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REVIEW ARTICLE

Effects of manufactured nanomaterials on algae: Implications and applications

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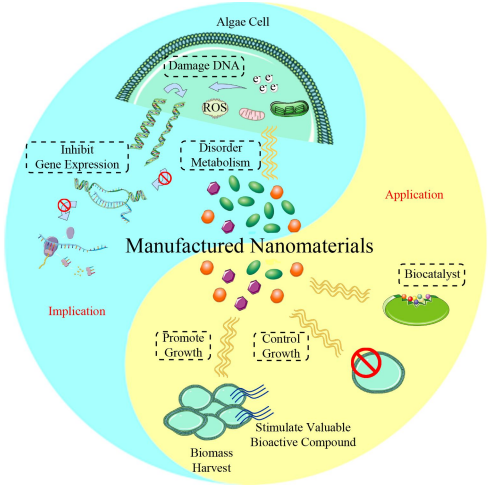
HIGHLIGHTS

- Summary of positive and negative effects of MNMs on algae.
- MNMs adversely affect algal gene expression, metabolite, and growth.
- MNMs induce oxidative stress, mechanical damage and light-shielding effects on algae.
- MNMs can promote production of bioactive substances and environmental remediation.

GRAPHIC ABSTRACT



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ABSTRACT

The wide application of manufactured nanomaterials (MNMs) has resulted in the inevitable release of MNMs into the aquatic environment along their life cycle. As the primary producer in aquatic ecosystems, algae play a critical role in maintaining the balance of ecosystems' energy flow, material circulation and information transmission. Thus, thoroughly understanding the biological effects of MNMs on algae as well as the underlying mechanisms is of vital importance. We conducted a comprehensive review on both positive and negative effects of MNMs on algae and thoroughly discussed the underlying mechanisms. In general, exposure to MNMs may adversely affect algae's gene expression, metabolites, photosynthesis, nitrogen fixation and growth rate. The major mechanisms of MNMs-induced inhibition are attributed to oxidative stress, mechanical damages, released metal ions and light-shielding effects. Meanwhile, the rational application of MNMs-algae interactions would promote valuable bioactive substances production as well as control biological and chemical pollutants. Our review could provide a better understanding of the biological effects of MNMs on algae and narrow the knowledge gaps on the underlying mechanisms. It would shed light on the investigation of environmental implications and applications of MNMs-algae interactions and meet the increasing demand for sustainable nanotechnology development.

1 Introduction

Manufactured nanomaterials (MNMs) refer to materials with a critical dimension of less than 100 nm on at least

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one geometric surface and high homogeneity, particularly manufactured products for application purposes, which are different from natural nanomaterials (e.g., protein molecules, viral particles, raw magnetite and ultrafine particles) (Lopez-Alonso et al., 2020). Based on the composition, MNMs can be divided into carbonaceous MNMs, metal/metal oxide MNMs, quantum dots and organic polymers (Haque and Ward, 2018). MNMs display unique physical and chemical properties at the nanoscale, such as high surface area, nanoscale size effects and quantum effects, etc. Given these unique properties, nanomaterials have been widely used in diverse applications, including agriculture, electronics, aerogels, aerospace, automotive, medicine, cosmetics and textiles (Zhang et al., 2020; Jiang et al., 2022). MNMs are estimated to be components of more than 2,000 commercial products, and this number is expected to grow significantly in the forthcoming years (Wang et al., 2021a). However, during the production, transportation, use and disposal of these products, MNMs are inevitably released into the environment (Keller et al., 2013).

The aquatic environment is the ultimate destination of almost all pollutants, including MNMs (Zhang et al., 2018a). MNMs can enter the aquatic environment through industrial wastewater, domestic sewage, and coastal recreation actives (e.g., swimming, diving) (Cedervall et al., 2012; Yue et al., 2017; Huang et al., 2021). In addition, MNMs are widely used to treat groundwater and other water bodies, which would be inevitably left in the water environment (Zhang and Elliott, 2006; Yang et al., 2021). Taking the global production of about 309000 tons of MNMs in 2010 as an example, it is estimated that 0.4%–7% of the nano-products eventually enter the water environment (Keller et al., 2013). The risk of MNMs to the aquatic ecosystem has been an increasing concern (Haque and Ward, 2018).

Algae is the primary producer in aquatic ecosystems, as it could produce oxygen for aquatic organisms via photosynthesis. In addition, algae are the key fundamental part of the food chain as they would generate organic carbon and biomass to supply as food sources for the aquatic ecosystems. Thus, the change of algal species composition and community structure would directly affect the aquatic ecosystems' energy flow, material circulation and information transmission, which plays an essential role in maintaining the balance of aquatic ecosystems (Rai et al., 2016; Li et al., 2020b; Grigoriev et al., 2021). Numerous studies have demonstrated that the exposure of MNMs induces adverse biological effects onto algae, which may further affect algae's gene expression, metabolism, photosynthesis, nitrogen fixation, and growth (Chen et al., 2019). Hence, investigations into the MNMs' effects on algae as well as the underlying mechanisms are critical in the ecological risk evaluation of MNMs. On the other hand, the biological interaction between MNMs and algae as well as the consequential effects may exhibit beneficial applications (e.g., hazard remediation(Guleri et al., 2020;Mohsenpour et al., 2021)), biomass production (Kartik et al., 2021), which has been overlooked in the previous reviews. Therefore, the current review aims to provide a full picture of the biological effects of MNMs on algae, including both negative implications and positive applications, which would provide a better understanding of mechanisms of MNMs' biological effects and help to meet the increasing demand in the sustainable development of nanotechnology.

