Chapter 3
Response of Plant Photosynthesis to Nanomaterials

Sashi Sonkar, Prakash Kumar Sarangi, Brijesh Pandey, Anand Prakash, and Akhilesh Kumar Singh

Abstract An enhancement in crop productivity is one of the crucial requirements in order to circumvent the increasing food demands globally. Crop productivity may be improved via plant nanobiotechnology that involve the integration of plant biotechnology with nanotechnology. The plant nanobiotechnology exploits the nanoparticles (NPs) for boosting the agricultural plant productivity via increasing growth, development as well as active photosynthesis rate of agricultural plants/crops. The photosynthetic performance is exceedingly susceptible biological activity under abiotic stresses. The photosynthetic process under abiotic stresses results in excessive formation of reactive oxygen species (ROS), which overwhelms the plants native ROS scavenging mechanism. However, the engineered NPs have been found to protect and boost the plants photosynthetic effectiveness by diminishing oxidative stress. However, the impact of NPs on photosynthetic effectiveness is found to varied between plants as well as even within species. They either improve plant photosynthetic effectiveness by enhancing the light-harvesting complexes or block routes through obstructing the electron transport chain. For instance, NPs like single-walled carbon nanotubes (SWCNTs) were found to boost photosynthesis by threefold. In contrast, NPs such as iron oxide as well as silver NPs were reported to impede photosynthesis. Overall, the study of the beneficial impacts of NPs on plant systems

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including photosynthesis is yet inadequate. This chapter provides an overview on the current status regarding the influence of NPs on photosynthesis in plants.

Keywords Light-harvesting complexes · Nanobiotechnology · Nanoparticles · Photosynthesis · Reactive oxygen species

3.1 Introduction

Nanoparticles (NPs) were among the most extensively investigated particles of the twenty-first century, fostering a new area of study known as "plant nanobiotechnology (Al-Khayri et al. 2021). NPs are particles that refer to small size natural or manufactured materials having dimensions ranging between 1 and 100 nm with extremely higher surface to volume area ratio (Mukhopadhyay 2014; Pandey et al. 2018; Porwal et al. 2020; Rani et al. 2020; Singh and Porwal 2020; Singh et al. 2018a; Singh et al. 2020; Porwal et al. 2021; Sonkar et al. 2021a). These NPs can modify their physicochemical characteristics over their parent bulk material (Rastogi et al. 2017). Because of their unique qualities and innovative features, NPs are widely utilized in the development of mankind as well as energy sectors (Nel et al. 2006). NPs may be manufactured from a range of bulk materials, and their activities are determined by their particle shape or/and size as well as chemical components (Brunner et al. 2006). Further, the rate of ingress of NPs into plant cells is determined by their surface features and size. The large size NPs are unable to penetrate the cell or impact cell metabolic processes, whereas smaller NPs enter easily (Kashyap et al. 2015; Sonkar et al. 2021b). However, some huge NPs were observed to create large pores to pass via plant cell walls (Rastogi et al. 2017). There are three sorts of NPs based on their derivation: engineered, accidental, and natural. Natural NPs are those that have occurred from the dawn of geological history and yet are still ubiquitous in the environment (mineral compositions, lunar dust, volcanic dust, and so on) (Monica and Cremonini 2009). Incidental NPs are anthropogenic particles produced by man-made industrial operations such as coal incineration, welding gases, as well as diesel exhaust. Engineered NPs are classified into four categories (Kataria et al. 2019; Singh et al. 2018b):

(a) Composites are NPs that have been blended with other NPs or with bigger bulky materials and come in a variety of shapes such as prisms, rods, tubes, and spheres.
(b) Dendrimers are nano-sized polymers that are made up of branching units that may be customized to conduct certain chemical activities.
(c) Metal-based materials include quantum dots, nano-aluminum, nano-zinc, nano-silver, nano-gold, and nano-scale metal oxides such as aluminium oxide, zinc oxide, and titanium dioxide.
(d) Multi-walled carbon nanotubes (MWCNTs), single-walled carbon nanotubes (SWCNTs), and fullerene are examples of carbon-based materials.

Overall, the development, as well as exploitation of NPs having greater volume to surface area ratio, are presently the key interest of nanotechnology towards boosting the competency of better penetration, interaction as well as reproducibility. This innovative approach is now enabled worldwide scientists to solve/resolve various global issues including food shortage together with agricultural hindrance/obstacles. This is supported by the fact that in the current scenario, plant nanobiotechnology is found to depict great potential in the agricultural field (Wu and Li 2022). For instance, it can enhance stress resistance of plant system through nanozymes mediated hunting of reactive oxygen species (ROS). The nanozymes are those NPs that can imitate antioxidant enzyme activities. It has been observed that cerium oxide NPs treated plants become more resistant/tolerant against salinity (Rossi et al. 2016; Wu et al. 2018; Liu et al. 2021), drought (Djanaguiraman et al. 2018), heat (Wu et al. 2017) as well as cold (Wu et al. 2017). Likewise, NPs like SWCNT enhanced threefold greater photosynthetic performance in the chloroplasts. This is owing to not only the speedy transportation of electrons but also the improved activity of signalling molecules like nitric oxide in plants. The nano-mesoporous silica compounds were also found to enhance the photosynthetic performance (Poddar et al. 2020).

