chl content in the aquatic flowering plant *Eichhornia crassipes* (Rani *et al.* 2016).

Zinc oxide nanoparticles (ZnO NPs)

Zinc oxide (ZnO) NPs are one of the most important NPs, because of their large surface area, low toxicity, and especially their unique physicochemical properties (Baker *et al.* 2019). A broad range of studies has shown that ZnO NPs may promote or disrupt photosynthesis (Table 2). For example, when *Anabaena* sp. plants were exposed to ZnO NPs, their photosynthesis and other metabolic activities were adversely affected (Tang *et al.* 2015). Other Zn NPs such as ZnS NPs also affect photosynthesis. For example, 125, 250, and 500 mg L^{-1} of ZnS NPs decreased the Chl content in pea plants, whereas these NPs increased the Chl content in mung beans compared to controls (Thapa *et al.* 2019). Enhanced Chl and/or carotenoid contents have been observed in different plant species subjected to ZnO NPs including *Solanum lycopersicum* (Singh *et al.* 2016), *Coriandrum sativum* (Pullagurala *et al.* 2018), and *Cucumis sativus* (Kataria *et al.* 2019).

Cerium oxide nanoparticles (CeO_2 NPs)

Cerium oxide is one of the most important nanoceria. CeO_2 can penetrate the leaf cells and also penetrate chloroplasts as well as thylakoids, which can suppress electron transportation to PSII (Conway *et al.* 2015). The application of CeO_2 NPs decreased the photosynthetic rate by reducing the Chl content in wheat (Wang *et al.* 2016). Exposure to 200 mg kg^{-1} CeO_2 NPs significantly decreased the photosynthetic rate and transpiration in *Cucumis sativus* (Tan *et al.* 2019). Treatment with 1,000–2,000 mg kg^{-1} of CeO_2 NPs also decreased the Chl content in *Lactuca sativa* (Lizzi *et al.* 2019). Likewise, CeO_2 NPs caused a decrease in photosynthesis in *Clarkia unguiculata* (Conway *et al.* 2015) and *Cucumis sativus* (Tighe-Neira *et al.* 2018). However, as we mentioned previously, NPs concentration and plant species are key players of the net outcome arising from NPs–plant interactions (Tighe-Neira *et al.* 2018, Abbas *et al.* 2020). For example exposure to 2,000 mg L^{-1} of CeO_2 NPs decreased the Chl content, plant growth, and photosynthesis in wheat, however, treatment with 1,000 mg L^{-1} of CeO_2 NPs was accompanied by the maximum photosynthetic rate, along with enhanced CO_2 assimilation quantum yield (φ_{CO2}) and stomatal conductance (Abbas *et al.* 2020). CeO_2 NPs may also cause a deformation in photosynthetic tissues. For example, wheat plants exposed to CeO_2 NPs (100 and 400 mg kg^{-1}) had swollen chloroplasts (Tan *et al.* 2019). Lower concentrations of CeO_2 NPs can have a positive effect on photosynthesis (Abbas *et al.* 2020). Treatment with 300 mg L^{-1} of CeO_2 NPs increased the Chl content, net photosynthetic rate, and Rubisco activity in *Fragaria ananassa* (Dai *et al.* 2020). The application of CeO_2 NPs can increase the uptake of Mg^{2+} ions, which are a key structural component of the Chl molecule. For instance, the application of 400 mg kg^{-1} of CeO_2 NPs increased photosynthesis in cucumber plants *via* increasing their Mg^{2+} uptake (Rossi *et al.* 2016). An increase in the Chl content and photosynthesis efficiency occurred when *Brassica napus* L. plants were subjected to 200 mg kg^{-1} of CeO_2 NPs (Zhao *et al.* 2020). Treatment with 500 mg L^{-1} of CeO_2 NPs had a positive effect on wheat growth by increasing photosynthesis, transpiration, and stomatal conductance (Abbas *et al.* 2020). The effect of CeO_2 NPs may also depend on the plant species. For example, CeO_2 NPs did not affect the photosynthetic activity of *Raphanus sativa* (Corral-Diaz *et al.* 2014), whereas decreased the Chl and carotenoid contents in *Phaseolus vulgaris* (Majumdar *et al.* 2016). Cao *et al.* (2017) investigated the impact of uncoated and PVP-coated CeO_2 NPs on soybean. Their results revealed that uncoated CeO_2 NPs had no significant impact on Chl *a* or Chl *b*, whereas PVP-coated CeO_2 NPs increased the Chl *a* contents of plants (Cao *et al.* 2017). CeO_2 NPs coated with citric acid also increased Chl *a* and Chl *b* contents in *Solanum lycopersicum* (Barrios *et al.* 2016). CeO_2 NPs application had no impact on the algae *Phaeodactylum tricornutum* and *Chlamydomonas reinhardtii* (Sendra *et al.* 2018).

Silicon nanoparticles (Si NPs)

Silicon (Si) NPs have the potential to increase plant performance (Rastogi *et al.* 2019a, Rahimi *et al.* 2021). A positive impact on photosynthesis and gas exchange has been documented in Si NPs–plant interactions (Mahto *et al.* 2019). For example, Si NPs increased the total Chl contents and therefore photosynthesis in *Zea mays* L. (Suriyaprabha *et al.* 2012). Also, SiO_2 NPs showed the same impact on plants as Si NPs (Siddiqui *et al.* 2014). It has been acknowledged that SiO_2 NPs display a positive impact on transpiration, stomatal conductance, PSII, and electron transport chain activity as well as the photosynthetic rate (Siddiqui *et al.* 2014, Mahto *et al.* 2019). Elevated contents of Chl *a* and Chl *b* were detected in sugarcane plants treated with SiO_2 NPs (Tayemeh *et al.* 2020). However, SiO_2 NPs caused no significant change in photosynthetic pigments of maize (Zhao *et al.* 2019). Treatment with 30 mg L^{-1} of Si quantum dots increased the Chl *a* and Chl *b* contents in *Lactuca sativa* plants (Li *et al.* 2020). SiC NPs, at concentrations below 150 mg L^{-1}, increased the light absorption, growth, and lipid accumulation in the microalga *Scenedesmus* sp., however, 250 mg L^{-1} of SiC NPs decreased the growth and lipid accumulation in this algal species (Ren *et al.* 2020).

Gold nanoparticles (Au NPs)

Au NPs are important because of their outstanding properties such as easy synthesis, low toxicity, and visibility by naked eyes due to their optical properties (Torres *et al.* 2018). Au NPs can have both negative and positive effects on the photosynthetic activities of plants (Mezacasa *et al.* 2020). Generally, wavelengths beyond 700 nm are not useful for photosynthesis, however, Au NPs can increase the light absorption not only along with the visible lights (400–700 nm) but in wavelengths above 700 nm (Eroglu

Table 2. The effects of ZnO nanoparticles (NPs) on photosynthesis machinery in different plant/algal species.

Plant/algal species	NPs concentration	NPs size	Growth medium	Effects	Reference
Arachis hypogaea	1,000 mg kg^{-1}	Not mentioned	Soil	Increasing Chl content	Kataria *et al.* (2019)
Cucumis sativus	400 and 800 mg kg^{-1}	Not mentioned	Soil	Increasing Chl content	Kataria *et al.* (2019)
Arabidopsis thaliana	Not mentioned	Not mentioned	Not mentioned	Improved carotenoids content, decreased in Chl and photosynthesis	Kataria *et al.* (2019)
Coriandrum sativum	100 mg kg^{-1}	24 ± 3 nm	Soil	Increasing Chl and carotenoids content and photosynthesis	Pullagurala *et al.* (2018)
Glycine max	Not mentioned	Not mentioned	Not mentioned	Decreasing Chl content	Pullagurala *et al.* (2018)
Rosmarinus officinalis	100 mg kg^{-1}	Not mentioned	Not mentioned	Enhanced carotenoids content	Pullagurala *et al.* (2018)
Zea mays	800 mg kg^{-1}	Not mentioned	Soil	Decreasing net photosynthetic rate	Zhao *et al.* (2015)
Abelmoschus esculentus	100 ppm	Not mentioned	Not mentioned	Increasing Chl *a*, Chl *b*, and total Chl in leaves	Salama *et al.* (2019)
Solanum lycopersicum	> 200 mg kg^{-1}	20–30 nm	Soil	Decreasing Chl content	Iftikhar *et al.* (2019)
Solanum lycopersicum	1.2 mM	1–100 nm	Sand culture	Significant increase in Chl *a* and Chl *b* contents	Singh *et al.* (2016)
Solanum lycopersicum	50 mg L^{-1}	20 and 100 nm	Soil	Increasing stomatal conductance and intracellular CO_2 levels	Faizan *et al.* (2021)
Saccharum officinarum L.	Not mentioned	< 100 nm	Not mentioned	Improving Chl index and PSII function	Elsheery *et al.* (2020)
Sesamum indicum	Not mentioned	Not mentioned	Zink deficient soil	Increasing photosynthesis pigments	Salama *et al.* (2019)
Anabaena flos-aquae	10^{-3}M	Not mentioned	Not mentioned	Increased in photosynthetic activity	da Rocha *et al.* (2020)
Anabaena sp.	0.74 ± 0.01 mg L^{-1}	40–50 nm	BG11 culture medium	Making disorder in photosynthesis and other metabolic activities	Tang *et al.* (2015)
Chlorella vulgaris	200 mg L^{-1}	Not mentioned	Not mentioned	Decreasing in respiration efficiency and photosynthesis, causing shading effect	Ren *et al.* (2020)

et al. 2013, Torres *et al.* 2018). For instance, the application of Au NPs resulted in an increased Chl content and photosynthesis in *Brassica juncea* L. (Mahto *et al.* 2019). By increasing the concentration of Au NPs, Chl production increased in *Vicia faba* (Mezacasa *et al.* 2020). In *Vigna radiata* plants exposed to 1 μg mg^{-1} of gold nanoparticles (GNPs), aspartate-capped GNPs (GNPA), BSA-capped GNPs (GNPB), and citrate-capped GNPs (GNPC), the Chl content increased in GNPB and GNPC treatments compared to the GNPA and controls (Das *et al.* 2017).

