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Plant nanobiotechnology: a new strategy to enhance crop photosynthesis

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In crops, photosynthesis is the basis of biomass accumulation and yield formation. With the ever-increasing global population and the increased need to meet the food demand, the ability to increase crop yield has become a pressing concern, especially considering that crop production has been threatened by increased biotic and abiotic stress. Previous studies have evaluated photosynthetic system structure and population photosynthesis based on agronomic and molecular biology. However, these methods require a long study period and a high cost. Therefore, identifying a fast, simple, and cheap strategy to improve plant photosynthesis is crucial for future crop production. Plant nanobiotechnology, as a new interdisciplinary field, provides remarkable insight into plant stress tolerance, chemical delivery, and transgenes. In this review, to provide new insights for future plant nanobiotechnological studies, we examine previous studies on photosynthesis and enhancing photosynthesis through plant nanobiotechnology and suggest possible strategies for increasing photosynthesis.

Environmental significance

Improving crop photosynthesis has been considered as one of the most promising approaches to further enhance crop yield in the future. As a new interdisciplinary field, plant nanobiotechnology provides remarkable insight into plant stress tolerance, chemical delivery, and transgenes. In this review, to provide new insights for future plant nanobiotechnological studies, we first reviewed previous studies on photosynthesis and enhancing photosynthesis through plant nanobiotechnology, and then suggest possible strategies for improving photosynthesis through nanobiotechnology in the future.

1. Introduction

Recently, climate change has significantly impacted agricultural production, negatively affecting nitrogen fertilizer utilization efficiency, disease resistance, carbon sequestration, and crop yield. To meet the food demand by 2050, crop yield needs to increase by 60–110% compared to 2005.[1] Therefore, improving crop yield per area is necessary to ensure food security, especially considering the ever-increasing global population and the decrease in agricultural land due to urbanization and soil degradation.

According to Monteith,[2] crop yield is dependent on the total incident solar radiation, light interception efficiency, light conversion efficiency, and partitioning efficiency during the growing season of crops. Due to the benefits of variety breeding and improved cultivation technologies, light interception efficiency and partitioning efficiency have significantly increased, nearing their theoretical maximum values of 0.9 and 0.6, respectively; however, there are still opportunities to improve light conversion efficiency.[3] Furthermore, Zhu *et al.*[3] found that when exposed to elevated CO_2 conditions, the augmented soybean yield was primarily attributed to increased light conversion efficiency, independent of both light interception efficiency and partitioning efficiency. Therefore, improving photosynthesis is a promising approach for further increasing crop yield.[4]

In recent years, plant nanobiotechnology has received increasing attention. Since Richard Feynman proposed the concept of using nanotechnology to control matter at the atomic level, it has made significant progress in medicine and industry. As for agronomy, nanotechnology applications are still in their infancy. To meet agricultural production and research

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demands, researchers have developed many multifunctional nanomaterials, including nano-fertilizers, nano-pesticides, nano-sensors, and nano-enzymes. Due to their small size and large surface area, nanomaterials have unique properties. For example, cerium oxide nanoparticles, which have both Ce^{3+} and Ce^{4+} valences on their surfaces and unpaired electrons, have great catalytic activity with reactive oxygen species (ROS) and have been reported to improve salt tolerance in cotton and *Arabidopsis*.[5,6] Similar nanomaterials, including CuO and Mn_3O_4, have been applied in rice and cucumbers.[7,8]

Although many studies have reviewed possible approaches for improving photosynthesis, none have considered the application of nanobiotechnology in enhancing plant photosynthesis.[9–19] In this review, we introduce the advances made in previous studies that attempted to improve photosynthesis, summarize recent findings, and explore future opportunities for enhancing photosynthesis through nanobiotechnology.

2. Approaches to improving photosynthesis

2.1. Leaf CO_2 diffusion

Carbon dioxide (CO_2) is a carbon resource for photosynthesis. After reaching the leaf surface, CO_2 must overcome the resistance imposed by stomata before entry into mesophyll cells, and reciprocal resistance is usually termed stomatal conductance (g_s).[20] Due to the critical role of stomata in controlling CO_2 and H_2O exchange between the internal leaf and the air surrounding the leaf, g_s plays an important role in leaf light and water use efficiency and is co-determined by stomatal anatomy and aperture.[21–23] In the last decade, increasing attention has been given to the genetic control of stomatal development and its effects on leaf photosynthesis and water use efficiency. For example, the overexpression of secreted epidermal patterning factor (EPF) peptides, including EPF1 and EPF2, or stomatal density and distribution 1 (SOD1) has been shown to decrease stomatal density in several crops, including rice, barley, tomato, and maize.[24,25] Tanaka *et al.*[26] demonstrated that overexpressing STOMAGEN, a positive regulator of stomatal development, increased stomatal density, g_s, and A in *Arabidopsis thaliana*; however, the enhancement of A did not translate into higher plant biomass, probably due to other factors such as increased water loss through increased stomatal density.