Farming is the foremost occupational backbone of the utmost of developing nations. Further, there is need to enhance agricultural yield by 60% from the 2005–2007 level to nourish a population of about 9 billion by 2050 (Lee 2011; van Ittersum et al. 2016; Porwal et al. 2021). Such rapid growth of population will give rise to severe issues pertaining to water, food as well as energy resources (Marchiol 2018). Consequently, instant sustainable intensification is required towards the enhancement of environmentally friendly agricultural yield in present cultivable land. The speedy rise in worldwide population results in excessive utilization of the limited natural sources like land, water as well as soil has been excessively exploited. This requires eco-friendly-based agricultural development having economic viability. Hence, apart from efforts in breeding programs, farm management as well as cultivation practices, there is a further need for the introduction of innovative approaches like nano-assisted agriculture for overall agricultural improvement (Singh et al. 2015; Prasad et al. 2014). The nano-assisted agriculture/farming has potential towards overcoming the forecasted food scarcity. The evolving area of nano-assisted farming has potential for increasing the plant resistance towards the abiotic stresses apart from improving plant breeding as well as farming (White and Gardea-Torresdey 2018; Pulizzi 2019). Therefore, apart from overcoming food scarcity, plant nanobiotechnology also depicts its considerable potential/impacts in sustainable farming.

Plants are vital for ecosystem functioning as primary producers because they transform energy from the sun into organic materials that may be utilized by later trophic levels of the food chain (McKee and Filser 2016). Plants represent a possible channel for the transportation of NPs (Rico et al. 2011). Further, it can accrue in consumers at various trophic levels along the food chain (Zhu et al. 2008). The rate of NP absorption and its impact on metabolic function as well as growth differ amongst plant species. Additionally, the quantity of NPs influences plant functions such as photosynthesis, growth, and germination. NPs either increase photosynthetic activities in plants and bacteria by enhancing the light-harvesting complexes or block routes by obstructing the electron transport chain (Kataria et al. 2019). Furthermore, NPs play a significant role in plant defense against a variety of abiotic challenges (Khan et al. 2017) by activating antioxidative enzymes that scavenge ROS (Wei and Wang 2013). Under abiotic stresses, photosynthesis is an exceedingly susceptible biological entity, where NPs have been demonstrated to protect the process and boost photosynthetic efficiency by lowering oxidative stress (Siddiqui et al. 2014). Figure 3.1 revealed the potential advantageous interactions of NPs with photosynthetic apparatus in plant system under ultraviolet B (UV-B) radiations as abiotic stress. Nevertheless, the reactions of various plant species to NPs varied (Qi et al. 2013; Giraldo et al. 2014; Barhoumi et al. 2015; da Costa and Sharma 2016; Wang et al. 2016, 2018; Wu et al. 2017; Li et al. 2018; Yanık and Vardar 2018; Ali et al. 2019; Dias et al. 2019; Soleymanzadeh et al. 2020; Swift et al. 2020; Elshoky et al. 2021; Faizan et al. 2021a, b; Rai-Kalal and Jajoo 2021; Rajput et al. 2021). NPs in the cultural medium produce oxidative stress, reduce biomass accumulation, photosynthesis, chlorophyll concentration, shoot length, root length as well as germination including nutrition to agricultural plants. NPs also alter gene expression involved in energy pathways, electron transport chain, cell organization, biosynthesis as well as abiotic and biotic stress responses. The impact of NPs on photosynthesis varied between plants and even within species (Kataria et al. 2019). This chapter throws light on the current status concerning the impact of NPs on plant photosynthesis.

3.2 Interaction of NPs with the Plant Systems

The factors responsible for NPs absorption in plant cells involve plant growth conditions, plant type as well as age. Furthermore, the physicochemical properties of the NPs (such as chemical composition, size, dimension, and stability in solution) were responsible for NP uptake, translocation, and accrual in the plant system (Snehal and Lohani 2018). In general, NPs enter the plant root through the lateral root connections and go to the xylem via the cortex and the pericycle. The plant system's interaction with NPs is mostly based on chemical reactions that result in lipid peroxidation, oxidative damage, ion transport activity, and the formation of ROS. When NPs reach plant cells, they react with carboxyl and sulfhydryl groups, altering protein activity (Kurepa et al. 2009). The transporter or pumps found in the cytoplasmic membrane of the roots primarily controlled nutrient and mineral absorption in plants. In certain circumstances, NPs bind to carrier proteins before passing via ions channels, aquaporins, or endocytosis (Snehal and Lohani 2018). Metals such as silicon in its silicic acid state are mostly taken by plants by diffusion (apoplastic transport). Nonetheless, specialized aquaporin (NIP2) is required for symplastic transport. Xylem is in care of an upwards flow of silicic acid to the aerial tissue system, which includes the shoot and leaves (Deshmukh et al. 2013; Snehal and Lohani 2018). Further, the uptake or absorption of NPs or their aggregates by plant cells is determined by their size, which should be smaller than the pore diameter (5–20 nm) so that they may readily reach the cell membrane after passing through the cell wall (Kumar et al.