2 Effects of MNMs on algae

MNMs would induce adverse biological effects onto algae, affecting algae's gene expression, metabolism, photosynthesis, nitrogen fixation, and growth.

2.1 MNMs affect algae's gene expression

MNMs induce biological effects onto algae's gene expression, particularly, the gene expression related to antioxidant synthesis, lipid synthesis, cell division and photosynthesis (Fig. 1). Middepogu et al. reported that nano-TiO_2 disrupted material and energy metabolisms in algal photosynthesis at the molecular level (Middepogu et al., 2018). The expression of genes related to lipid synthesis (*gdat*), carbohydrate synthesis (*cah2*) and cell division (*tdsH*) were all down-regulated, indicating that nano-TiO_2 suppressed the lipid and carbohydrate biosynthesis and cell division at the gene expression level. Similar results were reported in the *Chlorella pyrenoidosa*'s gene expression change to oxidized multi-walled carbon nanotubes (o-MWCNTs), as remarkable down-regulated were observed on the algal carbon fixation and photosynthesis-related genes (e.g., *CAH2* and *rbcL*) (Zhang et al., 2018b).

Furthermore, advances in "omics" technologies (e.g., transcriptomics, proteomics and metabolomics) facilitate the comprehensive analysis of stressor effects at subcellular levels (Lauritano et al., 2019; Balbi et al., 2021). Particularly, transcriptomics and proteomics could provide a better understanding of the stress effects and mechanisms of toxic action by analyzing the expression of genes and proteins within an organism. Pillai et al. investigated the effects of nano-Ag onto *Chlamydomonas reinhardtii* at the transcriptome and proteome levels, revealing an oxidative stress response at subcellular levels, even though no lipid peroxidation was observed at the biochemical level (Pillai et al., 2014).

2.2 MNMs affect algae's metabolism

As shown in Fig. 1, MNMs would affect the metabolic processes of algal cells by causing oxidative stress in algae, affecting the activity of enzymes involved in

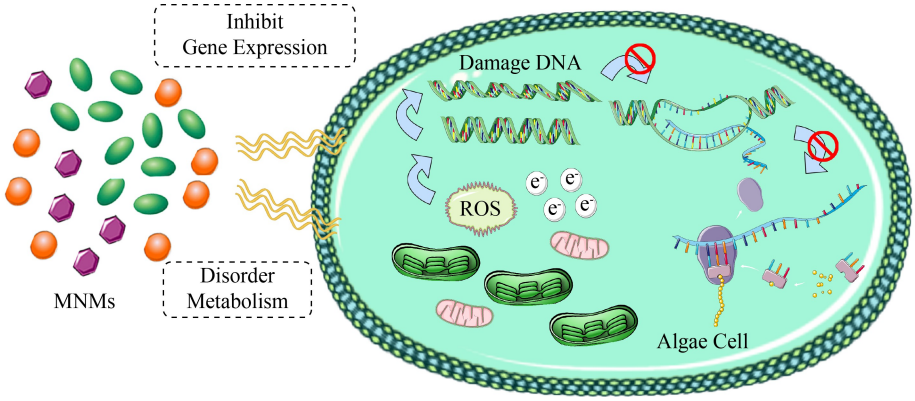

Fig. 1 MNMs affect algae's gene expression and metabolism.

metabolic processes, or affecting the expression of related genes, which would further induce the changes in levels or concentrations of macromolecules and metabolites (e.g., lipids, fatty acids, carotenoids, amino acids, polysaccharides) as well as the ratio of carbon, nitrogen and phosphorous in algal cells (Manier et al., 2013; Cherchi et al., 2015; Li et al., 2015a; Praveenkumar et al., 2015; Rhiem et al., 2015; Li et al., 2016; Zhang et al., 2016b). Cherchi et al. reported changes in *Cyanobacteria Anabaena's* intracellular C:N, C:P and N:P stoichiometries after exposure to nano-TiO_2 at varying dose concentrations (0–1 mg/L) and exposure duration (96 h–21 d) (Cherchi et al., 2015). Notably, the relative ratio of amide II, lipids, nucleic acids and carbohydrates to the cellular protein content (quantified as amide I stretch) changed significantly within the initial 96 h exposure.

Similar to transcriptome and proteomics, metabolomics is also helpful to evaluate the effects of nanomaterials on algae at the molecular level, and has been gradually applied in the field of ecotoxicology (Huang et al., 2018; Huang et al., 2019; Grigoriev et al., 2021). Taylor et al. investigated the potential toxicity of tightly constrained nano-CeO_2 to the unicellular green algae by using the metabolomics approach (Taylor et al., 2016). According to principal components analysis (PCA) of the mass spectrometry-based metabolomics data, there was a significant perturbation of metabolic function within the algal cells when exposed to nano-CeO_2 at supra-environmental concentrations.

2.3 MNMs affect algae's photosynthesis and nitrogen fixation

Photosynthesis activity is an important indicator for evaluating the MNMs' effects on algae. Chlorophyll content, the maximal electron transport rate (ETR_{max}) and primary light energy conversion efficiency of photosystem II (PSII) have been widely used as indicators of the external stressor's effects on the algal photosystem (Pillai et al., 2014; Masojidek et al., 2021). Several studies have shown that a higher concentration of MNMs (> 10 mg/L) can inhibit photosynthesis of algae by reducing chlorophyll content or affecting photoelectron transfer (Saison et al., 2010; Wei et al., 2010a; Sadiq et al., 2011a; Oukarroum et al., 2012; Pillai et al., 2014). Saison et al. investigated the change of *Chlamydomonas reinhardtii's* PSII after exposure to nano-CuO, and reported that both the content of chlorophyll and PSII electron transport rate significantly decreased, indicating strong inhibition of the PSII photochemistry (Saison et al., 2010). Likewise, it was reported that contents of chlorophyll decreased in *Haematococcus pluvialis* after the exposure to nano-Cu (Babazadeh et al., 2021).