In addition to stomatal anatomy, stomatal aperture under light is co-determined by blue light receptors, plasma membrane H^+-ATPases, and K^+ influx channels, among which the activated plasma membrane H^+-ATPases, induced by blue light, are required for stomatal opening because K^+ uptake through K^+ influx channels is dependent on plasma membrane hyperpolarization.[27] By overexpressing H^+-ATPase in guard cells in *Arabidopsis thaliana*, Wang *et al.*[27] found that compared to wild-type plants, transgenic plants had a wider stomatal aperture and higher g_s and A when exposed to high light conditions. Additionally, they observed that biomass accumulation significantly increased in transgenic plants compared to wild-type plants. Consistent with Wang *et al.*,[27] Zhang *et al.*[28] found that *OSA1* (*Oryza sativa* plasma membrane H^+-ATPase 1) overexpression resulted in increased g_s, A, and grain yield in rice plants. Kusumi *et al.*[29] found that slow anion channel 1 (*slac1*) mutants in rice resulted in increased g_s and A, which might be associated with obstructed anion outflow from the cytoplasm to the apoplast and, thus, a high level of hyperpolarization of the plasma membrane. These results suggest that manipulating stomatal development, plasma membrane H^+-ATPases, and/or ion channels is effective in improving g_s, and thus also in improving A. Another important factor in improving stomatal aperture is plant hydraulic conductance, which refers to the plant water transport capacity.[30] Numerous studies have confirmed the existence of positive relationships between plant hydraulic conductance and g_s and A in crops such as rice.[30,31] For example, Huang *et al.*[31] demonstrated that leaf hydraulic conductance was more significant than stomatal anatomy in determining g_s among different rice genotypes, indicating that plant hydraulic conductance plays a crucial role in stomatal opening in crops. This warrants further research to optimize plant hydraulic system for improving g_s and A in the future.

In addition to g_s, mesophyll conductance (g_m) is defined as the CO_2 diffusional capacity from substomatal cavities to carboxylation sites within the chloroplast. Similar to g_s, g_m is also a major limiting factor to photosynthesis in C_3 plants.[32] Previous studies have confirmed that the chloroplast surface area facing intercellular airspace (S_c) and cell wall thickness (T_{cw}) are the two most important leaf anatomical traits determining g_m, and larger S_c or lower T_{cw} is usually associated with a higher g_m.[31–34] Additionally, g_m is also tightly regulated by biochemical processes, such as the expression level and activity of aquaporin and carbonic anhydrase.[19,35,36]

Due to the vital role of S_c in determining g_m, some studies have investigated the improvement of g_m and A by manipulating mesophyll cell development. In a previous review, Ren *et al.*[37] suggested that an appropriate decrease in mesophyll cell size could contribute to a larger S_c and, thus, a higher g_m and leaf photosynthetic capacity without increasing the leaf thickness. Consistent with Ren *et al.*,[37] by manipulating cell cycle gene expression in *Arabidopsis* leaves, Lehmeier *et al.*[38] found that palisade cell density had a positive relationship with g_m among wild-type and transgenic plants. Further investigation indicated that increased g_m in transgenic plants was associated with a higher density network of shorter, smaller diameter air channels that are less connected in the palisade layer.[38] These results suggest that mesophyll cell development manipulation is a promising approach for maximizing g_m and leaf photosynthesis.

Compared with the manipulation of mesophyll cell development, the impacts of aquaporins on g_m have been thoroughly investigated between wild-type and aquaporin-overexpressing and knockout plants.[39–41] Since Uehlein *et al.*[42] reported the important role of aquaporins in controlling CO_2 transport across cell membranes, numerous studies have focused on the possible roles of aquaporins in regulating CO_2 transport and g_m.[35,39,41] For example, by overexpressing and silencing *NtAQP1* in tobacco, Flexas *et al.*[39] demonstrated that CO_2 transport at the leaf level was affected by aquaporins. Similar results have also been reported in other studies.[35] Furthermore, Xu *et al.*[41] found that rice aquaporin *OsPIP1;2* overexpression could lead to enhanced g_m, A, and grain yield in rice plants, suggesting that aquaporin overexpression is a feasible approach to further increase g_m and A in crops.