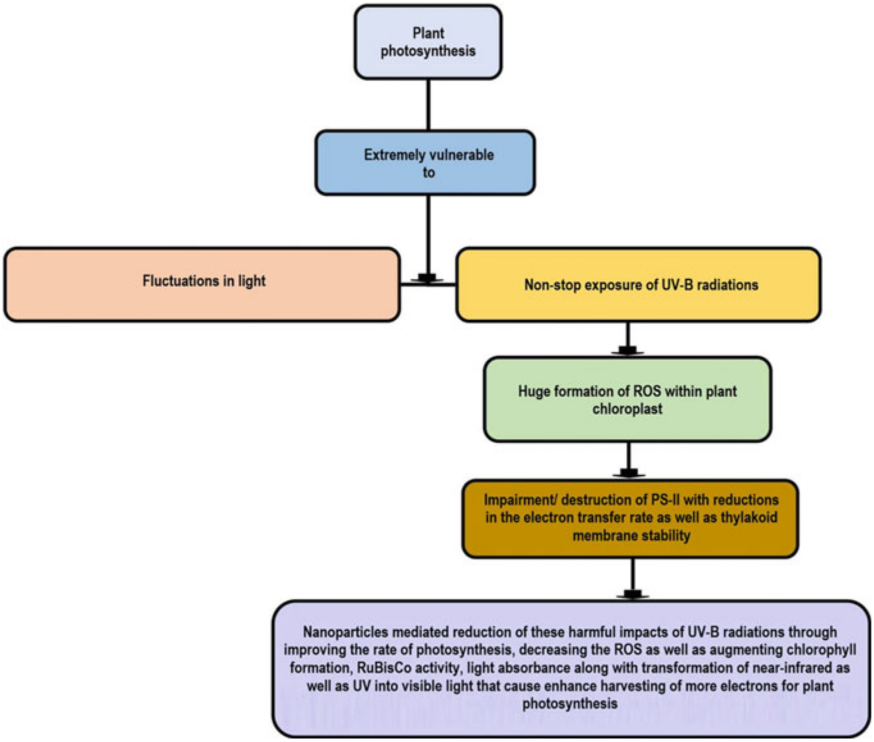

Fig. 3.1 Promising beneficial interactions amongst NPs and plant photosynthetic apparatus under UV-B radiations (Figure constructed by Akhilesh Kumar Singh)

2016). After forming complexes inside membrane transporters or root exudates, the NPs were transferred into the plants. The absorption of NPs by plants has also been documented, either by the stomata or the base of the trichome in leaves (Snehal and Lohani 2018). Following NP penetration into the cell membrane, additional transport occurs via either apoplastic or symplastic routes. NP mobilization following absorption within the plant cell might also be aided by plasmodesmata from one cell to another (Rico et al. 2011; Sanzari et al. 2019).

3.3 Role of NPs in Plant Photosynthesis

Photosynthesis is essentially the only mechanism of energy input in the living world. It is an anabolic process of manufacturing food inside the chlorophyll-containing cells from water as well as carbon dioxide with the assistance of solar light as a source of energy. Recent research is concerned about the participation of NPs and their impact on photosynthetic activity. Some of the favorable impacts of NPs on photosynthesis as well as plant growth have been documented for a variety of plant species (Zarate-Cruz et al. 2016; Cao et al. 2018). To study the rate of energy transformation in plants, the precise interaction of NPs with the molecular as well as ultrastructural components of the plant photosynthetic system must be developed (Tripathi et al. 2017). Hence, the association of NPs with plants and their influences on biological alterations of the photosynthetic system including plant physiological processes, draw attention for assessment and research.

Photosynthesis is more dependent on the structural arrangement of the involved cellular organelle, which is involved in regulating gaseous concentrations inside the cellular system and managing carbon dioxide transit to carboxylation sites (Mediavilla et al. 2001). Factors that influence photosynthetic activity include the regulatory proteins of the thylakoids, presence of photosynthetic pigment (chlorophyll *a* and *b*), activity of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCo), carbon dioxide aggregation, adequate grana development, structural stability of mesophyll cells as well as chloroplasts (Sáez et al. 2017). Accordingly, the favorable effects on photosynthesis efficiency with the modification of the aspects liable for photosynthetic yield offer an alternative approach for crop development (Foyer et al. 2017). In addition, solar energy is fundamentally turned into chemical energy via photosynthesis, generating several aspects of the photosynthetic process. NPs can have an influence on photosynthesis in both beneficial as well as harmful ways (Fig. 3.2). It modulates the light-harvesting complex of crops by boosting the reaction, inhibiting the electron transport system as well as altering the function of phosphoenolpyruvate carboxylase, carbonic anhydrase, and RuBisCo thus stopping the metabolic reaction (Kataria et al. 2019). Furthermore, researchers are actively striving to increase agricultural productivity through enhancing plant photosynthetic activity with implanted SWCNTs in chloroplasts. SWCNTs improve the biological detection of signaling chemicals such as nitric oxide and increase the rate of electron transport (Giraldo et al. 2014). Because NPs alter the functionality of photosynthetic components, extensive investigation is necessary to assess the effects of NPs on the final products of photosynthesis. The use of a silicon compound conjugate with photosystem II resulted in a steady photosynthetic reaction for oxygen evolution, which increased the activity of photosynthetic pigments and enzymes. The conjugate might potentially be used in artificial photosynthesis as photo-sensors (Siddiqui et al. 2015).