Copper nanoparticles (Cu NPs)

Both negative and positive impacts on plants have been established for Cu NPs. Cu accumulation (especially Cu NPs accumulation) in leaves may change the shape of plant stoma and chloroplasts, and also decrease the thylakoids in plants, such as *Oryza sativa* L., *Elodea densa*, and *Landoltia punctata* (Tighe-Neira *et al.* 2018). CuO NPs inhibited photosynthesis by affecting PSII, causing a decrease in electron transport rate, number of thylakoids, and transpiration in spring barley (Rajput *et al.* 2018). Application of 2,000 μg L^{-1} of CuO NPs caused cellular toxicity in tomato plants and significantly decreased their growth (Ahmed *et al.* 2018). CuO NPs (10,000 mg kg^{-1}) decreased the number and size of stoma in spring barley (Tan *et al.* 2019). Likewise, CuO NPs treatment had a significant negative impact on photosynthetic activities of *Quercus robur* (Rajput *et al.* 2018). Treatment with 500 mg kg^{-1} of CuO NPs decreased the total Chl contents in wheat (Tan *et al.* 2019). However, CuO NPs may have a positive effect on photosynthesis. For example, Cu NPs were demonstrated to increase the transpiration, stomatal conductance, and rate of electron transport chain in *Capsicum annuum* (Rawat *et al.* 2019). In addition, CuO NPs increased the Chl contents and photosynthetic activities in mung beans (Kataria *et al.* 2019). Treatment with CuO NPs inhibited photosynthesis and decreased the PSII operational quantum yield in the aquatic flowering plant *Lemna gibba* (gibbous duckweed) (Sharma and Uttam 2017). Total carotenoid content decreased significantly in duckweed upon exposure to a low concentration of CuO NPs (Tan *et al.* 2019). In the single-celled green alga *Chlamydomonas reinhardtii*, the Chl *a* and Chl *b* contents decreased by exposure to CuO NPs (Middepogu *et al.* 2018). Cu NPs did not significantly affect the maximal quantum yield of PSII (F_v/F_m) in barley (*Hordeum vulgare* L. landrace Arabi Aswad), however, enhanced flavonol content with concomitant improvement in ascorbate peroxidase activity was found to be insufficient to enforce a light control over the H_2O_2 content under Cu NPs stress conditions (Shaw *et al.* 2014).

Other metal nanoparticles

Other metal NPs have not been widely investigated in terms of their interactions with plants. Mn_3O_4 NPs can increase the photosynthetic potential of mesophyll protoplasts (Wang *et al.* 2020). Mn NPs were shown to positively affect photosynthesis in *Vigna radiata* by improving the photophosphorylation activity in the electron transport chain (Kataria *et al.* 2019). Similarly, Al_2O_3 NPs (20 nm) increased the electron chain efficiency, PSII performance, and photosynthesis in the aquatic plant *Lemna minor* (Ahmed *et al.* 2018). Chitosan NPs improved the net photosynthetic rate and CO_2 concentration of coffee (Kataria *et al.* 2019).

$Ni(OH)_2$ had no significant impact on soybeans and *Prosopis* sp., whereas NiO NPs decreased photosynthesis (Mishra *et al.* 2014). Ni ions displace Mg ions and alter the structure of Chl molecules, which was suggested to be the mechanism underlying the decreased photosynthetic efficiency in *Lycium barbarum* (Pinto *et al.* 2019). Application of 120 mg kg^{-1} of NiO NPs decreased the Chl contents in barley (Pinto *et al.* 2019). In the microalga *Pseudokirchneriella subcapitata*, NiO NPs decreased the electron transport rate and photosynthetic efficiency (Sousa *et al.* 2018).

Platinum (Pt) NPs decreased the Chl content and growth of the single-celled green algal species *Chlamydomonas reinhardtii* (Röhder *et al.* 2014) and *Pseudokirchneriella subcapitata* (Książyk *et al.* 2015). Nonetheless, our knowledge of the effects of Pt NPs on photosynthesis is quite limited (Tighe-Neira *et al.* 2018).

Selenium (Se) NPs increased the total Chl contents in *Punica grantum* cv. Malase Saveh (Zahedi *et al.* 2019). Moreover, Se NPs were proven to increase the leaf area in both cluster bean (300–400 mg L^{-1}) and orange trees (50 mg L^{-1}) (Zahedi *et al.* 2019). However, it has been acknowledged that Se (IV) reveals dual effects on pigments content, gas-exchange parameters, net photosynthetic rate (P_N), and PSII photochemical efficiency (F_v/F_m) of *Brassica napus* cultivars in a dose-dependent manner (Ulhassan *et al.* 2018, 2019a,b).

The protein-loaded mPEG-PLGA NPs increased the photosynthetic parameters such as Chl content in wheat (Gao *et al.* 2018). CdO NPs decreased CO_2 absorption and also inhibited energy transportation from PSII to Calvin cycle in barley (Večeřová *et al.* 2016). CdS NPs reduced the photosynthetic activities in *Euglena gracilis* by causing cell death (da Rocha *et al.* 2020). Photosynthesis, transpiration rate, and also stomatal conductance decreased in soybean and maize plants subjected to La_2O_3 NPs, however, these adverse effects were more severe in maize (C_4 plant), compared to soybean (C_3 plant) (Liu *et al.* 2020).

Magnetic nanoparticles

Nanoparticles with magnetic properties can be used to stimulate the photosynthetic activities of plants (Baker *et al.* 2019, Tombuloglu *et al.* 2019). Fe, Ni, Co, and their chemical combinations are some examples of magnetic NPs (Tombuloglu *et al.* 2019).

Iron is essential for plants and its deficiency can reduce the Chl content, leading to reduction or inhibition of photosynthesis (Mohammadi *et al.* 2018, 2020; Mahto *et al.* 2019). Fe NPs can also increase the photosynthetic potential of mesophyll (Wang *et al.* 2020). Treatment with Fe NPs increased the essential oil content of *Mentha piperita* (Askary *et al.* 2017). Enhanced Chl concentration was observed in *A. thaliana* plants treated with Fe NPs (Marusenko *et al.* 2013). Application of 30–60 ppm of Fe NPs increased the Chl surface in soybean (Thapa *et al.* 2019). Exposure to Fe NPs increased the photosynthetic rate, PSII activity, and shoot growth in spinach (*Spinacia oleracea*) (Jeyasubramanian *et al.* 2016, Wang *et al.* 2020). Fe NPs significantly increased the Chl *a* and Chl *b* contents in both *Vigna radiata* and *Hordeum vulgare* (Pagano *et al.* 2018, Tombuloglu *et al.* 2019). Fe NPs were also shown to promote the growth of *Capsicum annuum* plants (Tombuloglu *et al.* 2019). Fe NPs application enhanced the Chl contents in tree species, such as *Citrus maxima* (Li *et al.* 2018, Baker *et al.* 2019) and *Quercus macdougallii* (Tombuloglu *et al.* 2019). Fe_3O_4 NPs application also increased Chl *b* in *Zea mays* (Zhao *et al.* 2019). Application of 500 and 1,000 mg L^{-1} of Fe NPs increased the photosynthetic rate in soybean (Maswada *et al.* 2018). Fe_2O_3 NPs coated with citric acid also increased the photosynthetic rate in soybean (Kataria *et al.* 2019). As an example of negative Fe NPs–plant interactions, treatment with 72 µM of Fe_2O_3 NPs decreased the Chl *a* and Chl *b* contents in *A. thaliana* (Pagano *et al.* 2018). Exposure to superparamagnetic FeO NPs (SPION) increased the Chl content in subapical leaves of soybean (Ghafariyan *et al.* 2013, Kataria *et al.* 2019). However, these NPs showed a shading effect in the algal species *C. reinhartii*, leading to a significant reduction in photosynthesis (Hurtado-Gallego *et al.* 2020). Application of SPIONs also inhibited the Chl production and photosynthesis in the gibbous duckweed *Lemna gibba* (Hurtado-Gallego *et al.* 2020).

Cobalt (Co) NPs are another example of magnetic NPs that were demonstrated to have a positive effect on Chl *a*, Chl *b*, and total Chl of mung bean (*Vigna radiata*) (Ha *et al.* 2020).

Effects of nanoparticles on stressed plants

Environmental stresses can decrease the photosynthesis indices in plants, however, studies have shown that NPs can prevent or ameliorate the adverse effects of stresses on plants (Baiazidi-Aghdam *et al*. 2016, Sheikhalipour *et al*. 2021). For example, 1–1,000 mg L^{-1} of fullerenols NPs decreased the negative effects of water stress in canola (*Brassica napus*) (Verma *et al*. 2019). Exposure to 200–1,000 mg L^{-1} of CeO_2 NPs stimulated the photosynthesis machinery and the total Chl contents in salt-stressed (100 mM) canola plants (Rossi *et al*. 2016). In a different study, CeO_2 NPs application improved the salt stress tolerance of canola by promoting the formation of apoplastic barriers in roots (Rossi *et al*. 2017). Also, the application of SiO_2 NPs increased the Chl content and biomass of *Spinacia oleracea*, as well as mesophyll conductance in *Cucurbita pepo* under salt-stress conditions (Kataria *et al*. 2019, Zhao *et al*. 2020). Si NPs also increased the photosynthetic rate in salt-stressed cucumber and rice (Elsheery *et al*. 2020). The application of 100 mg L^{-1} of Fe_2O_3 NPs increased the photosynthetic rate in salt-stressed sorghum (Maswada *et al*. 2018).