Though most studies have demonstrated that MNMs could inhibit the photosynthesis of algae, there are exceptions. Some studies have found that MNMs can enhance photosynthetic performance of microalgae (Rodea-Palomares et al., 2012; Serag et al., 2013; Giraldo et al., 2014; Xu et al., 2018). Rodea-Palomares et al. reported that low concentrations (0.01–0.1 mg/L) of nano-CeO_2 increased the photosynthetic electron transport and chlorophyll a content in the freshwater alga *Pseudokirchneriella subcapitata* (Rodea-Palomares et al., 2012). Similarly, carbon nanotubes (CNTs) exhibited high efficiency in light energy capture, owing to the broader absorption spectrum than the chloroplast antenna pigments (Hagen and Hertel, 2003). It has been reported that CNTs could promote photosynthetic electron transport both *ex vivo* and *in vivo* (Lambreva et al., 2015) and increase photosynthetic activity (Giraldo et al., 2014). The underlying mechanisms of MNMs' positive effects on the photosynthetic activity might attribute to their widened spectral region for energy capturing (Lambreva et al., 2015) and higher chlorophyll content under the MNMs-induced stress (Chen and Smith, 2012). However, the presence of MNMs even at low concentrations (< 0.1 mg/L) would induce oxidative stress to algal organisms (Rodea-Palomares et al., 2012), which would further cause lipid peroxidation and cell death. In addition, to long-term effect of algae exposed to MNMs should be thoroughly studied to maximize the positive contribution of MNMs to algal photosynthetic performance and biomass accumulation (Giraldo et al., 2014).

In addition to affecting photosynthesis, MNMs would

affect the algal nitrogen fixation ability (Cherchi and Gu, 2010; Kumar et al., 2016). After exposure to nano-TiO_2, both the occurrence and intracellular levels of the nitrogen-rich cyanophycin grana proteins (CGPs) in cyanobacteria *Anabaena variabilis* increased with the increasing concentration and time of nano-TiO_2 exposure, indicating inhabitation in nitrogen fixation activity (Cherchi and Gu, 2010). Likewise, it was reported that nano-hexaconazole, a nanoscale polymer carrier for pesticides, caused inhibition in blue-green algae's activity of nitrogen assimilating enzymes (Kumar et al., 2016). On the other hand, the biological effects of MNMs to algae also vary under different nitrogen conditions. For example, the exposure to nano-TiO_2 under replete nitrogen conditions would decrease the growth and biomass of *Chlorella vulgaris*, while the exposure to nano-TiO_2 under limited nitrogen would lead to a more severe drop of the algal growth and biomass (Dauda et al., 2017). MNMs would induce negative effects on algal nutrient cycling and nitrogen fixation, which deserves more in-depth investigation.

2.4 MNMs affect algae's growth

As discussed above, the exposure to MNMs would affect algae's gene expression, metabolism, photosynthesis, and nitrogen fixation, which would eventually affect the growth of algal cells (Wang et al., 2011; Hazani et al., 2013; Nogueira et al., 2015; Sohn et al., 2015). We have summarized the adverse effects and mechanisms of MNMs on algae in Table 1. Generally, the inhibition of algae growth by MNMs is usually evaluated by the median effective concentration (EC_{50}), which may vary significantly with the MNMs type, exposure time or concentration, testing organisms, and algae age. For instance, the EC_{50} of metal quantum dots (QDs) was significantly higher than that of carbon QDs on *Chlorella pyrenoidosa* (Xiao et al., 2016). Besides, EC_{50} of MNMs on "mid-age" algae is usually lower than that of "young" and "old" algae (Metzler et al., 2011). Metzler et al. studied the effect of nano-TiO_2 on *Pseudokirchneriella subcapitata* and reported that as the algal age increased, there was an increase in EC_{50} from that in 3–5 d algae to 8-d algae, but a decrease of EC_{50} in 12–14 d algae (Metzler et al., 2011). Moreover, EC_{50} usually increases with exposure time. For example, EC_{50} of nano-TiO_2 inhibiting *Chlamydomonas reinhardtii* growth was 10 and 100 mg/L for 3-d and 10-d exposure, respectively (Gunawan et al., 2013).

In general, the higher exposure concentration of MNMs would induce stronger inhibition of algae growth (Schwab et al., 2011; Sohn et al., 2015). Wei (Wei et al., 2014) et al. reported that the growth inhibition of *Scenedesmus obliquus* were 6.27%, 11.2%, and 20.7% after 96-h exposure of 50, 100, 200 mg/L nano-SiO_2. Meanwhile, low-dosage MNMs exposure may also suppress algae growth, for example, the growth of *Chlorella kessleri* was hindered by up to 91.9% after the exposure to 26.7 mg/L C_{60} fullerene, which was only 70.2% when exposed to 40 mg/L C_{60} fullerene (Kubatova et al., 2013).

On the other hand, the exposure to low concentrations of MNMs may promote the growth of algae (Sohn et al., 2015; Tyne et al., 2015; Chen et al., 2019; Vargas-Estrada et al., 2020). For instance, Sohn et al. reported that the biomass of *Raphidocelis subcapitata* was elevated 1.47 times after 72-hour exposure of 12 mg/L single-walled carbon nanotubes (SWCNTs), which was attributed to hormesis (Sohn et al., 2015).