3.4 NPs and Their Diverse Impact on Plant Photosynthetic Systems

Nonmetallic NPs are biocompatible and less oxidizing. Consequently, they have little or no harmful effects on plant photosynthesis. Metallic NPs, on the other hand, tend to impede photosynthesis by generating ROS, which damages the different photosynthetic machineries (Poddar et al. 2020). The stimulated reactions generated by NPs varied amongst plant species as depicted in Table 3.1.

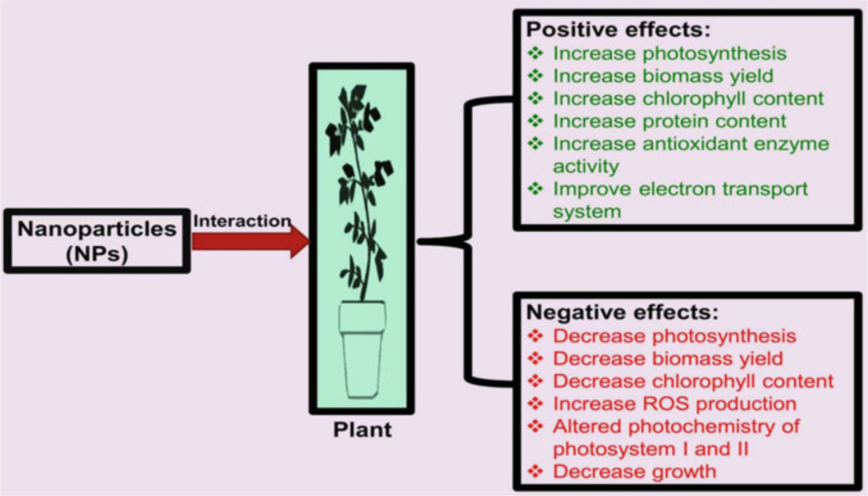

Fig. 3.2 Various positive and negative impacts of NPs on a plant's photosynthetic system (Figure constructed by Sashi Sonkar)

Qi et al. (2013) investigated the impact of TiO_2 NPs on the photosynthetic rate of tomatoes under exposure to mild heat stress. The photosynthetic and transpiration, as well as water conductance, get improved with the treatment of TiO_2 NPs. TiO_2 NPs not only boosted the regulation of photosystem II energy dissipation but also decreased the non-regulated photosystem II energy dissipation under mild heat stress. These findings suggest that TiO_2 NPs promote photosynthesis in leaf tissue under mild heat stress. Giraldo et al. (2014) reported that SWCNTs passively transport and irreversibly localize within the lipid envelope of extracted spinach chloroplasts, increasing maximum electron transport rates as well as promoting photosynthetic activity over three times higher than the control. Through a mechanism compatible with increased photoabsorption, the SWCNT and chloroplast assemblies also permit higher rates of leaf electron transfer in vivo. Delivering SWCNT-nanoceria [cerium oxide (CeO_2) NPs] or poly(acrylic acid)-nanoceria (PNC) complexes considerably reduces ROS concentrations inside removed chloroplasts. The toxicity of superparamagnetic iron oxide nanoparticles (SPION) in *Lemna gibba* L. plants subjected for 7 days to Fe_3O_4 (SPION-1), $Co_{0.2}Zn_{0.8}Fe_2O_4$ (SPION-2) or $Co_{0.5}Zn_{0.5}Fe_2O_4$ (SPION-3) at 0, 12.5, 25, 50, 100, 200, or 400 $\mu g\ mL^{-1}$ was examined. At less than 400 $\mu g\ mL^{-1}$ of SPION, toxicity was shown by a larger production of ROS, impairment of photosystem II activities, and reduction in chlorophyll content as well as suppression of growth rate. The exposure of SPION suspensions to *L. gibba* induced many changes to the entire plant cellular system, which might be attributed to both NP and metal ion absorption in the soluble fraction. The findings show that the SPION has a complicated toxic mode of action on the entire plant system, affecting its viability (Barhoumi et al. 2015). On the other hand, da Costa and Sharma

Table 3.1 Beneficial and detrimental effects of NPs on plant photosynthetic systems