Contents of photosynthetic pigments increased in lupin plants under salt stress upon exposure to ZnO NPs (Kataria *et al*. 2019). A combined application of micro- and nano-carbon increased the growth of chickpea plants in Cr-stressed soil (Kumar *et al*. 2020). The PSII activity, Chl content, and plant growth decreased in salt-stressed maize, whereas chitosan NPs mitigated these destructive effects (Yasmeen *et al*. 2018). Although salt stress had negative effects on the photosynthesis of *Dracocephalum moldavica*, TiO_2 NPs treatment reduced these negative effects (Gohari *et al*. 2020). Water deficit and salt-stressed cucumber plants treated with 200 mg kg^{-1} of Si NPs had significantly higher Chl contents compared to untreated plants; in fact, Si application increased the uptake of Mg, *i.e.*, a key element in Chl structure (Alsaeedi *et al*. 2019).

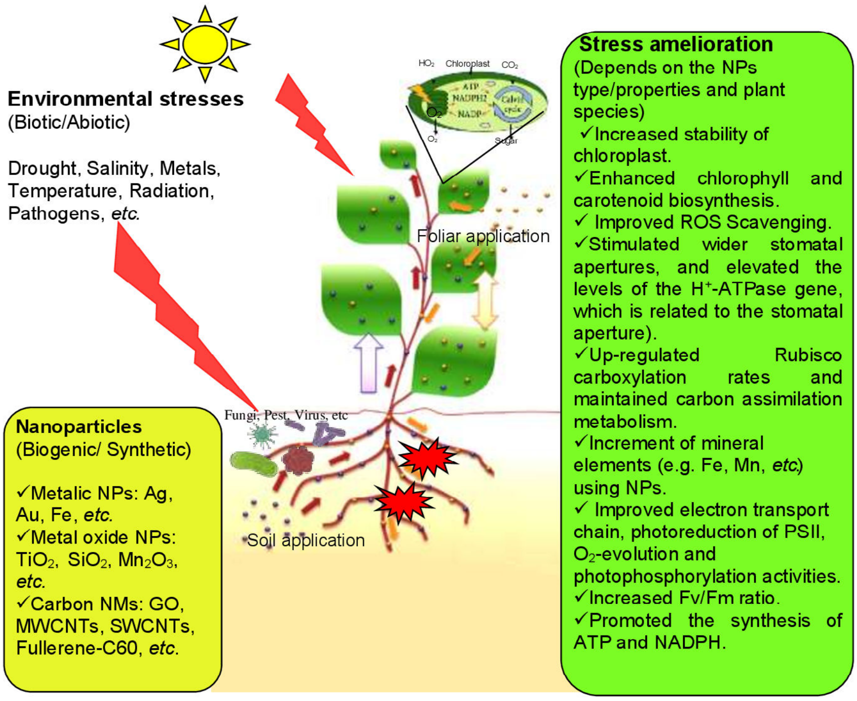
Drought stress decreased the Chl index and stomatal conductance in sorghum, whereas foliar Ce NPs application improved these photosynthetic parameters (Djanaguiraman *et al*. 2018). In addition, abiotic stresses (excess light, heat, and dark chilling) decreased photosynthesis in *A. thaliana*, while treatment with CeO_2 NPs increased photosynthesis (Wu *et al*. 2017). Exposure to 3,200 mg L^{-1} of SiO_2 NPs increased the growth of drought-stressed cotton plants (Zhao *et al*. 2020). UV-B-stressed wheat seedlings exhibited disrupted photosynthesis, whereas Si NPs application promoted their photosynthesis *via* altering the ROS equilibrium (Tripathi *et al*. 2017c). In cold-stressed chickpea, TiO_2 NPs treatment stabilized the cell metabolic processes such as photosynthesis (Hasanpour *et al*. 2015). TiO_2 NPs application led to an enhanced adaptation of chickpea plants to cold stress (Amini *et al*. 2017). However, NPs-treated plants can adapt or cope with environmental perturbations and unfavorable conditions, such as drought, salinity, trace elements, chilling, and heat stress (Ali *et al*. 2021) through different enzymatic and nonenzymatic reactions (Ahmadi *et al*. 2020, Ghorbanpour *et al*. 2020). For example, MWCNTs have been documented to be involved in upregulating stress-specific gene expression such as *HSP90* (Khodakovskaya *et al*. 2011). The possible mechanisms of augmented photosynthesis in stressed plants through the application of NPs (in optimum dose) are illustrated in Fig. 2.

Combined application of nanoparticles and soil amendments

The combined application of biochar and Ag NPs led to reduced negative impacts on rice plants, in comparison to plants only treated with Ag NPs; in fact, biochar amendment ameliorated the toxic effects of Ag NPs on photosynthetic and physiological parameters in these plants (Abbas *et al*. 2019). Treatment with a low concentration of ZnO NPs with amended citric acid increased the growth of cowpea (*Vigna unguiculata* L.) (Cyriac *et al*. 2020). The combination of diuron and CNTs also increased the growth of the green microalga *Chlorella vulgaris* (Schwab *et al*. 2013). Nonetheless, these sorts of combined applications may not necessarily lead to desirable outcomes. For example, treatment with CeO_2 NPs and alginate decreased the Chl *a* fluorescence in maize in all applied concentrations (Zhao *et al*. 2014). Moreover, the EC50 of ZnO NPs, against the filamentous cyanobacterium *Anabaena*, increased in the presence of humic acid (Tang *et al*. 2015).

Possible mechanisms underlying improvement of photosynthesis by NPs

Multiple mechanisms are involved in the augmentation of plant photosynthesis upon exposure to NPs, however, the exact mechanisms are not sufficiently clear or deeply understood (Kataria *et al*. 2019). The schematic illustration of NPs-induced changes in plant photosynthesis is presented in Fig. 3. As shown, NPs can expand the absorption wavelength range. The photosynthesis process is mainly dependent on the availability of the visible spectrum. However, specific NPs convert near-infrared (IR) and ultraviolet (UV) wavelengths to visible light, resulting in improved electron transport (Liu *et al*. 2019). Light-harvesting NPs may capture and transfer more electrons for tuning photosynthetic efficiency, specifically under light-insufficient conditions (Wu and Lin 2021). Moreover, NPs may enhance the photosynthetic performance mainly by light-dependent (Hill reaction) and light-independent (Calvin cycle) reactions (PSI and PSII activities), leading to greater oxygen evolution and photophosphorylation (Pradhan *et al*. 2015, Swift *et al*. 2019). The NPs-augmented photosynthetic efficiency may arise from the upregulation of key photosynthetic enzymes, such as Rubisco, Rubisco activase, fructose-1,6-bisphosphate phosphatase (FBPase), ribulose-5-phosphate kinase (RBPase), and NADP-glyceraldehyde-3-phosphate dehydrogenase (GPDHase), and phospho*enol*pyruvate carboxylase (PEPC) (Gao *et al*. 2006, Pradhan *et al*. 2015, Liu *et al*. 2019). It has been acknowledged that certain NPs play a vital role in stress defense mechanisms by scavenging stress-induced ROS in a dose-dependent manner (Corral-Diaz *et al*. 2014, Wu *et al*. 2018). Recently, nanobionics has been introduced as a powerful technique to increase the function of photosynthetic organelles of plants by augmenting the light-harvesting ability and enhancing the ROS-scavenging capacity under stress conditions (Giraldo *et al*. 2014, Ghorbanpour and Fahimirad 2017).



Drought, Salinity, Metals, Temperature, Radiation, Pathogens, *etc.*

Nanoparticles
(Biogenic/ Synthetic)

✓Metalic NPs: Ag, Au, Fe, *etc.*
✓Metal oxide NPs: TiO_2, SiO_2, Mn_2O_3, *etc.*
✓Carbon NMs: GO, MWCNTs, SWCNTs, Fullerene-C60, *etc.*

Stress amelioration
(Depends on the NPs type/properties and plant species)
✓Increased stability of chloroplast.
✓Enhanced chlorophyll and carotenoid biosynthesis.
✓ Improved ROS Scavenging.
✓Stimulated wider stomatal apertures, and elevated the levels of the H^+-ATPase gene, which is related to the stomatal aperture).
✓Up-regulated Rubisco carboxylation rates and maintained carbon assimilation metabolism.
✓Increment of mineral elements (e.g. Fe, Mn, *etc*) using NPs.
✓ Improved electron transport chain, photoreduction of PSII, O_2-evolution and photophosphorylation activities.
✓Increased Fv/Fm ratio.
✓Promoted the synthesis of ATP and NADPH.

Fig. 2. Possible regulating factors of augmented photosynthesis in stressed plants by application of nanoparticles (NPs) in optimum dose. Exposure to NPs increased the mitigating ability of photosynthetic machinery under different environmental stresses.

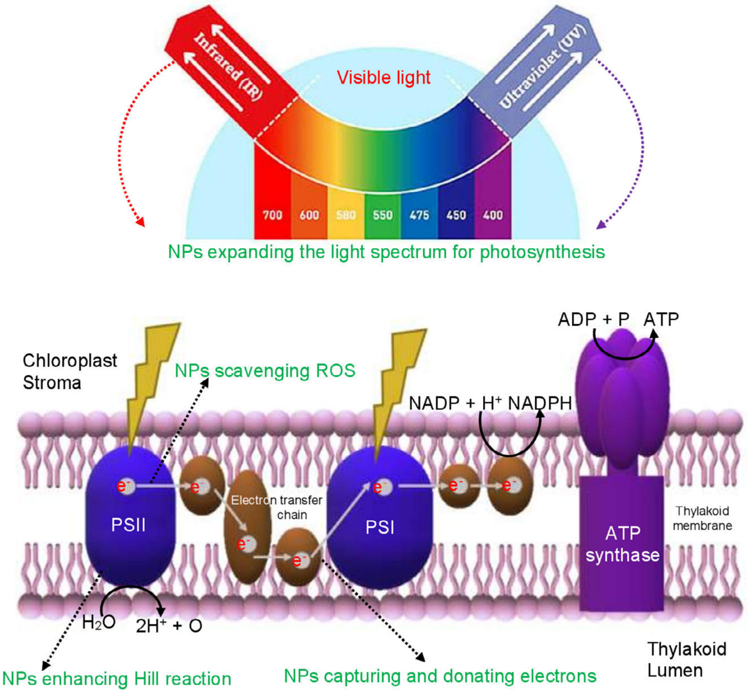


Fig. 3. Role of nanoparticles (NPs) in plant photosynthesis. This model depicts that NPs may augment the photosynthetic efficiency through (*1*) expanding the absorption wavelength range, (*2*) enhancing Hill reaction, (*3*) harvesting more electrons, (*4*) accelerating electron transfer, (*5*) scavenging ROS.