3 Mechanisms of MNMs' effect on algae

MNMs affect algae mainly by inducing mechanical damage and light-shielding effects in algae as well as releasing metal ions in water, and which could directly or indirectly induce oxidative stress in algae.

3.1 Mechanical damage

Owing to MNMs' high surface/interface potential, strong interaction between MNMs and algal cells (e.g., MNMs being adsorbed on the surface of algal cells, encapsulated algal cells) would induce mechanical damages (e.g., MNMs penetrate algal cells with a sharp edge and corner) (Chen et al., 2015; Zhang et al., 2016a; Zhao et al., 2017; Middepogu et al., 2018). Two-dimension MNMs, for example, reduced graphene oxide (rGO) and multi-layer graphene (MG) were reported to destroy membrane integrity of *Chlorella pyrenoidosa*, due to the direct contact of the edges of rGO and MG with algal cells (Zhao et al., 2017).

Moreover, MNMs were reported to enter the algal cells and destroy the subcellular structure (Dalai et al., 2013; Manier et al., 2013; Li et al., 2015a; Zhang et al., 2016a; Wang et al., 2021b). Iswarya et al. assessed the damage of anatase and rutile nano-TiO_2 to the membrane and subcellular structures of *Chlorella vulgaris*, and suggested that anatase nano-TiO_2 would damage algal cells' nucleus and cell membrane while rutile nano-TiO_2 would cause chloroplast and internal organelle damages (Iswarya et al., 2015). However, it is not always the case that MNMs would enter the algal cells, for instance, QDs were observed adsorbed on the surface of *Phaeodactylum tricornutum* and *Dunaliella salinaonly*, while no QDs were observed inside the algal cells (Morelli et al., 2013).

3.2 MNMs induced light-shielding effect

The interactions between MNMs and algal cells (e.g., heteroaggregation) may result in the attachment to the surface of the algal cells to absorb or block part of the light, inducing a light-shielding effect. The light-shielding effect of MNMs would further affect the photosynthesis

Table 1 Adverse effects and mechanisms of MNMs on algae

MNMs type	MNMs	Particle size	Dosage	Algae species	Effects	Mechanisms	EC_{50}	References
Carbonaceous MNMs	Graphene oxide (GO)	N/A	0.5, 2, 5, 10, 20, 50, 70, 100 mg/L	*Raphidocelis subcapitata*	Growth inhibition	Oxidative damage; shading effects; mechanical damage	96 h – EC_{50} = 20 mg/L	Nogueira et al., 2015
	GO	3.5 nm	0.5, 2, 5, 10, 20, 50, 70, 100 mg/L	*Raphidocelis subcapitata*	Growth inhibition	Oxidative damage; shading effects; mechanical damage	N/A	Nogueira et al., 2015
	GO	5 nm	N/A	*Chlorella vulgaris*	Cell division inhibition	N/A	N/A	Wahid et al., 2013
	Graphene	N/A	50 mg/L	*Chlorella pyrenoidosa*	Growth inhibition	Shading effects; mechanical damage	96 h – EC_{50} = 37.3 mg/L (GO)/34.0 mg/L (rGO)/ 62.2 mg/L(MG)	Zhao et al., 2017
	Carbon nanotubes (CNTs)	N/A	1–50 mg/L	*Chlorella vulgaris*	Growth inhibition; normal photosynthetic activity	Shading effects; the agglomeration of algal cells	96 h – EC_{50} = 1.8 mg/L (well dispersed suspensions)/ 24 mg/L (agglomerated suspensions)	Schwab et al., 2011
	CNTs	N/A	1–50 mg/L	*Pseudokirchneriella subcapitata*	Growth inhibition; normal photosynthetic activity	Shading effects; the agglomeration of algal cells	96 h – EC_{50} = 20 mg/L (well dispersed suspensions)/ 36 mg/L (agglomerated suspensions)	Schwab et al., 2011
	CNTs	4 nm inner and 5–20 nm outer diameter	0.85±0.12 mg CNTs/g algae dry weight	*Pseudokirchneriella subcapitata*	Biochemical composition alteration	Mechanical damage and internalization	N/A	Glomstad et al., 2016
	Single-walled carbon nanotubes (SWCNTs)	Length: ~20μm, diameter:1–	12–46.1 mg/L	*Chlorella vulgaris*	Growth inhibition	N/A	72 h – EC_{50} = 30.96 mg/L	Sohn et al., 2015
		Length: ~20 μm, diameter:1–1.2 nm	15–42.8 mg/L	*Raphidocelis subcapitata*	Growth inhibition	N/A	72 h – EC_{50} = 29.99 mg/L	Sohn et al., 2015
	Multi-walled carbon nanotubes (MWCNTs)	20–30 μm	0.1, 0.5, 1, 2.5, 5, 10 mg/L	*Dunaliella tertiolecta*	Growth inhibition	N/A	96 h – EC_{50} = (0.82±0.02) mg/L	Wei et al., 2010
	CNT (DWCNTs 80%, SWCNTs 15%, and MWCNTs 5%)	1–100 μm	0.1, 1, 10 and 50 mg/L	*Nitzchia palea*	Proteins/carbohydrates ratio increase; growth inhibition	N/A	48 h – EC_{50} = 7.5 mg/L	Verneuil et al., 2015

(*Continued*)