Type of plant species	Type of NPs treatment	Response	References
Arabidopsis (*Arabidopsis thaliana* (L.) Heynh.)	Ag NPs	Severely limit chlorophyll production and plant development, as well as induce oxidative damage	Li et al. (2018)
Arabidopsis (*Arabidopsis thaliana* (L.) Heynh.)	CeO_2 NPs	Increase photosynthesis by allowing for faster RuBisCo carboxylation	Wu et al. (2017)
Arabidopsis (*Arabidopsis thaliana* (L.) Heynh.)	ZnO NPs	Inhibit the expression of photosystem structural genes and chlorophyll biosynthesis genes, resulting in the inhibition of chlorophyll biosynthesis and a decrease in photosynthesis effectiveness in the plants	Wang et al. (2016)
Barley (*Hordeum sativum* L.)	ZnO NPs	Diminish photosynthetic activity and impair the structural organization of the photosynthetic machinery	Rajput et al. (2021)
Mung bean (*Vigna radiata* (L.) Wilczek)	Carbon dots (CDs)	Promotes photosynthesis and plant growth. Increase electron transfer in photosystem, RuBisCo activity, and chlorophyll concentration	Wang et al. (2018)
Pea (*Pisum sativum* L.)	ZnO-Si NPs and ZnO NPs	Reduce the deleterious effects of salt stress on the membrane integrity, stomata closure, pigment content, and photochemistry of photosystems I and photosystems II	Elshoky et al. (2021)
Rice (*Oryza sativa* L.)	CuO NPs	Decreases the concentration of photosynthetic pigment, the maximum quantum yield of photosystem II photochemistry, stomatal conductance, transpiration rate, and photosynthetic rate	da Costa and Sharma (2016)
Rice (*Oryza sativa* L.)	ZnO NPs	Improves mineral nutrient content, antioxidant enzyme activity, protein content, photosynthesis, and biomass	Faizan et al. (2021b)

(continued)

Table 3.1 (continued)

Type of plant species	Type of NPs treatment	Response	References
Spinach (*Spinacia oleraceae* L.)	Single-walled carbon nanotubes (SWCNTs)	Improves the antioxidant system, photoabsorption, and electron transport in chloroplasts	Giraldo et al. (2014)
Strawberry (*Fragaria* × *ananassa* Duch. cv. ‘Gaviota’)	Se NPs	Improves antioxidant apparatus, salicylic acid, photosynthesis, and ion hemostasis under salt stress	Soleymanzadeh et al. (2020)
Swollen duckweed (*Lemna gibba* L.)	Superparamagnetic iron oxide nanoparticles (SPION)	Effecting viability and shut down of whole photosynthesis process to a huge extent. Higher production of ROS, impairment of photosystem II activities, and reduction in chlorophyll content as well as suppression of growth rate	Barhoumi et al. (2015)
Tomato (*Lycopersicon esculentum* Mill.)	TiO_2	Increased photosynthesis through managing energy dissipation, which resulted in leaf cooling by increasing stomatal opening	Qi et al. (2013)
Tomato (*Lycopersicon esculentum* Mill.)	ZnO NPs	Increase photosynthetic features, chlorophyll content, leaf area, biomass, root length, and shoot length of tomato. Reduces the deleterious effects of salt stress on plant development and increases protein content as well as antioxidative enzyme activity such as catalase, superoxide dismutase, and peroxidase under salt stress	Faizan et al. (2021a)
Wheat (*Triticum aestivum* L.)	CDs	Enhances photosynthesis and boosts crop output, resulting in an 18% upsurge in grain production	Swift et al. (2020)

(continued)

Table 3.1 (continued)

Type of plant species	Type of NPs treatment	Response	References
Wheat (*Triticum aestivum* L.)	Si NPs	Improves leaf gas exchange characteristics and chlorophyll *a* and *b* concentrations while decreasing oxidative stress in leaves as evidenced by increased peroxidase and superoxide dismutase abilities and reduced electrolyte leakage in the leaf	Ali et al. (2019)
Wheat (*Triticum aestivum* L.)	TiO_2 NPs	Reduction in both the light-independent and light-dependent phases of photosynthesis, as well as a decrease in chlorophyll content, the maximum and effective efficiency of photosystem II, starch content, intercellular CO_2 concentration, stomatal conductance, transpiration rate, and net photosynthetic rate	Dias et al. (2019)
Wheat (*Triticum aestivum* L.)	ZnO NPs	Increase seed water intake, which resulted in increased α-amylase activity. The concentration of photosynthetic pigments (total chlorophyll, chlorophyll *b*, and chlorophyll *a* content) was dramatically increased	Rai-Kalal and Jajoo (2021)
Wheat (*Triticum aestivum* L. cv Demir 2000)	Al_2O_3 NPs	Triggers oxidative stress in plants and damages photosynthetic pigment systems. Reduces catalase activity while increasing proline content, lipid peroxidation, superoxide dismutase activity, and hydrogen peroxide content	Yanık and Vardar (2018)