Conclusions and future perspectives

Although nanoparticles (NPs) are widely used in different industries, their potential applications in certain fields such as agriculture and plant science are underestimated. Due to their nanoscale and unique physicochemical properties, NPs can easily and effectively affect diverse biochemical pathways in plant cells. Nanoparticles can act as stress inhibitors and/or stress inducers. The net outcome of NPs–plant interactions depends on different factors, such as size, concentration, surface charge, and type of NPs, plant species, growth medium, *etc*. Among all other metabolic activities, photosynthesis is one of the significant physiological processes of plants that is vital for the survival of plants, and humans, hence, it is crucial to explore and characterize the impact NPs on photosynthetic pathways and biosynthesis of photosynthetic pigments. This comprehensive review of the literature showed that NPs might have both positive and negative effects on photosynthesis. Positive effects can be attributed to increases in the biosynthesis of Chl, the activity of Rubisco enzyme, the performance of PSII, enhanced light-harvesting complex (LHC), and CO_2 harvesting, as well as broadening the chloroplast photoabsorption spectrum, whereas the negative effects can occur due to damages to chloroplast structures, decreases in the biosynthesis of Chl and electron transport rate by changing several genes and enzymes such as carbonic anhydrase and PEPC. These possible impacts provide insights into the potential applications of NPs to boost photosynthesis in crops, or strategies/considerations to reduce the negative environmental footprint of NPs. Most studies have focused on the overall outcome of NPs on photosynthesis (*e.g.*, contents of photosynthetic pigments, photosynthetic rate, PSII activity, *etc*.), while little is known about the details of the NPs–chloroplast interactions (*e.g.*, NPs entry to the chloroplast, main target molecules, and enzymes affected, *etc*.), which need to be investigated. Furthermore, nearly all studies have been conducted under controlled environmental conditions (glasshouses and laboratories), while it is crucial to explore the impacts of NPs on photosynthetic parameters of plants under field (natural) conditions. Exposure to NPs increases the tolerance level of plants against various biotic and abiotic environmental stresses, but the mechanisms underlying this regulation are not fully understood yet. Further investigations are required to better understand the regulation of gene expression in plants exposed to various metal/metal-oxide and carbon-based NPs under stressful conditions. Mechanisms, by which chloroplasts may be engineered with NPs to extend their functions, called nanobionics, await further investigation.

References

Abbas Q., Liu G.J., Yousaf B. *et al*.: Effects of biochar on uptake, acquisition and translocation of silver nanoparticles in rice (*Oryza sativa* L.) in relation to growth, photosynthetic traits and nutrients displacement. – Environ. Pollut. **250**: 728-736, 2019.

Abbas Q., Liu G.J. Yousaf B. *et al*.: Biochar-assisted transformation of engineered-cerium oxide nanoparticles: Effect on wheat growth, photosynthetic traits and cerium accumulation. – Ecotox. Environ. Safe. **187**: 109845, 2020.

Ahmad B., Shabbir A., Jaleel H. *et al*.: Efficacy of titanium dioxide nanoparticles in modulating photosynthesis, peltate glandular trichomes and essential oil production and quality in *Mentha piperita* L. – Curr. Plant Biol. **13**: 6-15, 2018.

Ahmadi S.Z, Ghorbanpour M., Aghaee A., Hadian J.: Deciphering morpho-physiological and phytochemical attributes of *Tanacetum parthenium* L. plants exposed to C60 fullerene and salicylic acid. – Chemosphere **259**: 127406, 2020.

Ahmed B., Khan M.S., Musarrat J.: Toxicity assessment of metal oxide nano-pollutants on tomato (*Solanum lycopersicon*): A study on growth dynamics and plant cell death. – Environ. Pollut. **240**: 802-816, 2018.

Ali A., Mehmood A., Khan N.: Uptake, translocation, and consequences of nanomaterials on plant growth and stress adaptation. – J. Nanomater. **2021**: 6677616, 2021.

Alsaeedi A., El-Ramady H., Alshaal T. *et al*.: Silica nanoparticles boost growth and productivity of cucumber under water deficit and salinity stresses by balancing nutrients uptake. – Plant Physiol. Bioch. **139**: 1-10, 2019.

Amini S., Maali-Amiri R., Mohammadi R., Kazemi-Shahandashti S.-S.: cDNA-AFLP analysis of transcripts induced in chickpea plants by TiO_2 nanoparticles during cold stress. – Plant Physiol. Bioch. **111**: 39-49, 2017.

Amooaghaie R., Tabatabaei F., Ahadi A.: Alterations in *HO-1* expression, heme oxygenase activity and endogenous NO homeostasis modulate antioxidant responses of *Brassica nigra* against nano silver toxicity. – J. Plant Physiol. **228**: 75-84, 2018.

Askary M., Talebi S.M., Amini F., Bangan A.D.B.: Effect of NaCl and iron oxide nanoparticles on *Mentha piperita* essential oil composition. – Environ. Exp. Biol. **14**: 27-32, 2017.

Baiazidi-Aghdam M.T., Mohammadi H., Ghorbanpour M.: Effects of nanoparticulate anatase titanium dioxide on physiological and biochemical performance of *Linum usitatissimum* (Linaceae) under well watered and drought stress conditions. – Braz. J. Bot. **39**: 139-146, 2016.

Baker S., Satish S., Prasad N., Chouhan R.S.: Nano-agromaterials: Influence on plant growth and crop protection. – In: Thomas S., Grohens Y., Pottathara Y.B. (ed.): Industrial Applications of Nanomaterials. Pp. 341-363. Elsevier Academic Press, Amsterdam 2019.

Barrios A.C., Rico C.M., Trujillo-Reyes J. *et al*.: Effects of uncoated and citric acid coated cerium oxide nanoparticles, bulk cerium oxide, cerium acetate, and citric acid on tomato plants. – Sci. Total Environ. **563-564**: 956-964, 2016.

Cao Z., Stowers C., Rossi L. *et al*.: Physiological effects of cerium oxide nanoparticles on the photosynthesis and water use efficiency of soybean (*Glycine max* (L.) Merr.). – Environ. Sci.-Nano **4**: 1086-1094, 2017.

Chandra S., Pradhan S., Mitra S. *et al*.: High throughput electron transfer from carbon dots to chloroplast: a rationale of enhanced photosynthesis. – Nanoscale **6**: 3647-3655, 2014.

Chen J., Liu B., Yang Z. *et al*.: Phenotypic, transcriptional, physiological and metabolic responses to carbon nanodot exposure in *Arabidopsis thaliana* (L.). – Environ. Sci.-Nano **5**: 2672-2685, 2018.

Chen L., Wang C., Yang S. *et al*.: Chemical reduction of graphene enhances in vivo translocation and photosynthetic inhibition in pea plants. – Environ. Sci.-Nano **6**: 1077-1088, 2019.

Chen L., Zhou L., Liu Y. *et al*.: Toxicological effects of nanometer titanium dioxide (nano-TiO_2) on *Chlamydomonas reinhardtii*. – Ecotox. Environ. Safe. **84**: 155-162, 2012.

Choi S.A., Jeong Y., Lee J. *et al*.: Biocompatible liquid-type carbon nanodots (C-paints) as light delivery materials for cell growth and astaxanthin induction of *Haematococcus pluvialis*. – Mater. Sci. Eng. C **109**: 110500, 2020.

Conway J.R., Beaulieu A.L., Beaulieu N.L. *et al*.: Environmental stresses increase photosynthetic disruption by metal oxide nanomaterials in a soil-grown plant. – ACS Nano **9**: 11737-11749, 2015.

Corral-Diaz B., Peralta-Videa J.R, Alvarez-Parrilla E. *et al*.: Cerium oxide nanoparticles alter the antioxidant capacity but do not impact tuber ionome in *Raphanus sativus* (L). – Plant Physiol Bioch. **84**: 277-285, 2014.

Cox A., Venkatachalam P., Sahi S., Sharma N.: Silver and titanium dioxide nanoparticle toxicity in plants: a review of current research. – Plant Physiol. Bioch. **107**: 147-163, 2016.

Cyriac J., Melethil K., Thomas B. *et al*.: Synthesis of biogenic ZnO nanoparticles and its impact on seed germination and root growth of *Oryza sativa* L. and *Vigna unguiculata* L. –

Mater. Today: Proc. **25**: 224-229, 2020.

da Rocha A., Menguy N., Yéprémian C. *et al*.: Ecotoxicological studies of ZnO and CdS nanoparticles on *Chlorella vulgaris* photosynthetic microorganism in Seine river water. – Nanomaterials **10**: 227, 2020.

Dai Y., Chen F., Yue L. *et al*.: Uptake, transport, and transformation of CeO_2 nanoparticles by strawberry and their impact on the rhizosphere bacterial community. – ACS Sustain. Chem. Eng. **8**: 4792-4800, 2020.