MNMs type	MNMs	Particle size	Dosage	Algae species	Effects	Mechanisms	EC_{50}	References
Metal/Metal Oxide MNMs	Nano-Au	633 nm	0.005125, 0.01025, 0.0205,0.041, 0.082 mg/L	*Desmodesmus subspicatus*	Growth inhibition	N/A	72 h – EC_{50} = 0.028 mg/L	DĚDkovÁ et al., 2014
	Nano-Au	633 nm	0.005125, 0.01025, 0.0205,0.041, 0.082 mg/L	*Selenastrum bibraianum*	Growth inhibition	N/A	72 h – EC_{50} = 0.014 mg/L	DĚDkovÁ et al., 2014
	Nano-Ag	50 nm	10, 50, 100, 200 mg/L	*Chlorella vulgaris*	Cell stability decreased	Oxidative damage	N/A	Hazani et al., 2013
	Nano-Au	10, 20,40, 60 and 80 nm	5–8 mg/L	*Pseudokirchneriella subcapitata*	Growth inhibition	N/A	72 h – EC_{50} = 0.72 mg/L (average)	Angela et al., 2014
	Nano-Au	N/A	10, 100, 200, 500 nM	*Chlamydomonas reinhardtii*	ATP and photosynthesis plummeting	Oxidative damage	N/A	Pillai et al., 2014
	Nano-Au	50 nm	0–10 mg/L	*Chlorella vulgaris*	Chlorophyll content decrease; growth inhibition (viable algal cells decrease)lipids peroxidation	Oxidative damage	N/A	Oukarroum et al., 2012
	Nano-Au	20, 40, 100 nm	0.05–20 μM.	*Thalassiosira pseudonana*	Growth inhibition	Releasing metal ions	N/A	Burchardt et al., 2012
	Nano-Au	20, 40, 100 nm	0.05–20 μM.	*Synechococcus sp.*	Growth inhibition	Releasing metal ions	N/A	Burchardt et al., 2012
	Nano-CuO	N/A	0.1, 0.5, 0.8, 1, 2 mg/L	*Microcystis aeruginosa*	DNA damage	Mechanical damage and internalization; oxidative damage	72 h – EC_{50} = 0.47 mg/L	Angela et al., 2014
	Nano-TiO_2	935±33 (*s*) nm	0, 0.2, 2, 10, 50, and 250 mg/L	*Pseudokirchneriella subcapitata*	Growth inhibition	N/A	96 h – EC_{50} = 8.7 mg/L (with a UV filter)/ 6.3 mg/L (with 3 h pre-exposure to UV)	Wang et al., 2011
	Nano-TiO_2	10 nm (primary size) /192±0.8 nm (NM aggregates)	0–500 mg/L	*Anabaena variabilis*	Growth inhibition; nitrogen fixation activity inhibition	N/A	96 h – EC_{50} = 0.62 mg/L	Cherchi and Gu, 2010
	Nano-TiO_2	4–30nm	0, 10, 30, 100, 250,500, 600, and 1000 mg/L	*Pseudokirchneriella subcapitata*	Growth inhibition	Surface coverage; oxidative damage	96 h – EC_{50} = 113±18 mg/L	Metzler et al., 2011
	Nano-TiO_2	5–10 nm	0, 5, 10, 20, and 30 mg/L	*Karenia brevis*	Growth inhibition; cell membrane destroyed	Oxidative damage; mechanical damage	72 h – EC_{50} = 10.69 mg/L	Li et al., 2015
	Nano-TiO_2	5–10 nm	0, 5, 10, 20, and 30 mg/L	*Skeletonema costatum*	Growth inhibition; MDA contents increase	Oxidative damage	72 h – EC_{50} = 7.37 mg/L	Li et al., 2015

(*Continued*)

MNMs type	MNMs	Particle size	Dosage	Algae species	Effects	Mechanisms	EC_{50}	References
Quantum Dots (QDs)	Carbon QDs (PEG_{2000} -CQDs, CA-CQDs, and Gly-CQDs)	<10 nm	0, 5, 10, 50, 100, and500 mg/L	*Microcystis aeruginosa*	Growth inhibition	N/A	N/A	Yan, 2015
	CdSe QDs	3.2 nm	Short-term exposure experiments: 20–320 nM.Long-term exposure experiments: 0.04–1.0 nM	*Phaeodactylum tricornutum*	Growth inhibition; SOD and CAT activities were increased; ascorbate peroxidase (APX) and glutathione reductase (GR) activities were not significantly affected	Oxidative damage	N/A	Morelli et al., 2012
	CdTe-QDs	<10 nm	0, 5, 10, 50, 100, and 500 mg/L	*Microcystis aeruginosa*	Growth inhibition; chlorophyll-a accumulation inhibition	N/A	N/A	Yan, 2015
	CQDs (N, S doped CQDs, N doped CQDs, no doped CQDs)	–	0, 1, 5, 10, 50, 100 mg/L,0, 5, 10, 50, 100, 500 mg/L, 0, 5, 10, 50, 100, 500 mg/L, respectively	*Chlorellapyrenoidosa*	Growth inhibition; Chla contents and protein contents were decreased; SOD activity and MDA contents were increased	Oxidative damage	96 h – EC_{50} = 38.56, 185.83, 232.47 mg/L, respectively	Xiao et al., 2016
	Metal QDs (CdTe QDs, CdS QDs, $CuInS_2$ /ZnS QDs)	–	0, 0.01, 0.02, 0.1, 0.2, 1 mg/L, 0, 0.75, 1.5, 7.5, 15, 75mg/L, 0, 10, 20, 100, 200, 1000 mg/L, respectively	*Chlorellapyrenoidosa*	Growth inhibition; Chla contents and protein contents were decreased; SOD activity and MDA contents were increased	Oxidative damage	96 h – EC_{50} = 0.015, 4.88, 459.5 mg/L, respectively	Xiao et al., 2016