Although many studies have suggested that g_m is negatively correlated with T_{cw},[31,33,34] no study has attempted to improve g_m by decreasing T_{cw} in crops. Previous studies have shown that the T_{cw} of crops is almost the lowest in terrestrial plants.[34,43] Recently, studies have begun to examine the impacts of cell wall composition on g_m, and mixed results have been obtained depending on the species used and the experimental conditions.[44] For instance, Ellsworth *et al.*[45] found that compared to wild-type rice, g_m and A significantly decreased in rice mutants with obstructions in cell wall mixed-linkage glucan synthesis, suggesting that cell wall composition plays a vital role in determining g_m. More recently, Salesse-Smith *et al.*[46] found that tobacco plants overexpressing *AtCGR3* (*Arabidopsis* Cotton Golgi-related 3) showed increased g_m and A under field conditions, which was caused by the increased cell wall porosity and decreased cell wall thickness. Unfortunately, to date, no studies have reported the positive effects of manipulating cell wall composition on g_m and A in cereal crops, which merits further research.

2.2. Rubisco characteristics

As the most abundant protein on Earth, Rubisco is a bifunctional enzyme that can either catalyze RuBP with CO_2 to produce 3-phosphoglycerate or catalyze RuBP with O_2 to synthesize toxic 2-phosphoglycolate. Moreover, Rubisco plays a central role in the Calvin cycle and leaf photosynthesis.[47] To protect plants from 2-phosphoglycolate, 2-phosphoglycolate needs to be promptly metabolized at the expense of releasing CO_2 and consuming ATP for NH_3 re-assimilation, which is called photorespiration.[48] Previous studies have suggested that the CO_2 concentration inside the chloroplast and the relative specificity of Rubisco for CO_2 over O_2 ($S_{c/o}$) are the main factors influencing photorespiration.[49] Therefore, Rubisco activity and $S_{c/o}$ are promising targets for enhancing A in crops.

Before participating in the CO_2 reduction reaction, the catalytic sites of Rubisco should be free from the inactivated state resulting from inhibitors, such as 2-carboxy-D-arabinitol 1-phosphate and xylulose-1,5-bisphosphate, which are highly dependent on Rubisco activase (RCA).[47] Yamori *et al.*[50] found no significant difference in A between transgenic rice overexpressing maize RCA and the wild-type rice when the leaf temperature was <25 °C; however, overexpressing transgenic rice showed a higher A than wild-type rice when the leaf temperature increased to 40 °C. This suggests that, at normal temperatures, Rubisco activity may not be a significant limiting factor to A in rice. However, at high temperatures, improving Rubisco activity is a promising approach to increasing A in rice. Similarly, Kumar *et al.*[51] found that the expression of thermostable chimeric RCA in *Arabidopsis thaliana* contributed to a higher A, larger biomass, and higher seed yield at moderately high temperatures. Therefore, RCA manipulation can be beneficial in improving A, especially under high temperatures.

Another potential target for Rubisco to enhance A is $S_{c/o}$, which is dominated by the inherent characteristics of Rubisco. By surveying Rubisco catalytic properties among 25 genotypes in the triticeae family, including wild relatives of bread wheat at 25 and 35 °C, Prins *et al.*[52] found variations in Rubisco's catalytic properties among closely related genotypes and concluded that this variation could be further explored to improve wheat photosynthesis. Moreover, by modeling the response of photosynthesis to varying CO_2 concentrations, Prins *et al.*[52] suggested that photosynthesis could be increased in wheat by replacing superior Rubisco enzymes at 25 and 35 °C. Similarly, Sharwood *et al.*[53] demonstrated significant variability in Rubisco characteristics among different C_3, C_3–C_4 intermediate, and C_4 species and found that the CO_2 fixation rate was lower in Rubisco from nicotinamide adenine dinucleotide malic enzyme (NAD-ME) species than in adenine dinucleotide phosphate malic enzyme (NADP-ME) and phosphoenolpyruvate carboxykinase (PCK) species. Additionally, the reduction in $S_{c/o}$ with temperature occurred more quickly in NAD-ME species than in NADP-ME and PCK species.[53] These results suggest that the manipulation of Rubisco's characteristics is a promising target for further improving crop photosynthesis. Sharwood *et al.*[53] suggested that amino acid substitutions in the large subunit of Rubisco account for the observed catalytic variation in Rubisco, which deserves further attention. However, the results of Prins *et al.*[52] and Sharwood *et al.*[53] showed inherent negative relationships between Rubisco's catalytic rate and $S_{c/o}$, which could somewhat impede the improvement of Rubisco.