Das S., Debnath N., Pradhan S., Goswami A.: Enhancement of photon absorption in the light-harvesting complex of isolated chloroplast in the presence of plasmonic gold nanosol – a nanobionic approach towards photosynthesis and plant primary growth augmentation. – Gold Bull. **50**: 247-257, 2017.

Dauda S., Chia M.A., Bako S.P.: Toxicity of titanium dioxide nanoparticles to *Chlorella vulgaris* Beyerinck (Beijerinck) 1890 (Trebouxiophyceae, Chlorophyta) under changing nitrogen conditions. – Aquat. Toxicol. **187**: 108-114, 2017.

Djanaguiraman M., Nair R.,. Giraldo J.P., Prasad P.V.V.: Cerium oxide nanoparticles decrease drought-induced oxidative damage in sorghum leading to higher photosynthesis and grain yield. – ACS Omega **3**: 14406-14416, 2018.

El Naschie M.S.: Nanotechnology for the developing world. – Chaos Solitons Fractals **30**: 769-773, 2006.

Elsheery N.I., Sunoj V.S.J., Wen Y. *et al*.: Foliar application of nanoparticles mitigates the chilling effect on photosynthesis and photoprotection in sugarcane. – Plant Physiol. Bioch. **149**: 50-60, 2020.

Eroglu E., Eggers P.K., Winslade M. *et al*.: Enhanced accumulation of microalgal pigments using metal nanoparticle solutions as light filtering devices. – Green Chem. **15**: 3155-3159, 2013.

Etxeberria E., Gonzalez P., Baroja-Fernandez E., Romero J.P.: Fluid phase endocytic uptake of artificial nano-spheres and fluorescent quantum dots by sycamore cultured cells: evidence for the distribution of solutes to different intracellular compartments. – Plant Signal. Behav. **1**: 196-200, 2006.

Fahimirad S., Ajalloueian F., Ghorbanpour M.: Synthesis and therapeutic potential of silver nanomaterials derived from plant extracts. – Ecotox. Environ. Safe. **168**: 260-278, 2019.

Faizan M., Faraz A., Mir A.R., Hayat S.: Role of zinc oxide nanoparticles in countering negative effects generated by cadmium in *Lycopersicon esculentum*. – J. Plant Growth Regul. **40**: 101-115, 2021.

Falco W.F., Scherer M.D., Oliveira S.L. *et al*.: Phytotoxicity of silver nanoparticles on *Vicia faba*: Evaluation of particle size effects on photosynthetic performance and leaf gas exchange. – Sci. Total Environ. **701**: 134816, 2020.

Fan X., Xu J., Lavoie M. *et al*.: Multiwall carbon nanotubes modulate paraquat toxicity in *Arabidopsis thaliana*. – Environ. Pollut. **233**: 633-641, 2018.

Faraji J., Sepehri A.: Exogenous nitric oxide improves the protective effects of TiO_2 nanoparticles on growth, antioxidant system, and photosynthetic performance of wheat seedlings under drought stress. – J. Soil Sci. Plant Nutr. **20**: 703-714, 2020.

Gade A., Ingle A., Whiteley C., Rai M.: Mycogenic metal nanoparticles: progress and applications. – Biotechnol. Lett. **32**: 593-600, 2010.

Gao F.Q., Hong F.S., Liu C. *et al*.: Mechanism of nano-anatase TiO_2 on promoting photosynthetic carbon reaction of spinach: inducing complex of Rubisco-Rubisco activase. – Biol. Trace Elem. Res. **111**: 239-253, 2006.

Gao F.Q., Liu C., Qu C.X. *et al*.: Was improvement of spinach growth by nano-TiO_2 treatment related to the changes of Rubisco activase? – Biometals **21**: 211-217, 2008.

Gao H., Qin Y., Guo R. *et al*.: Enhanced plant growth promoting role of mPEG-PLGA-based nanoparticles as an activator protein PeaT1 carrier in wheat (*Triticum aestivum* L.). – J. Chem. Technol. Biotechnol. **93**: 3143-3151, 2018.

Ghafariyan M.H., Malakouti M.J., Dadpour M.R. *et al*.: Effects of magnetite nanoparticles on soybean chlorophyll. – Environ. Sci. Technol. **47**: 10645-10652, 2013.

Ghazaei F., Shariati M.: Effects of titanium nanoparticles on the photosynthesis, respiration, and physiological parameters in *Dunaliella salina* and *Dunaliella tertiolecta*. – Protoplasma **257**: 75-88, 2020.

Ghorbanpour M., Fahimirad S.: Plant nanobionics: a novel approach to overcome the environmental challenges. – In: Ghorbanpour M., Varma A. (ed.): Medicinal Plants and Environmental Challenges. Pp. 247-257. Springer, Cham 2017.

Ghorbanpour M., Hadian J.: Multi-walled carbon nanotubes stimulate callus induction, secondary metabolites biosynthesis and antioxidant capacity in medicinal plant *Satureja khuzestanica* grown *in vitro*. – Carbon **94**: 749-759, 2015.

Ghorbanpour M., Hatami M.: Spray treatment with silver nanoparticles plus thidiazuron increases anti-oxidant enzyme activities and reduces petal and leaf abscission in four cultivars of geranium (*Pelargonium zonale*) during storage in the dark. – J. Hortic. Sci. Biotech. **89**: 712-718, 2014.

Ghorbanpour M., Khaltabadi Farahani A.H., Hadian J.: Potential toxicity of nano-graphene oxide on callus cell of *Plantago major* L. under polyethylene glycol-induced dehydration. – Ecotox. Environ. Safe. **148**: 910-922, 2018.

Ghorbanpour M., Mohammadi H., Kariman K.: Nanosilicon-based recovery of barley (*Hordeum vulgare*) plants subjected to drought stress. – Environ. Sci.-Nano **7**: 443-461, 2020.

Giraldo J.P., Landry M.P., Faltermeier S.M. *et al*.: Plant nanobionics approach to augment photosynthesis and biochemical sensing. – Nat. Mater. **13**: 400-408, 2014.

Gogotsi Y. (ed.): Nanomaterials Handbook. 1st Edition. Pp. 800. CRC Press, Boca Raton 2006.

Gohari G., Mohammadi A., Akbari A. *et al*.: Titanium dioxide nanoparticles (TiO_2 NPs) promote growth and ameliorate salinity stress effects on essential oil profile and biochemical attributes of *Dracocephalum moldavica*. – Sci. Rep.-UK **10**: 912, 2020.

Gong Y., Zhao J.: Small carbon quantum dots, large photosynthesis enhancement. – J. Agr. Food Chem. **66**: 9159-9161, 2018.

Ha N.T.M., Do C.M., Hoang T.T. *et al*.: The effect of cobalt and silver nanoparticles on overcoming leaf abscission and enhanced growth of rose (*Rosa hybrida* L. 'Baby Love') plantlets cultured in vitro. – Plant Cell Tiss. Org. Cult. **141**: 393-405, 2020.

Hajian M.H., Ghorbanpour M., Abtahi F., Hadian J.: Differential effects of biogenic and chemically synthesized silver-nanoparticles application on physiological traits, antioxidative status and californidine content in California poppy (*Eschscholzia californica* Cham). – Environ. Pollut. **292**: 118300, 2022.

Hasanpour H., Maali-Amir R., Zeinali H.: Effect of TiO_2 nanoparticles on metabolic limitations to photosynthesis under cold in chickpea. – Russ. J. Plant Physiol. **62**: 779-787, 2015.

Hatami M., Ghorbanpour M.: Effect of nanosilver on physiological performance of *Pelargonium* plants exposed to dark storage. – J. Hortic. Res. **21**: 15-20, 2013.

Hatami M., Ghorbanpour M.: Defense enzymes activity and biochemical variations of *Pelargonium zonale* in response to nanosilver particles and dark storage. – Turk. J. Biol. **38**:

130-139, 2014.

Hatami M., Ghorbanpour M., Salehiarjomand H.: Nano-anatase TiO_2 modulates the germination behavior and seedling vigority of the five commercially important medicinal and aromatic plants. – J. Biol. Environ. Sci. **8**: 53-59, 2014.

Hatami M., Hadian J., Ghorbanpour M.: Mechanisms underlying toxicity and stimulatory role of single-walled carbon nanotubes in *Hyoscyamus niger* during drought stress simulated by polyethylene glycol. – J. Hazard. Mater. **324**: 306-320, 2017.

Hatami M., Hosseini S.M., Ghorbanpour M., Kariman K.: Physiological and antioxidative responses to GO/PANI nanocomposite in intact and demucilaged seeds and young seedlings of *Salvia mirzayanii*. – Chemosphere **233**: 920-935, 2019b.

Hatami M., Kariman K., Ghorbanpour M.: Engineered nanomaterial-mediated changes in the metabolism of terrestrial plants. – Sci. Total Environ. **571**: 275-291, 2016.

Hatami M., Naghdi Badi H., Ghorbanpour M.: Nano-elicitation of secondary pharmaceutical metabolites in plant cells: a review. – J. Med. Plants **18**: 6-36, 2019a.

Hong F.S., Yang P., Gao F.Q. *et al*.: Effect of nano-anatase TiO_2 on spectral characterization of photosystem particles from spinach. – Chem. Res. Chin. Univ. **21**: 196-200, 2005.

Hu C., Liu L., Li X. *et al*.: Effect of graphene oxide on copper stress in *Lemna minor* L.: evaluating growth, biochemical responses, and nutrient uptake. – J. Hazard. Mater. **341**: 168-176, 2018.

Hu J., Wu X., Wu F. *et al*.: Potential application of titanium dioxide nanoparticles to improve the nutritional quality of coriander (*Coriandrum sativum* L.). – J. Hazard. Mater. **389**: 121837, 2020.

Huang J., Cheng J., Yi J.: Impact of silver nanoparticles on marine diatom *Skeletonema costatum*. – J. Appl. Toxicol. **36**: 1343-1354, 2016.