Note: N/A refers to data not provided in the original report.

of algae, which directly or indirectly affects the growth and reproduction of algae (Schwab et al., 2011; Hazeem et al., 2020; Thiagarajan et al., 2021; Wang et al., 2021b). Sadiq et al. reported that the existence of nano-Al_2O_3 had a certain light-shielding effect on *Scenedesmus* sp. and *Chlorella* sp., inhibiting the synthesis of photosynthetic pigments and thus suppressing algae growth (Sadiq et al., 2011b). Similarly, graphene oxide (GO) was reported to exhibit a light-shielding effect onto *Chlorella vulgaris* (Zhao et al., 2016), while CNT was also demonstrated to inhibit the growth of *Chlorella vulgaris* due to the light-shielding effect (Schwab et al., 2011).

However, there have been debates on the role of the light-shielding effect in MNMs induced toxicity (Saison et al., 2010; Wang et al., 2011). Aruoja et al. found no significant growth inhibition when using nano-TiO_2 to block the light source (Aruoja et al., 2009). Likewise, the light-shielding effect was not observed in the toxicity study of nano-TiO_2 on *Scenedesmus obliquus* (Li et al., 2020a). The MNMs induced shading effects may depend on the properties of MNMs, for example, the black flake-like MNMs (e.g., GO) may have a stronger light-shielding effect.

3.3 MNMs released metal ions

Metal-containing MNMs, especially nano-Ag, nano-ZnO, nano-PbS, nano-Cu_2O, etc., would gradually release metal ions along the environmental process (Gunasekaran et al., 2020; Ahmed et al., 2021; Kong et al., 2021; Xiong et al., 2021b), which may also induce biological effects to algae. Particularly, some researchers suggested that the toxicity of MNMs to algae is dominated by MNMs-induce dissolved metal ions (Franklin et al., 2007; Wong et al., 2010). Franklin et al. reported that the toxicity of nano-ZnO to *Pseudokirchneriella subcapitata* was statistically similar to that of $ZnCl_2$, suggesting Zn^{2+} released by the dissolution of nano-ZnO lead to the major toxic effect (Franklin et al., 2007). Likewise, Li et al. reported less toxicity on alga *Euglena gracilis* exposed to nano-Ag, compared to $AgNO_3$ (Li et al., 2015b). The proteinaceous pellicle of algae could effectively inhibit the uptake of MNMs, while the dissolved ions could mitigate into algal cells and induce biological effects (e.g., suppress the photosynthetic yield).

On the contrary, compared to the released metal ions, some researchers considered the role of MNMs is more critical in causing the biological effects onto algae (Navarro et al., 2008; Manzo et al., 2013). Manzo et al. reported that nano-ZnO induced significantly higher than that of bulk ZnO, though similar amount of Zn^{2+} was detected in both exposures, demonstrating the critical role of MNMs in the toxicity effect on algae (Manzo et al., 2013). Similarly, it's reported that nano-ZnO exhibited higher toxicity to green algae *Chlorella sp* compared to the bulk-ZnO and Zn^{2+}, which was attributed to the fact that nano-ZnO entrapped and wrapped the algal cells and may contribute to the algal growth inhibition (Ji et al., 2011). Thus, the MNMs released metal ions should not be considered as the sole reason for MNMs' negative effects to algae, while the "nano-effect" of MNMs (e.g., light-shielding effect, mechanical damage) might be dominant contributors (Chen et al., 2019).

3.4 MNMs induced ROS generation

Oxidative stress has been widely considered as one of the dominant mechanisms in the toxic effect of MNMs on algae (Xiao et al., 2016; Santschi et al., 2017; Chen et al., 2019). MNMs have unique physicochemical properties (e.g., photocatalytic, oxidative capability), which may trigger reactive oxygen species (ROS) formation in algal cells via direct and indirect chemical reactions (Ouabadi et al., 2013; von Moos and Slaveykova, 2014).

Generally, the intracellular ROS could be generated via directly contact-mediated approach, or indirectly through dissolved ions. The direct MNMs-mitochondria contacts could compromise the organelle membrane integrity, which would release of Ca^{2+} ions from interior stores and further activate the ROS-generating Ca^{2+}/calmodulin-dependent enzymes (Santschi et al., 2017). Additional direct pathways may associate with the interactions between MNMs and membrane-bound enzymes to trigger ROS formation (Navarro et al., 2008). Meanwhile, the indirect pathways are involved in the interactions between algae and leached MNM constituents such as metals and organics, which further engage in redox cycling that yield ROS (e.g., H_2O_2, $O^{2-}\cdot$, $OH\cdot$) production (Ouabadi et al., 2013). Studies have revealed that the amount of MNMs generated ROS exhibited linear correlations with their toxicity to biological organisms (Li et al., 2012). For example, the exposure of nano-Ag had increased the ROS generation in *Chlorella vulgaris*, and resulted in stronger toxic effects (Hazeem et al., 2019). The exceeded intracellular ROS would engage in unrestricted oxidation of biological molecules and cellular components (e.g., lipid peroxidation), and eventually result in losing cell function and apoptosis (Rocha et al., 2015; Glomstad et al., 2016; Liu et al., 2018).

4 Implications and applications of MNMs' on algae

The effects of MNMs on algae could be either positive or negative, as posing ecological risks (e.g., intracellular biochemical composition change, metabolism alteration, nitrogen-fixation inhibition, photosynthesis suppression, growth reduction) and potential applications (e.g., enhanced production of valuable bioactive substances, control of biological and chemical pollutants).