(2016) evaluated the effects of copper (II) oxide NPs (CuO NPs) on the biochemical and physiological behavior of rice plants. At high concentrations of CuO NPs, the biomass, root and shoot length, and germination rate were decreased, whereas Cu absorption in the shoots and roots improved. The increment of CuO NP was documented in the cells, particularly in the chloroplasts, and was associated with a decrease in the number of thylakoids per grana. The concentration of photosynthetic pigment, the maximum quantum yield of photosystem II photochemistry, stomatal conductance, transpiration rate, and photosynthetic rate, all decreased with no photosystem II photochemical quenching at 1000 mg L^{-1} of CuO NPs. Increased proline as well as malondialdehyde levels, indicated osmotic and oxidative stress. Superoxide dismutase as well as ascorbate peroxidase expression levels, were similarly enhanced. Their findings indicated the detrimental impact of Cu buildup in roots and shoots, which resulted in the loss of photosynthesis. Zinc oxide NPs (ZnO NPs) were shown to be toxic to a variety of plant species. Likewise, Wang et al. (2016) investigated the impact of ZnO NPs on *Arabidopsis* plant photosynthesis and biomass accumulation. Treatment with 300 and 200 mg L^{-1} ZnO NPs lowers growth by 80 as well as 20%, correspondingly over untreated system. Chlorophyll a and b content was reduced by more than 50%, although carotenoid content was mostly unaltered in *Arabidopsis* plants treated with 300 mg L^{-1} ZnO NPs. Furthermore, in 300 mg L^{-1} ZnO NPs-supplemented plants show the transpiration rate, net photosynthesis, leaf stomatal conductance, and intercellular carbon dioxide concentration rate were all lowered by more than 50%. The expression levels of chlorophyll synthesis genes including *magnesium-chelatase subunit D (CHLD), Mg-protoporphyrin IX methyltransferase (CHLM), copper response defect 1 (CRD1), chlorophyll synthase (CHLG), and chlorophyll a oxygenase (CAO)*, as well as photosystem structure gene such as *photosystem I subunit K (PSAN), photosystem I subunit K (PSAK), photosystem I subunit E-2 (PSAE2)*, and *photosystem I subunit D-2 (PSAD2)* were reduced about five-folds in 300 mg L^{-1} ZnO NPs treated plants, according to quantitative analysis using reverse transcription-polymerase chain reaction. On the contrary, enhanced expression of numerous carotenoid synthesis genes, including *zetacarotene desaturase (ZDS), phytoene desaturase (PDS), phytoene synthase (PSY), and geranyl geranyl pyrophosphate synthase 6 (GGPS6)*, was found in plants treated with ZnO NPs. These findings suggest that the toxicological effects of ZnO NPs observed in *Arabidopsis* were most likely caused by the inhibitory activities of the expression of photosystem structural genes as well as chlorophyll biosynthesis genes, resulting in the inhibition of chlorophyll biosynthesis with a decrease in photosynthesis effectiveness in the plants. Wu et al. (2017) revealed that nanoceria increase photosynthesis and ROS scavenging in *Arabidopsis thaliana* (L.) Heynh. when exposed to high levels of light (2000 mol m^{-2} s^{-1} for 1.5 h), heat (35 °C for 2.5 h), and dark chilling (4 °C for 5 days). Non-endocytic mechanisms transfer PNC into chloroplasts. PNC with a low Ce^{3+}/Ce^{4+} ratio (35%) lowers leaf ROS levels by 52%, including hydroxyl radicals, superoxide anion, and hydrogen peroxide. When plants with PNC were subjected to abiotic stress, they showed an increase in RuBisCo carboxylation (61%), carbon absorption (67%), and quantum yield (19%) of PS II over plants without NPs. However, PNC with a high $Ce3^{+}/Ce^{4+}$ ratio (60.8%) increase leaf ROS levels and do not protect photosynthesis from oxidative damage during abiotic stress. Li et al. (2018) explores the interactions of silver NPs (Ag NPs) and diclofop-methyl (DM) on the antioxidant system, photosynthesis, and physiological morphology of *Arabidopsis thaliana* (L.) Heynh. Treatment with Ag NPs (0.5 mg L^{-1}), on the other hand, was shown to severely limit chlorophyll production and plant development, as well as induce more severe oxidative damage in plants than the effects reported in a hydroponic solution containing both Ag NPs and DM. Meanwhile, relative transcript levels of photosynthesis-related genes (*pgrl1B, pgrl1A, rbcL,* and *psbA*) in the combined group were found to be somewhat higher than transcript levels in the Ag NPs group, to sustain ATP production at normal levels to heal light damage. Wang et al. (2018) investigate the effects of carbon dots (CDs) on photosynthesis and plant growth of mung bean. A dose–response impact was observed on biomass stem elongation, root elongation, and mung bean sprout growth. CDs at optimum levels also improve the seed moisture levels and root vitality which may have aided plant development and growth. Furthermore, mung bean sprouts treated with CDs had a rise in carbohydrates content (21.9%) as compared to the control condition. They postulated that the rise in carbohydrates was due to the involvement of CDs in photosynthesis. Further research demonstrated that CDs could improve photosystem activity by increasing the transfer of electrons. Other important photosynthetic parameters, including RuBisCo activity and chlorophyll concentration, are similarly affected by CDs treatment. These results hold a lot of potential for agricultural productivity and biological study. Yanık and Vardar (2018) evaluated the impact of aluminium oxide NPs (Al_2O_3 NPs) on wheat (*Triticum aestivum* L. cv Demir 2000) in which wheat roots were treated to varying concentrations of Al_2O_3 NPs (5, 25, and 50 mg mL^{-1}) for 96 h. The impacts of Al_2O_3 NPs were investigated using a variety of metrics, including anthocyanin content, photosynthetic pigment, total proline, lipid peroxidation, catalase, and superoxide dismutase activity, and H_2O_2 concentration. In comparison to the control, Al_2O_3 NPs induced a dose-dependent reduction in catalase activity while increasing proline content, lipid peroxidation, superoxide dismutase activity, and H_2O_2 content. Furthermore, at the dosage of 50 mg mL^{-1}, anthocyanin, carotenoids, chlorophyll a, and total chlorophyll content decreased. Finally, after 96 h, Al_2O_3 NPs triggered oxidative stress in wheat. Similarly, Ali et al. (2019) studied the effects of silicon NPs (Si NPs) on wheat (*Triticum aestivum* L.) growth under heavy metal stress of cadmium as well as cadmium (Cd) accumulation in grains. The results revealed that Si NPs considerably enhanced, compared to the control, the dry biomass grains (27–74%), spike (25–69%), roots (11–49%), and shoots (10–51%) in soil-applied and by 31–96%, 34–87%, 14–59%, and 24–69% in foliar spray Si NPs, correspondingly. Si NPs improved leaf gas exchange characteristics and chlorophyll *a* and *b* concentrations while decreasing oxidative stress in leaves as evidenced by increased peroxidase and superoxide dismutase abilities and reduced electrolyte leakage in leaf under Si NPs treatments over control. As compared with the control, the soil-applied Si NPs reduced the Cd concentrations in grains roots, shoots, and by 22–83%, 10–59%, and 11–53%, respectively, whereas the foliar spray of Si NPs reduced the Cd contents in grains, roots, and shoots by 20–82%, 19–64%, and