2.3. Light capture and transport

Light is the energy source for the normal operation of all photosynthetic autotrophic organs; therefore, light capture and transport play essential roles in regulating plant photosynthesis. Plants can only use light at wavelengths ranging from 400 to 700 nm, and more than half of the light intercepted by plants is reflected, transmitted, or wasted, leading to relatively low light use efficiency.[3,54] Interestingly, it was reported that some cyanobacteria can use far-red light by synthesizing chlorophyll *f* pigments.[55] Therefore, if the cyanobacterial genes encoding chlorophyll *f* biosynthesis are inserted into crops, improvements in crop photosynthesis and yield should be expected. Recently, Zhen and Bugbee[56] investigated the effects of far-red light on leaf and canopy photosynthesis in diverse crop species and found that adding far-red photons (up to 40%), which was equal to adding 400–700 nm photons, to a background of shorter wavelength photons contributed to enhanced canopy photosynthesis. These results suggest that producing crops through biotechnology using a broader light spectrum that can be used by green organs is a feasible approach to improving crop photosynthesis.

Under natural conditions, the light that plants receive is constantly changing because of upper leaf shading, changes in the sun's incidence angle, and cloud movement. Therefore, leaves are frequently exposed to low-to-high and high-to-low light transitions, resulting in low light use efficiency. The slow relaxation of non-photochemical quenching (NPQ) from high-to-low light conditions leads to a considerable waste of electrons that could otherwise be used by photochemical quenching.[57] In a previous study, by overexpressing violaxanthin de-epoxidase, zeaxanthin epoxidase, and PSII subunit S in tobacco, Kromdijk *et al.*[57] found that compared to wild-type plants, transgenic plants showed increased quantum efficiency of PSII and lower NPQ under fluctuating light conditions, which resulted in a significantly increased biomass in transgenic plants under field conditions. However, when plants were grown under steady-state conditions, the advantages of transgenic plants disappeared,[57] suggesting that crop photosynthesis and yield could be further improved by manipulating NPQ under dynamic light conditions.

The sustained production of ATP and NADPH is a prerequisite for the operation of the Calvin cycle, in which ATP synthase and the cytochrome b_6/f complex play critical roles. Rott *et al.*[58] found that the ATP synthase content had positive relationships with ATP synthase activity and the leaf photosynthetic rate in tobacco. Similarly, Yamori *et al.*[59] demonstrated that the electron transport rate and leaf photosynthetic rate increased with increasing ATP synthase content and Rieske FeS content (an essential component of the cytochrome b_6/f complex), suggesting that ATP synthase and the cytochrome b_6/f complex are major limiting factors to electron transport and photosynthesis in crops. Besides, Yamori *et al.*[60] also found that an increase in the Rieske FeS content was associated with the improved electron transport rate in rice plants, which resulted in enhanced photosynthesis, growth, and yield. Therefore, overexpressing ATP synthase and the cytochrome b_6/f complex may be a promising approach for further increasing crop photosynthesis.

3. Plant nanobiotechnology provides new insights for enhancing photosynthesis

Although biological technologies can effectively enhance plant photosynthesis,[61,62] they require long-term promotion periods, have high costs, and provide limited universality. Therefore, a simple and cheap method for enhancing photosynthesis is meaningful for increasing crop yield. As an emerging interdisciplinary field, plant nanobiotechnology offers unique ideas for improving photosynthesis.

3.1. Nanomaterials enhance CO_2 absorption and concentration

As previously discussed, CO_2 carboxylation sites are deep within plant leaves, and CO_2 encounters several hindrances such as cell membranes and cell walls. Increasing the CO_2 concentration and transporting CO_2 to carboxylation sites can improve photosynthesis.