4.1 Implications of MNMs on algae

As discussed above, MNMs would induce manifold

biological effects on algae, including intracellular biochemical composition change, metabolism alteration, nitrogen-fixation inhibition, photosynthesis suppression, and growth reduction. Due to the long-term exposure of MNMs at environmentally relevant concentrations, the alteration of algae's photosynthesis, nitrogen fixation and the ratio of C, N, P may further influence the general biogeochemical processes (e.g., carbon and nitrogen cycling) (Cherchi and Gu, 2010; Cherchi et al., 2015). Furthermore, MNMs-engaged biomass change of algae would break the balance of interspecies equilibriums and community dynamics in aquatic ecosystems (Oukarroum et al., 2012; Cherchi et al., 2015).

On the other hand, as the major primary producers in aquatic ecosystems, algae may promote the bioaccumulation of MNMs via the food chain due to the algae-MNMs interaction (e.g., adsorption, internalization) (Rhiem et al., 2015; Xin et al., 2021). It has been proved that MNMs can be transferred from low to high trophic levels along the food chain, and further accumulated in high trophic organisms (Zhao and Wang, 2010; Campos et al., 2013; Bhuvaneshwari et al., 2018). For example, Bouldin et al. fed *Ceriodaphnia dubia* with CdSe QDs exposed *Pseudokirchneriella subcapitata*, and found the existence of CdSe QDs in the *Ceriodaphnia dubia* (Bouldin et al., 2008). In addition, studies have shown that the bio-enrichment of MNMs via the food web is significantly greater than that through water (Zhao and Wang, 2010; Campos et al., 2013). It's reported that more than 70% of nano-Ag accumulated in the *Daphnia magna* was through ingestion of algae (Zhao and Wang, 2010). The trophic transfer, bioaccumulation and bio-enrichment of MNMs via the food web would eventually pose a great threat to the ecosystem and public health.

4.2 Applications of MNMs' effect on algae

4.2.1 Enhance the production of valuable bioactive substances

As shown in Fig. 2, algae could produce a variety of bioactive substances (e.g., fatty acids, steroids, carotenoids, polysaccharides, lectins, mycoplasma-like amino acids, halogenated compounds) through different metabolic pathways (Almendinger et al., 2021), which also serves as the adaption to the environmental change. As discussed above, the exposure of MNMs would alter the metabolism of algae, which may tune certain metabolic pathways to enhance the production of valuable bioactive substances. As a high-value antioxidant, astaxanthin (AXT) has been widely used in cosmetics, health care products, medical and other industries (Du et al., 2021). AXT could be produced by *Haematococcus pluvialis*, however, the yield is very limited. Recently, nano-Au was innovatively used to stimulate *Haematococcus pluvialis* to produce AXT at a single cell level, providing a successful MNMs-enhanced biorefinery process (Praveenkumar et al., 2015).

On the other hand, algae is considered as a unique feedstock to produce biofuel (Saber et al., 2016; Yap et al., 2021), while the efficiency and cost-reduction of the cultivation and harvesting steps remain key obstacles (Jones and Mayfieldt, 2012; Kim et al., 2013; Fazal et al., 2021). Due to the MNMs-algae interactions, the biofuel production could be promoted via the induction of intracellular lipid accumulation by nutrient competition and/or stress environments (Farooq et al., 2016; Kim et al., 2016; Liu et al., 2016; He et al., 2017), enhancement of cell growth and/or pigment by light scattering (Torkamani et al., 2010; Pattarkine and Pattarkine, 2012; Eroglu et al., 2013), increased cell separation efficiency and processing time in culture media (Borlido et al., 2013; Hu et al., 2013), and integrated one-pot harvest/cell division (Lee et al., 2014).

4.2.2 Control of biological pollutants

Though algae are an important part of the ecosystem, however, they would also generate biological pollutants (e.g., eutrophication and biofouling). Since MNMs could inhibit the growth of algal cells, which would be beneficial to control eutrophication or inhibit biofouling (Fig. 2).

Due to the excellent aggregation and sedimentation

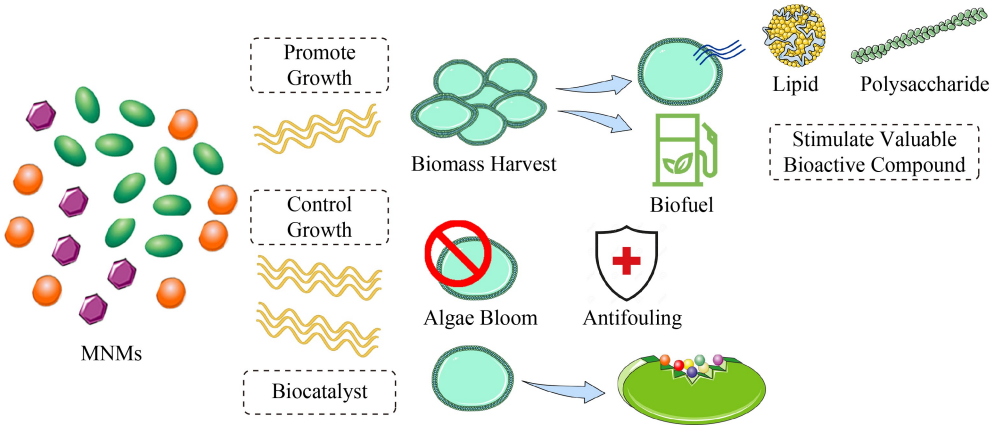

Fig. 2 Potential applications of MNMs' effect on algae.