16–58%, correspondingly. Si concentrations in shoots as well as roots, rose considerably after foliar and soil Si NP treatment over control. Their findings revealed that Si NPs might increase wheat output but also lower Cd contents in grains. Dias et al. (2019) examine the impact of titanium dioxide NPs (TiO_2 NPs) on photosynthesis in wheat (*Triticum aestivum* L.). The results exhibited a reduction in both the light-independent and light-dependent phases of photosynthesis, as well as a decrease in chlorophyll *a* content, the maximum and effective efficiency of photosystem II, starch content, intercellular CO_2 concentration, stomatal conductance, transpiration rate, and net photosynthetic rate. However, no changes in RuBisCo activity, non-photochemical, and photochemical quenching levels, or total soluble sugar content were reported. Their findings support the hypothesis that induced degradation in chlorophyll *a* concentration hampered electron transport through photosystem II and that stomatal constraint hampered CO_2 uptake. The decrease in starch concentration appears to be a result of its breakdown as a method to keep total soluble sugar levels stable. As a result, it was claimed that photosynthetic-related endpoints are sensitive and relevant biomarkers for determining TiO_2 NP cytotoxicity. Soleymanzadeh et al. (2020) explored the impact of selenium NPs (Se NPs) (10 and 100 μM) on phenylpropanoids, antioxidant system, ion homeostasis, and photosynthetic efficiency in strawberry (*Fragaria* × *ananassa* Duch. cv. 'Gaviota') subjected to salinity stress. Salinity caused a decrease in Ca and K contents and a rise in Na concentration, which were alleviated by the administration of Se NPs. Furthermore, the Se NPs application at 10 μM reduced the NaCl-induced lesion to PS II performance, which contributed to an enhancement in water-splitting complex function under salt stress. Exposure to Se NPs at a concentration of 100 μM caused mild stress, as measured by rises in lipid peroxidation rate and hydrogen peroxide. Under salinity conditions, the Se NPs 10 M treatment boosted the amount of phenylpropanoid derivatives (caffeic acid, catechin, and salicylic acid) and catalase activity while decreasing the content of oxidants. Consequently, using Se NPs at the appropriate concentration can be an efficient way to treat indications of salt stress by improving antioxidant apparatus, salicylic acid (a critical signaling defense hormone), photosynthesis, and ion hemostasis. Swift et al. (2020) investigate the uptake of carbon dots in *Triticum aestivum* L. 'Apogee' (dwarf bread wheat) enhances photosynthesis and boosts crop output, resulting in an 18% upsurge in grain production. The glucose-functionalization improves NPs absorption, photo-protection, and pigment synthesis, resulting in higher yields. This demonstrates the potential of a functional nanomaterial for enhancing photosynthesis as a means of increasing agricultural output. Elshoky et al. (2021) evaluate the effects of zinc oxide NPs (ZnO NPs) coated with a silicon shell (ZnO-Si NPs) and bare (ZnO NPs) on the growth of *Pisum sativum* L. under salt and physiological stress conditions. The experimental results showed that foliar spray with ZnO-Si NPs and 200 mg L^{-1} ZnO NPs did not affect the functions of both photosystems, membrane integrity, and stomata structure under physiological conditions, whereas 400 mg L^{-1} ZnO-Si NPs had a positive effect on the photochemistry of photosystem I and effective quantum yield of photosystem II. On the alternative, minimal phytotoxic effects were seen following spraying with 400 mg L^{-1} ZnO NPs, which was associated with an increase in non-photochemical quenching and promotion of the cyclic electron flow around the photosystem I. The findings also revealed that both types of NPs (except 400 mg L^{-1} ZnO NPs) reduce the deleterious effects of 100 mM NaCl on the membrane integrity, stomata closure, pigment content, and photochemistry of photosystems I and II. The protective effect was greater after spraying with ZnO-Si NPs than after spraying with ZnO NPs, which might be attributed to the existence of a Si covering shell. Faizan et al. (2021a) examines the impact of zinc oxide NPs (ZnO NPs) in the modulation of salt tolerance in tomato (*Lycopersicon esculentum* Mill.). Their findings revealed that foliar spraying ZnO NPs at different concentrations, namely 10, 50, and 100 mg L^{-1} in the presence or absence of NaCl (150 mM), significantly increased photosynthetic attributes, chlorophyll content, leaf area, biomass, root length, and shoot length of tomato. Furthermore, the use of ZnO NPs reduces the deleterious effects of salt stress on plant development and increases protein content as well as antioxidative enzyme activity such as catalase, superoxide dismutase, and peroxidase under salt stress. Finally, ZnO NPs have a vital function in the reduction of NaCl toxicity in tomato plants. As a result, ZnO NPs can be employed to improve tomato development and alleviate the negative effects of salt stress. Faizan et al. (2021b) investigates the effects of 50 mg L^{-1} zinc oxide NPs (ZnO NPs) on plant growth, photosynthetic activity, elemental status, and antioxidant activity in rice (*Oryza sativa* L.) under cadmium stress. However, under cadmium toxicity, rice plants fed with ZnO NPs showed significantly enhanced root dry weight (12.24%), shoot dry weight (23.07%), root fresh weight (30%), and shoot length (34%). Furthermore, the ZnO NPs treatment has beneficial impacts on photosynthesis. ZnO NPs also significantly reduced cadmium-induced increases in malondialdehyde and hydrogen peroxide contents. Biochemical and physiological analysis revealed that ZnO NPs increased the enzymatic activities of superoxide dismutase (59%), and catalase (52%) as well as proline (17%), all of which metabolize ROS; these increases corresponded to changes in malondialdehyde and hydrogen peroxide accretion after ZnO NPs implementation. Eventually, the application of ZnO NPs to rice leaves improves mineral nutrient content, antioxidant enzyme activity, protein content, photosynthesis, biomass, and reduces cadmium levels. This is mostly owing to the decreased oxidative damage using ZnO NPs. Rai-Kalal and Jajoo (2021) indicate that seed priming with zinc oxide NPs (ZnO NPs) has a substantial favorable influence on seed vigor index and germination performance in wheat cultivar H-I 1544 when compared to hydroprimed and unprimed (control) seeds. Furthermore, nanopriming increased seed water intake, which resulted in increased α-amylase activity. The concentration of photosynthetic pigments (total chlorophyll, chlorophyll b, and chlorophyll a content) in nanoprimed plants was dramatically increased. A significant drop in the activity of superoxide dismutase, catalase, peroxidase, and the degree of lipid peroxidation was detected, which might be attributable to lower ROS levels in nanoprimed plants compared to controls. Rajput et al. (2021) evaluate the toxicity of zinc oxide NPs (ZnO NPs) on spring barley anatomical and physiological indicators. ZnO NPs hindered development by changing chlorophyll fluorescence emissions and producing trichome and stomatal morphological deformations, modifications to cellular structures, particularly abnormalities in the chloroplasts, and disruptions to the thylakoid and grana organizations. The number of chloroplasts per cell in barley leaf cells treated with ZnO NPs was lower as compared to control. Zn content buildup in plant tissues caused by ZnO NPs was demonstrated to diminish photosynthetic activity and impair the structural organization of the photosynthetic machinery.