Engineered nano zero-valent iron induces *Arabidopsis thaliana* plasma membrane H^+-ATPase activation, and high H^+-ATPase activities decrease apoplastic pH and widen stomata.[63] By determining the stomatal relative gene expression levels, the expression level of *AHA2* was found to be 5-fold higher after nano zero-valent iron treatment than before.[63] Alidoust and Isoda[64] found similar results, showing that Fe_2O_3 nanoparticle-treated soybean leaves had a wider stomatal aperture and stronger photosynthesis. Li *et al.*[65] applied carbon dots to crops and enhanced crop photosynthesis. Horseradish peroxidase and H_2O_2 can degrade carbon dots to CO_2 and hormone analogs, thereby increasing the CO_2 concentration and improving photosynthesis.[66,67] A similar function has also been reported by Huang *et al.*,[68] who found that applying ^{14}C-labeled graphene to plants increased the CO_2 concentration within the leaf. Graphene has also been reported to improve plant resilience and photosynthesis. For example, it enhances photosynthesis and the antioxidative defense system while alleviating salinity and alkalinity stresses in alfalfa (*Medicago sativa* L.) by regulating gene expression. C_4 crops, such as maize, assimilate CO_2 more efficiently than C_3 crops. Based on the mechanism by which C_4 crops assimilate CO_2, a method to absorb and release intercellular CO_2 has been developed. Li *et al.*[69] have selected metal–organic frameworks as the CO_2 concentrate materials and applied them to microalgae; metal–organic frameworks located at the microalgae membrane absorb CO_2. Microalgae excrete carbonic anhydrase and then bond with CO_2 from the metal–organic framework; the final product is bicarbonate. Furthermore, Li *et al.*[69] reported a metal–organic framework with the function of enhancing Rubisco activity. With metal–organic framework treatment, microalgae showed a 1.9-fold improvement in photosynthesis compared to those without metal–organic framework treatment.[69]

3.2. Nanomaterials enhance Rubisco's activities and pigment amount

Rubisco activity is positively correlated with photosynthetic rate, and enhancing Rubisco activity is a crucial pathway for improving photosynthesis. Gao *et al.*[70] found that engineered TiO_2 nanoparticles not only acted in light harvesting and electric transfer but also enhanced Rubisco activity and amount, and TiO_2 nanoparticle-treated *Spinacia oleracea* plants presented a 42% increase in Rubisco and a 2.5-fold increase in activity. Purified Rubisco was used to study the effect of TiO_2 nanoparticles on its secondary structure. After being treated with TiO_2 nanoparticles, *Spinacia oleracea* Rubisco's secondary structure showed increased α-helix, β-sheet, and β-turn content, while the random coil content was markedly decreased.[70] Similarly, Fe nanoparticles also enhanced the Rubisco content and promoted substantial seed growth in crops.[71] Li *et al.*[66,67] investigated the mechanisms by which carbon dots improve crop photosynthesis, and after treatment with carbon dots, rice, *Trifolium repens* L., and *Arabidopsis thaliana* plants exhibited higher Rubisco activity.

In cucumber, Song *et al.*[72] reported that TiO_2 could increase the total content of chlorophyll, an essential light harvest pigment in the chloroplast. A similar result was observed in tomatoes, where chlorophyll content increased in tomato leaves treated with cubic TiO_2 and hexagonal ZnO nanoparticles.[73] Foliar-sprayed mesoporous SiO_2 has been shown to increase the chlorophyll content in wheat,[74] and similar results have been reported in soybeans.[75,76] In another study, Pradhan *et al.*[77] found that *Vigna radiata* plants treated with square-shaped manganese nanoparticles had higher photosynthetic rates, water splitting, and photophosphorylation compared to a control.

3.3. Nanomaterials enhance light harvesting

The solar energy that Earth receives can be divided into three parts: ultraviolet, visible, and infrared light. Plants can only use visible light, which comprises 52% of solar energy, but they cannot use ultraviolet or infrared light.[78] Specifically, plants cannot use green light with 30% visible energy.[79] Plants can absorb up to 90% of the wavelength but transmit over half of the total energy.[80,81] Semiconductor quantum dots (SQDs) are particles with sizes ranging from 1 to 100 nm, and appropriately energetic photons can cause their excitation. After absorbing photons, electrons are excited from the valence band into the conduction band, forming a positively charged hole. The coupled excited electron–hole pair then relaxes back to the valence state and emission of a red-shifted photon, resulting in the fluorescence observed in SQDs. In some cases, photoexcited electrons escape and are transferred to another acceptor, such as redox-like enzymes.[82] Compared with enzymes in cells, SQDs have more stable properties and can be excited over a wider wavelength range. SQDs can be excited by light wavelengths ranging from ultraviolet to infrared and emission electromagnetic radiation.[65] Their small size indicates that they can access the cell wall and bond with organics to act as a more efficient antenna for harvesting light. Excited electrons or emission photosynthesis-available wavelength light can then transmit efficiently to the photosynthesis electron transfer chain.[83] With technological advancements, there is an opportunity to combine engineered nanomaterials with natural photosynthesis systems to enhance the photosynthesis rate, which may be better than that of natural and artificial systems alone.