properties in aqueous suspension (Hartmann et al., 2010; Campos et al., 2013; Chowdhury et al., 2013) as well as photocatalytic potential (Metzler et al., 2012), MNMs have been increasingly used to eliminate the bloom algae via surface-mediated reactions and adsorption (Wang et al., 2015; da Silva et al., 2016). Particularly, nano-TiO_2 and iron-containing MNMs are considered the most effective MNMs for the control of red tide algae (Wang et al., 2015; da Silva et al., 2016; Fan et al., 2018; Song et al., 2021). However, MNMs may also adversely affect other species in the ecosystem when treating algae bloom. Da Silva et al. investigated the performance of nano-TiO_2 on remediating eutrophic waters under a microcosm experiment, and had eliminated the algal blooms (da Silva et al., 2016). Meanwhile, Silva et al. also reported that *Daphnia magna*, *Lemna minor* and *Chironomus riparius* exhibited significant inhibition, suggesting more attention should be paid to assessing the potential impact of MNMs on the entire ecosystem.

Moreover, studies have revealed that the engagement of MNMs (e.g., nano-TiO_2, nano-CuO, nano-Ag) could effectively control the biofouling induced by algae (Fonseca et al., 2010; Graziani et al., 2013; Verma et al., 2014). Biofilms would form along with the algal colonization, causing the biofouling on the surface of marine vessels and infrastructure (e.g., bridge), which may further induce decay and damage to materials (Scheerer et al., 2009).

4.2.3 Enhanced remediation of chemical pollutants

Algal photolysis has been proved as a promising alternative way to remove aquatic environmental contaminants (Wang et al., 2017; Samara Sanchez-Sandoval et al., 2021; Xiong et al., 2021a), which can produce photogenerated reactive radicals to accelerate the degradation of pollutants (Sun et al., 2020; Premnath et al., 2021; Wei et al., 2021). Similarly, photocatalytic MNMs have been widely applied for environmental remediation (Tan et al., 2020; Chen et al., 2021; Ding et al., 2021). Thus, the remediation efficiency could be significantly enhanced via the synergistic effect by combining MNMs and algae (Cai et al., 2017; Wang et al., 2017; Chen et al., 2018; Jing et al., 2018; Chang and Wu, 2019).

Researchers have fixed the MNMs together with algal cells on engineered templates (e.g., fibers mat) to promote the degradation of pollutants. For example, algae-TiO_2/Ag bio-nano hybrid material was developed by loading algal cells on the ultrafine TiO_2/Ag chitosan hybrid nanofiber mat, which has significantly improved the photo-removal of Cr(VI) under visible light irradiation (Wang et al., 2017). The organic substances released by algae could consume photo-excited holes and ·OH efficiently, which attenuated the electron-hole recombination and enhanced the photocatalytic reduction of Cr(VI) on TiO_2. Meanwhile, the release of intracellular substances (chlorophylls, carboxylate acids) could be served as photosensitizers to improve the generation of ROS, which enhanced the photoreduction of Cr(VI) in the system.

Likewise, algae could act as carriers to have MNMs fixed onto the algae biological templates (Tu et al., 2012). Cai et al. immobilized nano-TiO_2 on *Chlorella vulgaris* cells via the hydrothermal method, and sensitization of the photosynthesis pigment boosted nano-TiO_2's photodegradation efficiency under the visible light (Cai et al., 2017).

5 Conclusion and perspectives

Being widely applied in multiple fields, MNMs could be released into the aquatic environments along the life cycle, inducing critical effects on algae. We conducted a comprehensive review on both positive and negative impacts of MNMs on algae and thoroughly discussed the underlying mechanisms. In general, exposure to MNMs may adversely affect algae's gene expression, metabolism, photosynthesis, nitrogen fixation and growth rate. The major mechanisms of MNMs-induced inhibition are attributed to oxidative stress, mechanical damages, released metal ions and light-shielding effects.

On the other hand, rational utilization of the MNMs-induced effects would promote the production of valuable bioactive substances as well as control biological and chemical pollutants. MNMs could be used to stimulate algae to produce useful bioactive substances (e.g., antioxidants, biofuel), while the MNMs-algae interaction could effectively enhance the efficiency of environmental remediation process (e.g., degradation of contaminants, control of eutrophication and biofouling.

However, there are still knowledge gaps that need to be addressed to gain a comprehensive understanding of the effect of MNMs on algae as well as the associated implications and applications. The risks of MNMs on algae in the natural ecosystem should be thoroughly assessed prior to the applications. Particularly, MNMs would be involved in environmental processes, which may induce weathering and aging effects on MNMs, further changing the physicochemical properties and effective concentration of MNMs. More in-depth investigations should be conducted to address the migration, transformation, and aging of MNMs under realistic environmental conditions. It also poses huge demand on the quantitative information of the environmental background concentration of MNMs in aquatic ecosystems, which is still missing. It is an urgent need to advance analytical instruments and protocols to quantitatively analyze the actual environmental concentrations and size distributions of MNMs.

Meanwhile, the toxicity assessment of MNMs on algae should be evaluated under environmentally relevant conditions, which should fully consider the heterogeneous joint toxicity effect of MNMs and other environmental factors,

including hypoxia, acidification, temperature, heavy metal, persistent organic pollutants and micro-plastics (Liu and Wang, 2020; Liu et al., 2022). In addition, the biological effects of MNMs on algae should be carried out in real or simulated ecosystems with certain complexity and biodiversity, which is essential to improve the rationality and effectiveness of the data to obtain the whole picture of MNMs' ecological risks.

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