Hurtado-Gallego J., Pulido-Reyes G., González-Pleiter M. *et al*.: Toxicity of superparamagnetic iron oxide nanoparticles to the microalga *Chlamydomonas reinhardtii*. – Chemosphere **238**: 124562, 2020.

Hussain S., Iqbal N., Brestic M. *et al*.: Changes in morphology, chlorophyll fluorescence performance and Rubisco activity of soybean in response to foliar application of ionic titanium under normal light and shade environment. – Sci. Total Environ. **658**: 626-637, 2019.

Hussain S., Shafiq I., Chattha M.S. *et al*.: Effect of Ti treatments on growth, photosynthesis, phosphorus uptake and yield of soybean (*Glycine max* L.) in maize-soybean relay strip intercropping. – Environ. Exp. Bot. **187**: 104476, 2021.

Iftikhar A., Ali S., Yasmeen T. *et al*.: Effect of gibberellic acid on growth, photosynthesis and antioxidant defense system of wheat under zinc oxide nanoparticle stress. – Environ. Pollut. **254**: 113109, 2019.

Jeyasubramanian K., Thoppey U.U.G., Hikku G.S. *et al*.: Enhancement in growth rate and productivity of spinach grown in hydroponics with iron oxide nanoparticles. – RSC Adv. **6**: 15451-15459, 2016.

Jia W., Zhai S., Ma C. *et al*.: The role of different fractions of humic acid in the physiological response of amaranth treated with magnetic carbon nanotubes. – Ecotox. Environ. Safe. **169**: 848-855, 2019.

Johal M.S., Johnson L.E.: Understanding Nanomaterials. Pp. 528. CRC Press, Boca Raton 2018.

Joshi A., Sharma L., Kaur S. *et al*.: Plant nanobionic effect of multi-walled carbon nanotubes on growth, anatomy, yield and grain composition of rice. – BioNanoScience **10**: 430-445, 2020.

Kataria S., Jain M., Rastogi A. *et al*.: Role of nanoparticles on photosynthesis: avenues and applications. – In: Tripathi D.K., Ahmad P., Sharma S., Dubey N.K. (ed.): Nanomaterials in Plants, Algae and Microorganisms. Pp. 103-127. Academic Press, London 2019.

Khodakovskaya M.V., de Silva K., Nedosekin D.A. *et al*.: Complex genetic, photothermal, and photoacoustic analysis of nanoparticle-plant interactions. – P. Natl. Acad. Sci. USA **108**: 1028-1033, 2011.

Książyk M., Asztemborska M., Stęborowski R., Bystrzejewska-Piotrowska G.: Toxic effect of silver and platinum nanoparticles toward the freshwater microalga *Pseudokirchneriella subcapitata*. – B. Environ. Contam. Tox. **94**: 554-558, 2015.

Kumar A., Gahoi P., Verma N.: Simultaneous scavenging of Cr(VI) from soil and facilitation of nutrient uptake in plant using a mixture of carbon microfibers and nanofibers. – Chemosphere **239**: 124760, 2020.

Li J., Hu J., Xiao L. *et al*.: Interaction mechanisms between α-Fe_2O_3, γ-Fe_2O_3 and Fe_3O_4 nanoparticles and *Citrus maxima* seedlings. – Sci. Total Environ. **625**: 677-685, 2018.

Li X., Schirmer K., Bernard L. *et al*.: Silver nanoparticle toxicity and association with the alga *Euglena gracilis*. – Environ. Sci.-Nano **2**: 594-602, 2015.

Li Y., Li W., Zhang H. *et al*.: Amplified light harvesting for enhancing Italian lettuce photosynthesis using water soluble silicon quantum dots as artificial antennas. – Nanoscale **12**: 155-166, 2020.

Liang L., Tang H., Deng Z. *et al*.: Ag nanoparticles inhibit the growth of the bryophyte, *Physcomitrella patens*. – Ecotox. Environ. Safe. **164**: 739-748, 2018.

Liu Y., Yue L., Wang C. *et al*.: Photosynthetic response mechanisms in typical C_3 and C_4 plants upon La_2O_3 nanoparticle exposure. – Environ. Sci.-Nano **7**: 81-92, 2020.

Liu Y., Yue L., Wang Z., Xing B.: Processes and mechanisms of photosynthesis augmented by engineered nanomaterials. – Environ. Chem. **16**: 430-445, 2019.

Lizzi D., Mattiello A., Marchiol L.: Impacts of cerium oxide nanoparticles ($n$$CeO_2$) on crop plants: a concentric overview. – In: Tripathi D.K., Ahmad P., Sharma S., Dubey N.K. (ed.): Nanomaterials in Plants, Algae and Microorganisms. Pp. 311-324. Academic Press, London 2019.

Mahto R., Chatterjee N., Priya T., Singh R.K.: Nanotechnology and its role in agronomic crops. – In: Hasanuzzaman M. (ed.): Agronomic Crops. Pp. 605-636. Springer, Singapore 2019.

Majumdar S., Peralta-Videa J.R., Trujillo-Reyes J. *et al*.: Soil organic matter influences cerium translocation and physiological processes in kidney bean plants exposed to cerium oxide nanoparticles. – Sci. Total Environ. **569-570**: 201-211, 2016.

Marusenko Y., Shipp J., Hamilton G.A. *et al*.: Bioavailability of nanoparticulate hematite to *Arabidopsis thaliana*. – Environ. Pollut. **74**: 150-156, 2013.

Maswada H.F., Djanaguiraman M., Prasad P.V.V.: Seed treatment with nano-iron (III) oxide enhances germination, seeding growth and salinity tolerance of sorghum. – J. Agron. Crop Sci. **204**: 577-587, 2018.

Matouke M.M., Elewa D.T., Abdullahi K.: Binary effect of titanium dioxide nanoparticles ($n$$TiO_2$) and phosphorus on microalgae (*Chlorella ellipsoides* Gerneck, 1907). – Aquat. Toxicol. **198**: 40-48, 2018.

Mezacasa A.V., Queiroz A.M., Graciano D.E. *et al*.: Effects of gold nanoparticles on photophysical behaviour of chlorophyll and pheophytin. – J. Photoch. Photobio. A **389**: 112252, 2020.

Middepogu A., Hou J., Gao X., Lin D.: Effect and mechanism of TiO_2 nanoparticles on the photosynthesis of *Chlorella pyrenoidosa*. – Ecotox. Environ. Safe **161**: 497-506, 2018.

Mishra V., Mishra R.K., Dikshit A., Pandey A.C.: Interactions of nanoparticles with plants: an emerging prospective in the agriculture industry. – In: Ahmad P., Rasool S. (ed.): Emerging Technologies and Management of Crop Stress Tolerance. Pp. 159-180. Academic Press, Amsterdam 2014.

Missaoui T., Smiri M., Chmingui H., Hafiane A.: Effects of nanosized titanium dioxide on the photosynthetic metabolism of fenugreek (*Trigonella foenum-graecum* L.). – C. R. Biol. **340**: 499-511, 2017.

Mohammadi H., Amani-Ghadim A.R., Matin A.A., Ghorbanpour M.: Fe^0 nanoparticles improve physiological and antioxidative attributes of sunflower (*Helianthus annuus*) plants grown in soil spiked with hexavalent chromium. – 3 Biotech **10**: 19, 2020.

Mohammadi M., Hatami M., Feghezadeh K., Ghorbanpour M.: Mitigating effect of nano-zerovalent iron, iron sulfate and EDTA against oxidative stress induced by chromium in *Helianthus annuus* L. – Acta Physiol. Plant. **40**: 69, 2018.

Morelli E., Gabellieri E., Bonomini A. *et al.*: TiO_2 nanoparticles in seawater: Aggregation and interactions with the green alga *Dunaliella tertiolecta*. – Ecotox. Environ. Safe. **148**: 184-193, 2018.

Movafeghi A., Khataee A., Abedi M. *et al.*: Effects of TiO_2 nanoparticles on the aquatic plant *Spirodela polyrrhiza*: evaluation of growth parameters, pigment contents and antioxidant enzyme activities. – J. Environ. Sci. **64**: 130-138, 2018.

Nair P.M.G., Chung I.M.: Physiological and molecular level effects of silver nanoparticles exposure in rice (*Oryza sativa* L.) seedlings. – Chemosphere **112**: 105-113, 2014.

Nam S.-H., Kwak J.I., An Y.-J.: Quantification of silver nanoparticle toxicity to algae in soil via photosynthetic and flow-cytometric analyses. – Sci. Rep.-UK **8**: 292, 2018.

Nogueira P.F.M., Nakabayashi D., Zucolotto V.: The effects of graphene oxide on green algae *Raphidocelis subcapitata*. – Aquat. Toxicol. **166**: 29-35, 2015.

Ogunkunle C.O., Adegboye E.F., Okoro H.K. *et al.*: Effect of nanosized anatase TiO_2 on germination, stress defense enzymes, and fruit nutritional quality of *Abelmoschus esculentus* (L.) Moench (okra). – Arab. J. Geosci. **13**: 120, 2020.

Pagano L., Maestri E., Caldara M. *et al.*: Engineered nanomaterial activity at the organelle level: Impacts on the chloroplasts and mitochondria. – ACS Sustain. Chem. Eng. **6**: 12562-12579, 2018.

Park S., Ahn Y.J.: Multi-walled carbon nanotubes and silver nanoparticles differentially affect seed germination, chlorophyll content, and hydrogen peroxide accumulation in carrot (*Daucus carota* L.). – Biocatal. Agric. Biotechnol. **8**: 257-262, 2016.

Peharec Štefanić P., Cvjetko P., Biba R. *et al.*: Physiological, ultrastructural and proteomic responses of tobacco seedlings exposed to silver nanoparticles and silver nitrate. – Chemosphere **209**: 640-653, 2018.