Studies on the interaction between plants and nanomaterials have shown that using fluorescent nanomaterials to convert infrared and ultraviolet light into red and blue light can effectively strengthen the intensity of photosynthesis.[65] In 2010, Nabiev *et al.*[84] used quantum dots as antennas to improve light harvesting and transmit more energy to reaction centers, thus increasing plant photosynthesis.[84] Similarly, Li *et al.*[65] suggested that synthesized dual-emission carbon dots that emit red and blue light with ultraviolet excitation could enhance photosynthesis. Using isolated chloroplasts and dichlorophenol–indophenol experiments, Li *et al.*[65] verified that dual-emission carbon dots improved the electron transfer efficiency of isolated chloroplasts. Other researchers have doped up-conversion materials into carbon dots using the anti-Stokes shift to convert infrared light into red and blue light. Xu *et al.*[85] found that applying these materials to soybean root systems effectively improved the photosynthesis rate. Jiang *et al.* used UCNP and CD doping to achieve multi-band light energy conversion and utilization.[86] The researchers incorporated UCNP@CDs into films to improve photosynthesis in both isolated chloroplasts and living plants. The treated *Arabidopsis thaliana* exhibited a 12% increase in photosynthesis by integrating photon up- and down-conversion to produce efficient light-harvesting materials. These findings provide new perspectives on the use of nanomaterials to enhance plant photosynthesis.

3.4. Nanomaterials enhance photosynthetic electron transfer

Using nanomaterials to enhance photosynthetic electron transfer efficiency is another pathway for improving photosynthesis. There are two energy conversion processes in photosynthesis: optical conversion to electric energy and electric conversion to chemical energy.[54] In the previous section, some studies were presented on nanomaterials that help plants harvest more available light using the process of optical conversion to electric energy. However, after photosynthetic pigments absorb photons, electric power is transported through a series of photosynthetic electron transfer proteins accompanied by H_2O photolysis and O_2 generation. The photosynthetic rate depends on the electron transport efficiency in the photosynthetic electron transport chain, and improving electron transport efficiency can effectively enhance photosynthesis.

Chandra *et al.*[87] synthesized semiconductor carbon dots using ascorbic acid as a raw material in a one-step hydrothermal method and functionalized carbon dots using 2,2-(ethylenedioxy) bis(e-thylamine) to obtain better biocompatibility and water solubility. The synthesized carbon quantum dots efficiently enter plant cells, localize in chloroplasts, and generate strong conjugation. Carbon dots functionalized using 2,2-(ethylenedioxy) bis(e-thylamine) absorb light energy and convert it into electric energy, efficiently transferring electrons to the photosynthetic electron transport chain. Accepted electron transfer affects the photosynthetic electron transport chain and induces more robust photosynthesis.[87] A study on the conjugation effect have evaluated the interaction between nanomaterials and plants, including the use of nanosensors.[88] The mechanism by which nanomaterials conjugate with plants and enhance energy transfer

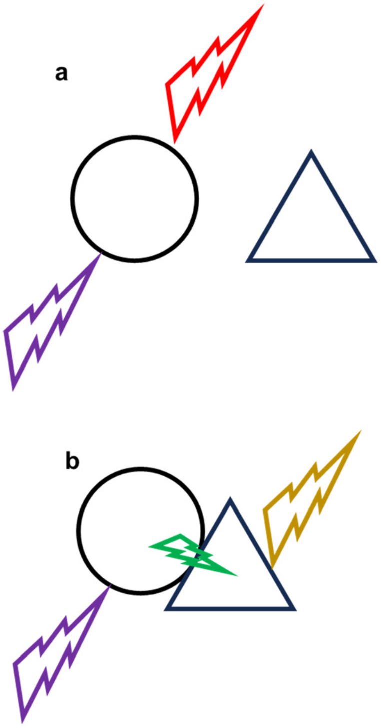

Fig. 1 Förster resonance energy transfer diagram. a. No Förster resonance energy transfer. When the distance is >1/2 Förster distance, the fluorescent substrate (circular) absorbs violet light and emits red light, while the triangular substrate does not emit fluorescence. b. Förster resonance energy transfer. When the two substrates are combined, the complex can absorb violet light, and the emitted light changes as a result of energy transfer.

is based on electric behavior. Specifically, the donor is engineered to bond with the receptor (<0.5 Foster distance) and has match excitation (receptor) and emission (donor) spectra (Fig. 1); the energy transfers from donor to receptor, accompanied by electric energy, with minimal energy loss. It is evident that engineered nanomaterials enhance photosynthesis through surface plasmon resonance.[89–91] Sharma and Kar[92] reported that gold nanoparticles could be conjugated with aspartate, citrate, and bovine serum albumin in *Vigna radiata*, exhibiting an enhanced photosynthetic rate. Conjugated gold nanoparticles not only enhance the electric transfer rate but also cause stronger photophosphorylation and oxygen evolution.[92] Similar results were found by Li *et al.*[65] and Giraldo *et al.*[93] In these studies, carbon dots and single-wall carbon nanotubes were used to enhance photosynthetic electron transfer efficiency, thus improving the plant photosynthetic rate.[65,93]