3.5 Conclusion and Prospects

There is a requirement for considerable enhancement in crop productivity to meet food scarcity. The nano-aided farming/agriculture has potential to circumvent food scarcity. NPs offer potential strategies towards the enhancement of plant photosynthesis, which in turn can increase crop productivity. This is supported by the fact that NPs can be exploited for transformation of near-infrared as well as UV into visible light. This is expected to cause enhanced harvesting of more electrons for plant photosynthesis, particularly in light inadequate conditions and, thereby enhancing photosynthetic performance. However, it is yet to be completely exploited. Metallic NPs often reduce the rate of photosynthesis by causing oxidative stress inside the chloroplast. A non-metallic nanoparticle increases photosynthesis by increasing the rate of electron transport inside the chloroplast and provides a defense system against oxidative stress. Considering this, there is need to carefully design/engineer NPs that may lead to a generation of more effective NPs with positive impacts on plant photosynthetic performance. In addition, more research is required to investigate the process of operation of NPs, their interactions with biological molecules, and their influence on regulating the expression in plant species. In addition, there are new concerns that arise to address the biological consequences of NPs to fill the significant gaps in research of NPs phytotoxicity and many unsolved problems. Based on these considerations, it is critical to establish both the deleterious and beneficial effects of NPs on photosynthetic activities in plant species. Plant resistance to abiotic stress is improved by NPs, although the processes underlying this response are still not fully known. More research at the molecular level is required to comprehend the role and importance of NPs at the subcellular level.

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