Perez-de-Luque A.: Interaction of nanomaterials with plants: What do we need for real applications in agriculture? – Front. Env. Sci. **5**: 12, 2017.

Pinto M., Soares C., Pinto A.S., Fidalgo F.: Phytotoxic effects of bulk and nano-sized Ni on *Lycium barbarum* L. grown *in vitro* – Oxidative damage and antioxidant response. – Chemosphere **218**: 507-516, 2019.

Pradhan S., Patra P., Mitra S. *et al.*: Copper nanoparticle (CuNP) nanochain arrays with a reduced toxicity response: a biophysical and biochemical outlook on *Vigna radiata*. – J. Agr. Food Chem. **63**: 2606-2617, 2015.

Pullagurala V.L.R., Adisa I.O., Rawat S. *et al.*: ZnO nanoparticles increase photosynthetic pigments and decrease lipid peroxidation in soil grown cilantro (*Coriandrum sativum*). – Plant Physiol. Bioch. **132**: 120-127, 2018.

Qi M., Liu Y., Li T.: Nano-TiO_2 improve the photosynthesis of tomato leaves under mild heat stress. – Biol. Trace Elem. Res. **156**: 323-328, 2013.

Qian H., Peng X., Han X. *et al.*: Comparison of the toxicity of silver nanoparticles and silver ions on the growth of terrestrial plant model *Arabidopsis thaliana*. – J. Environ. Sci. **25**: 1947-1956, 2013.

Rahayu I., Darmawan W., Zaini L.H., Prihatini E.: Characteristics of fast-growing wood impregnated with nanoparticles. – J. Forestry Res. **31**: 677-685, 2020.

Rahimi S., Hatami M., Ghorbanpour M.: Silicon-nanoparticle mediated changes in seed germination and vigor index of marigold (*Calendula officinalis* L.) compared to silicate under PEG-induced drought stress. – Gesunde Pflanzen, 2021.

Rajput V., Minkina T., Fedorenko A. *et al.*: Toxicity of copper oxide nanoparticles on spring barley (*Hordeum sativum* distichum). – Sci. Total Environ. **645**: 1103-1113, 2018.

Rani P.U., Yasur J., Loke K.S., Dutta D.: Effect of synthetic and biosynthesized silver nanoparticles on growth, physiology and oxidative stress of water hyacinth: *Eichhornia crassipes* (Mart) Solms. – Acta Physiol. Plant. **38**: 58, 2016.

Rastogi A., Tripathi D.K., Yadav S. *et al.*: Application of silicon nanoparticles in agriculture. – 3 Biotech **9**: 90, 2019a.

Rastogi A., Zivcak M., Tripathi D.K. *et al.*: Phytotoxic effect of silver nanoparticles in *Triticum aestivum*: Improper regulation of photosystem I activity as the reason for oxidative damage in the chloroplast. – Photosynthetica **57**: 209-216, 2019b.

Rawat S., Adisa I.O., Wang Y. *et al.*: Differential physiological and biochemical impacts of nano vs micron Cu at two phenological growth stages in bell pepper (*Capsicum annuum*) plant. – NanoImpact **14**: 100161, 2019.

Ren H.Y., Dai Y.Q., Kong F. *et al.*: Enhanced microalgal growth and lipid accumulation by addition of different nanoparticles under xenon lamp illumination. – Bioresource Technol. **297**: 122409, 2020.

Rico C.M., Majumdar S., Duarte-Gardea M. *et al.*: Interaction of nanoparticles with edible plants and their possible implications in the food chain. – J. Agr. Food Chem. **59**: 3485-3498, 2011.

Röhder L.A., Brandt T., Sigg L., Behra R.: Influence of agglomeration of cerium oxide nanoparticles and speciation of cerium(III) on short term effects to the green algae *Chlamydomonas reinhardtii*. – Aquat Toxicol. **152**: 121-130, 2014.

Rossi L., Zhang W., Lombardini L., Ma X.: The impact of cerium oxide nanoparticles on the salt stress responses of *Brassica napus* L. – Environ. Pollut. **219**: 28-36, 2016.

Rossi L., Zhang W., Ma X.: Cerium oxide nanoparticles alter the salt stress tolerance of *Brassica napus* L. by modifying the formation of root apoplastic barriers. – Environ. Pollut. **229**: 132-138, 2017.

Salama D.M., Osman S.A., Abd El-Aziz M. *et al.*: Effect of zinc oxide nanoparticles on the growth, genomic DNA, production and the quality of common dry bean (*Phaseolus vulgaris*). – Biocatal. Agric. Biotechnol. **18**: 101083, 2019.

Salama H.M.H.: Effects of silver nanoparticles in some crop plants, common bean (*Phaseolus vulgaris* L.) and corn (*Zea mays* L.). – Int. J. Biotechnol. Res. **3**: 190-197, 2012.

Samadi N., Yahyaabadi S., Rezayatmand Z.: Effect of TiO_2 and TiO_2 nanoparticle on germination, root and shoot length and photosynthetic pigments of *Mentha piperita*. – Int. J. Plant Soil Sci. **3**: 408-418, 2014.

Samadi S., Saharkhiz M.J., Azizi M. *et al.*: Multi-walled carbon nanotubes stimulate growth, redox reactions and biosynthesis of antioxidant metabolites in *Thymus daenensis* Celak. *in vitro*. – Chemosphere **249**: 126069, 2020.

Samadi S., Saharkhiz M.J., Azizi M. *et al*.: Single-wall carbon nano tubes (SWCNTs) penetrate *Thymus daenensis* Celak. plant cells and increase secondary metabolite accumulation *in vitro*. – Ind. Crop. Prod. **165**: 113424, 2021.

Sami F., Siddiqui H., Hayat S.: Impact of silver nanoparticles on plant physiology: A critical review. – In: Hayat S., Pichtel J., Faizan M., Fariduddin Q. (ed.): Sustainable Agriculture Reviews 41. Pp. 111-127. Springer, Cham 2020.

Santos S.M.A., Dinis A.M., Rodrigues D.M.F. *et al*.: Studies on the toxicity of an aqueous suspension of C60 nanoparticles using a bacterium (gen. *Bacillus*) and an aquatic plant (*Lemna gibba*) as *in vitro* model systems. – Aquat. Toxicol. **142-143**: 347-354, 2013.

Schwab F., Bucheli T.D., Camenzuli L. *et al*.: Diuron sorbed to carbon nanotubes exhibits enhanced toxicity to *Chlorella vulgaris*. – Environ. Sci. Technol. **47**: 7012-7019, 2013.

Schwab F., Zhai G., Kern M. *et al*.: Barriers, pathways and processes for uptake, translocation and accumulation of nanomaterials in plants – Critical review. – Nanotoxicology **10**: 257-278, 2015.

Sendra M., Moreno-Garrido I., Blasco J., Araújo C.V.M.: Effect of erythromycin and modulating effect of CeO_2 NPs on the toxicity exerted by the antibiotic on the microalgae *Chlamydomonas reinhardtii* and *Phaeodactylum tricornutum*. – Environ. Pollut. **242**: 357-366, 2018.

Serag M.F., Kaji N., Gaillard C. *et al*.: Trafficking and subcellular localization of multiwalled carbon nanotubes in plant cells. – ACS Nano **5**: 493-499, 2011.

Sharifi-Rad J., Quispe C., Butnariu M. *et al*.: Chitosan nanoparticles as a promising tool in nanomedicine with particular emphasis on oncological treatment. – Cancer Cell Int. **21**: 318, 2021.

Sharma P., Bhatt D., Zaidi M.G.H. *et al*.: Silver nanoparticle-mediated enhancement in growth and antioxidant status of *Brassica juncea*. – Appl. Biochem. Biotech. **167**: 2225-2233, 2012.

Sharma S., Uttam K.N.: Rapid analyses of stress of copper oxide nanoparticles on wheat plants at an early stage by laser induced fluorescence and attenuated total reflectance Fourier transform infrared spectroscopy. – Vib. Spectrosc. **92**: 135-150, 2017.

Shaw A.K, Ghosh S., Kalaji H.M. *et al*.: Nano-CuO stress induced modulation of antioxidative defense and photosynthetic performance of Syrian barley (*Hordeum vulgare* L.). – Environ. Exp. Bot. **102**: 37-47, 2014.

Sheikhalipour M., Esmaielpour B., Behnamian M. *et al*.: Chitosan–selenium nanoparticle (Cs–Se NP) foliar spray alleviates salt stress in bitter melon. – Nanomaterials **11**: 684, 2021.

Siddiqui M.H., Al-Whaibi M.H., Faisal M., Al Sahli A.A.: Nano-silicon dioxide mitigates the adverse effects of salt stress on *Cucurbita pepo* L. – Environ. Toxicol. Chem. **33**: 2429-2437, 2014.

Singh A., Singh N.B., Hussain I. *et al*.: Green synthesis of nano zinc oxide and evaluation of its impact on germination and metabolic activity of *Solanum lycopersicum*. – J. Biotechnol. **233**: 84-94, 2016.

Singh T., Shukla S., Kumar P. *et al*.: Application of nanotechnology in food science: Perception and overview. – Front. Microbiol. **8**: 1501, 2017.

Sousa C.A., Soares M.H.V.M., Soares E.V.: Toxic effects of nickel oxide (NiO) nanoparticles on the freshwater alga *Pseudokirchneriella subcapitata*. – Aquat. Toxicol. **204**: 80-90, 2018.

Spinoso-Castillo J.L., Chavez-Santoscoy R., Bogdanchikova N. *et al*.: Antimicrobial and hormetic effects of silver nanoparticles on in vitro regeneration of vanilla (*Vanilla planifolia* Jacks. ex Andrews) using a temporary immersion system. – Plant Cell Tiss. Org. Cult. **129**: 195-207, 2017.