4. Conclusion and prospects

The main limiting factors for improving photosynthesis are limited light energy capture and carbon dioxide fixation. Although cultivation and molecular breeding can improve photosynthesis to a certain extent, there is a theoretical upper limit, and the transformation period is longer. Plant nanobiology provides new ideas for the continuous improvement of photosynthesis, as summarized in Fig. 2. In this review, we discuss existing research on the use of plant nanobiotechnologies for enhancing photosynthesis, including light energy conversion, increasing Rubisco activity, and delivering CO_2 donors (Table 1). However, the continuous improvement of photosynthesis can not only widen the available light range and increase the intercellular

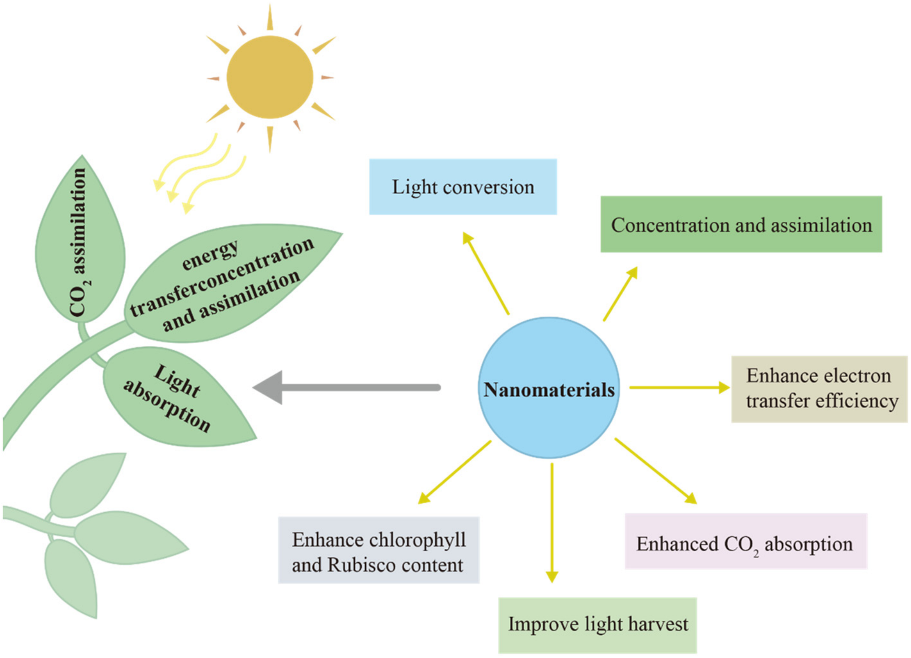

Fig. 2 Primary mechanism through which nanomaterials enhance plant photosynthesis.

Table 1 Impacts of nanomaterials on photosynthesis summarized from published studies

Nanomaterials	Mechanisms	Ref.
	Improvement of light energy capture	
Carbon dots	Excited by ultraviolet and emission red/blue light	Li *et al.*, 2021 (ref. 65)
Quantum dots	As antennas to improve light harvesting and transmit more energy to reaction centers	Nabiev *et al.*, 2010 (ref. 84)
Up-conversion materials	Convert infrared light into red and blue light	Xu *et al.*, 2022 (ref. 85)
	Improvement of electron transport	
Carbon dots	Absorb light energy and convert it into electric energy	Chandra *et al.*, 2014 (ref. 87)
Gold nanoparticles	Conjugated with aspartate, citrate, and bovine serum albumin in *Vigna radiata*	Sharma and Kar, 2019 (ref. 92)
Single-wall carbon nanotubes	Enhance photosynthetic electron transfer efficiency	Giraldo *et al.*, 2014 (ref. 93)
TiO_2 nanoparticles	Enhance light harvesting and electric transfer; increase Rubisco's secondary structure to present more α-helix, β-sheet, and β-turn content; and decrease the random coil contents	Gao *et al.*, 2006 (ref. 70)
	Enhancement of enzyme and pigment activity/content	
Fe nanoparticles	Enhance Rubisco content	Feng *et al.*, 2022 (ref. 71)
Carbon dots	Enhance Rubisco activity	Li *et al.*, 2018, 2019 (ref. 66 and 67)
TiO_2 nanoparticles	Increase cucumber total chlorophyll content	Song *et al.*, 2020 (ref. 72)
Cubic TiO_2 and hexagonal ZnO nanoparticle	Increase chlorophyll content	Raliya *et al.*, 2015 (ref. 73)
Mesoporous SiO_2	Increase chlorophyll content	Ayman *et al.*, 2020 (ref. 74)
Cerium oxide nanoparticles	Increase chlorophyll content	Cao *et al.*, 2017 (ref. 75)
Fe-based nanomaterial	Increase chlorophyll content	Wang *et al.*, 2022 (ref. 76)
	Enhancement of CO_2 concentration inside leaves	
Nano zero-valent iron	Widen stomata	Kim *et al.*, 2015 (ref. 63)
Fe_2O_3 nanoparticle	Widen stomata	Alidoust and Isoda, 2013 (ref. 64)
Carbon dots	Degraded to CO_2 and hormone analogs	Li *et al.*, 2018, 2019 (ref. 66 and 67)
Graphene	Increase the CO_2 concentration	Huang *et al.*, 2018 (ref. 68)
Metal–organic frameworks	Concentrate CO_2	Li *et al.*, 2023 (ref. 69)

CO_2 concentration but also prolong the light duration and regulate stomatal opening and closing.

In theory, nanomaterials with light conversion capabilities, CO_2 concentration capabilities, and the ability to decompose into raw materials for photosynthesis have the potential to improve plant photosynthesis. However, many of these materials have been ignored. This is often because laboratory attempts to use nanomaterials to improve photosynthesis have shown only minimal differences. At the same time, the lengthy experimental period may also contribute to the neglect of promising nanomaterials. Therefore, finding ways to quickly verify the biological effects of nanomaterials is important. Conventional methods involve measuring gas exchange rates and fresh weight accumulation in leaves, but these can be affected by respiration. Therefore, we propose that using *in vitro* chloroplasts to explore the effect of nanomaterials on plant photosynthesis might be more suitable.

In fact, engineered nanomaterials with the same core may also exhibit opposite effects. For example, CeO_2, a widely studied agricultural nanomaterial, improves drought resistance in sorghum when applied to roots,[94] but causes stomatal closure in rice when applied to leaves.[95] At the same time, engineered nanomaterials may accumulate in the fruit. A study on cucumber found that CeO_2-treated cucumber plants had Ce accumulation in the fruit and had poorer fruit quality.[96] The reasons for these completely opposite results may be related to the application method, the physical and chemical properties of the nanomaterials (such as particle size or surface functional groups and potential), and the crystal structure of the nanomaterial core.[97–99] Therefore, in the design and application of nanomaterials, we should take these factors into account to avoid unexpected effects.

Long afterglow material can continue to glow after excitation light stops, and its synthesis technology has matured. There have been studies on the implantation of long afterglow materials into the gap between plant leaves to form glowing plants. Therefore, there is the possibility of using long afterglow materials to store light energy and release it at night. Previous studies have shown that agricultural nanomaterials can regulate the inflow of K^+ in plant leaf cells through ROS signals, and K^+ is an important ion controlling stomatal opening and closing. Therefore, the use of agricultural nanomaterials to regulate K^+ inflow to promote stomatal opening and obtain greater stomatal conductance is a feasible scheme.

Traditional means of enhancing photosynthesis mainly focus on enhancing light utilization and improving CO_2 capture. However, research in plant nanobiology primarily concentrates on enhancing light utilization. Therefore, using nanomaterials to enhance plant CO_2 capture might be a feasible strategy. CO_2 can be compressed with CO_2-sensitive materials to increase the intercellular CO_2 concentration. Alternatively, the Rubisco enzyme can be modified to reduce its affinity for O_2 and enhance CO_2 assimilation. These strategies may provide new evidence for the interaction between nanomaterials and plants. In addition, we propose a possible way to prolong the light time and regulate stomatal opening and closing to improve plant photosynthesis.

Compared with traditional methods, using plant nanobiotechnology to improve the photosynthetic capacity of plants offers several advantages such as a shorter action period and quicker results. However, reducing the cost remains a significant challenge, including that for the synthesis, purification, conversion, application, and ecological assessment of agricultural nanomaterials, and the increase in photosynthetic capacity conferred by nanobiotechnologies may lead to higher costs. Therefore, further research is needed to address these cost issues and optimize the application of nanobiotechnology to improve plant photosynthesis.

Data availability

The datasets used or analyzed during the current study are available from the corresponding author on reasonable request.

Author contributions

JL: conceptualization, methodology, writing – draft. DZ: methodology, writing. YZ: validation. LB: software. TM: methodology. LZ: software. GH: methodology, writing – draft.

Conflicts of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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