Suriyaprabha R., Karunakaran G., Yuvakkumar R. *et al*.: Growth and physiological responses of maize (*Zea mays* L.) to porous silica nanoparticles in soil. – J. Nanopart. Res. **14**: 1294, 2012.

Swapna M.S., Raj V., Devi H.V.S., Sankararaman S.: Optical emission diagnosis of carbon nanoparticle-incorporated chlorophyll for sensing applications. – Photoch. Photobio. Sci. **18**: 1382-1388, 2019.

Swift T.A., Oliver T.A.A., Galan M.C., Whitney M.: Functional nanomaterials to augment photosynthesis: evidence and considerations for their responsible use in agricultural applications. – Interface Focus **9**: 20180048, 2019.

Tan W., Deng C., Wang Y. *et al*.: Interaction of nanomaterials in secondary metabolites accumulation, photosynthesis, and nitrogen fixation in plant systems. – Compr. Anal. Chem. **84**: 55-74, 2019.

Tang Y., Li S., Lu Y. *et al*.: The influence of humic acid on the toxicity of nano-ZnO and Zn^{2+} to the *Anabaena* sp. – Environ. Toxicol. **30**: 895-903, 2015.

Tao X., Yu Y., Fortner J.D. *et al*.: Effects of aqueous stable fullerene nanocrystal (nC_{60}) on *Scenedesmus obliquus*: evaluation of the sub-lethal photosynthetic responses and inhibition mechanism. – Chemosphere **122**: 162-167, 2015.

Tayemeh M.B., Esmailbeigi M., Shirdel I. *et al*.: Perturbation of fatty acid composition, pigments, and growth indices of *Chlorella vulgaris* in response to silver ions and nanoparticles: A new holistic understanding of hidden ecotoxicological aspect of pollutants. – Chemosphere **238**: 124576, 2020.

Thapa M., Singh M., Ghosh C.K. *et al*.: Zinc sulphide nanoparticle (nZnS): A novel nano-modulator for plant growth. – Plant Physiol. Bioch. **142**: 73-83, 2019.

Tian H., Ghorbanpour M., Kariman K.: Manganese oxide nanoparticle-induced changes in growth, redox reactions and elicitation of antioxidant metabolites in deadly nightshade (*Atropa belladonna* L.). – Ind. Crop. Prod. **126**: 403-414, 2018.

Tighe-Neira R., Carmora E., Recio G. *et al*.: Metallic nanoparticles influence the structure and function of the photosynthetic apparatus in plants. – Plant Physiol. Bioch. **130**: 408-417, 2018.

Tkalec M., Cvjetko P., Biba R. *et al*.: Impact of silver nanoparticles on photosynthesis in tobacco plants. – Toxicol. Lett. **280**: S184, 2017.

Tombuloglu H., Slimani Y., Tombuloglu G. *et al*.: Uptake and translocation of magnetite (Fe_3O_4) nanoparticles and its impact on photosynthetic genes in barley (*Hordeum vulgare* L.). – Chemosphere **226**: 110-122, 2019.

Torrent L., Iglesias M., Marguí E. *et al*.: Uptake, translocation and ligand of silver in *Lactuca sativa* exposed to silver nanoparticles of different size, coatings and concentration. – J. Hazard. Mater. **384**: 121201, 2020.

Torres R., Diz V.E., Lagorio M.G.: Effects of gold nanoparticles on the photophysical and photosynthetic parameters of leaves and chloroplasts. – Photoch. Photobio. Sci. **17**: 505-516, 2018.

Tripathi A., Liu S., Singh P.K. *et al*.: Differential phytotoxic responses of silver nitrate ($AgNO_3$) and silver nanoparticle (AgNps) in *Cucumis sativus* L. – Plant Gene **11**: 255-264, 2017a.

Tripathi D.K., Singh S., Singh S. *et al*.: Nitric oxide alleviates silver nanoparticles (AgNps)-induced phytotoxicity in *Pisum sativum* seedlings. – Plant Physiol. Bioch. **110**: 167-177, 2017b.

Tripathi D.K., Singh S., Singh V.P. *et al.*: Silicon nanoparticles more effectively alleviated UV-B stress than silicon in wheat (*Triticum aestivum*) seedlings. – Plant Physiol. Bioch. **110**: 70-81, 2017c.

Ulhassan Z., Ali S., Gill R.A. *et al.*: Comparative orchestrating response of four oilseed rape (*Brassica napus*) cultivars against the selenium stress as revealed by physiochemical, ultrastructural and molecular profiling. – Ecotox. Environ. Safe. **161**: 634-647, 2018.

Ulhassan Z., Gill R.A., Ali S. *et al.*: Dual behavior of selenium: Insights into physio-biochemical, anatomical and molecular analyses of four *Brassica napus* cultivars. – Chemosphere **225**: 329-341, 2019a.

Ulhassan Z., Huang Q., Gill R.A. *et al.*: Protective mechanisms of melatonin against selenium toxicity in *Brassica napus*: insights into physiological traits, thiol biosynthesis and antioxidant machinery. – BMC Plant Biol. **19**: 507, 2019b.

Večeřová K., Večeřa Z., Dočekal B. *et al.*: Changes of primary and secondary metabolites in barley plants exposed to CdO nanoparticles. – Environ. Pollut. **218**: 207-218, 2016.

Verma S.K., Das A.K., Gantait S. *et al.*: Applications of carbon nanomaterials in the plant system: a perspective view on the pros and cons. – Sci. Total Environ. **667**: 485-499, 2019.

Wang A., Jin Q., Xu X. *et al.*: High-throughput screening for engineered nanoparticles that enhance photosynthesis using mesophyll protoplasts. – J. Agr. Food Chem. **68**: 3382-3389, 2020.

Wang C., Zhang H., Ruan L. *et al.*: Bioaccumulation of ^{13}C-fullerenol nanomaterials in wheat. – Environ. Sci.-Nano **3**: 799-805, 2016.

Wang H., Zhang M., Song Y. *et al.*: Carbon dots promote the growth and photosynthesis of mung bean sprouts. – Carbon **136**: 94-102, 2018.

Winkelmann K., Bernas L., Swiger B., Brown S.: Measurement of chlorophyll loss due to phytoremediation of Ag nanoparticles in the first-year laboratory. – J. Chem. Educ. **94**: 751-757, 2017.

Wong M.H., Misra R.P., Giraldo J.P. *et al.*: Lipid exchange envelope penetration (LEEP) of nanoparticles for plant engineering: a universal localization mechanism. – Nano Lett. **16**: 1161-1172, 2016.

Wu H., Lin Z.: Recent advances in nano-enabled agriculture for improving plant performance. – Crop J., 2021. (In press)

Wu H., Shabala L., Shabala S., Giraldo J.P.: Hydroxyl radical scavenging by cerium oxide nanoparticles improves *Arabidopsis* salinity tolerance by enhancing leaf mesophyll potassium retention. – Environ. Sci.-Nano **5**: 1567-1583, 2018.

Wu H., Tito N., Giraldo J.P.: Anionic cerium oxide nanoparticles protect plant photosynthesis from abiotic stress by scavenging reactive oxygen species. – ACS Nano **11**: 11283-11297, 2017.

Xu X., Mao X., Zhuang J. *et al.*: PVA-coated fluorescent carbon dot nanocapsules as an optical amplifier for enhanced photosynthesis of lettuce. – ACS Sustain. Chem. Eng. **8**: 3938-3949, 2020.

Yang F., Liu C., Gao F. *et al.*: The improvement of spinach growth by nano-anatase TiO_2 treatment is related to nitrogen photoreduction. – Biol. Trace Elem. Res. **119**: 77-88, 2007.

Yasmeen F., Raja N.I., Ilyas N., Komatsu S.: Quantitative proteomic analysis of shoot in stress tolerant wheat varieties on copper nanoparticle exposure. – Plant Mol. Biol. Rep. **36**: 326-340, 2018.

Younes N.A., Dawood M.F.A., Wardany A.A.: Biosafety assessment of graphene nanosheets on leaf ultrastructure, physiological and yield traits of *Capsicum annuum* L. and *Solanum melongena* L. – Chemosphere **228**: 318-327, 2019.

Zahedi S.M., Hosseini M.S., Meybodi N.D.H. *et al.*: Foliar application of selenium and nano-selenium affects pomegranate (*Punica granatum* cv. Malase Saveh) fruit yield and quality. – S. Afr. J. Bot. **124**: 350-358, 2019.

Zhai G., Walters K.S., Peate D.W. *et al.*: Transport of gold nanoparticles through plasmodesmata and precipitation of gold ions in woody poplar. – Environ. Sci. Technol. Lett. **1**: 146-151, 2014.

Zhang L., Goswami N., Xie J. *et al.*: Unraveling the molecular mechanism of photosynthetic toxicity of highly fluorescent silver nanoclusters to *Scenedesmus obliquus*. – Sci. Rep.-UK **7**: 16432, 2017.

Zhao L., Lu L., Wang A. *et al.*: Nano-biotechnology in agriculture: Use of nanomaterials to promote plant growth and stress tolerance. – J. Agr. Food Chem. **68**: 1935-1947, 2020.

Zhao L., Peralta-Videa J.R., Peng B. *et al.*: Alginate modifies the physiological impact of CeO_2 nanoparticles in corn seedlings cultivated in soil. – J. Environ. Sci. **26**: 382-389, 2014.

Zhao L., Sun Y., Hernandez-Viezcas J.A. *et al.*: Monitoring the environmental effects of CeO_2 and ZnO nanoparticles through the life cycle of corn (*Zea mays*) plants and in situ μ-XRF mapping of nutrients in kernels. – Environ. Sci. Technol. **49**: 2921-2928, 2015.

Zhao L., Zhang H., White J.C. *et al.*: Metabolomics reveals that engineered nanomaterial exposure in soil alters both soil rhizosphere metabolite profiles and maize metabolic pathways. – Environ. Sci.-Nano **6**: 1716-1727, 2019.