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Review

Influence of Light Irradiation on Nitrification in Microalgal–Bacterial Systems for Treating Wastewater

Shimin Lu [1,2], Yayuan Li [1,3], Xingguo Liu [1,2], Guofeng Cheng [1,2], Zehui Yuan [1,3] and Fan Wu [1,2,*]

[1] Fishery Machinery and Instrument Research Institute, Chinese Academy of Fishery Sciences, Shanghai 200092, China; lushimin@fmiri.ac.cn (S.L.); m200100135@st.shou.edu.cn (Y.L.); chengguofeng@fmiri.ac.cn (G.C.); m220100167@st.shou.edu.cn (Z.Y.)
[2] Key Laboratory of Aquaculture Facilities Engineering, Ministry of Agriculture and Rural Affairs, Shanghai 200092, China
[3] College of Fisheries and Life, Shanghai Ocean University, Shanghai 201306, China
* Correspondence: wufan@fmiri.ac.cn

Abstract: The use of bacterial and microalgal consortia to remove nitrogen from wastewater has garnered attention as a potential alternative to conventional systems. This approach not only reduces energy consumption but also aids in nutrient recovery. Light is essential for algae photosynthesis; however, nitrifying bacteria are also influenced by light radiation. This mini-review summarizes the current knowledge concerning photoinhibition, the light stimulation of ammonia-oxidizing bacteria (AOB), resistance to light radiation, the implementation of microalgal–bacterial systems, and the possible mechanisms involved. *Nitrosomonadaceae* AOB and *Nitrospiraceae* nitrite-oxidizing bacteria (NOB) often coexist in a microalgal–bacterial system. Studies have suggested that AOB can tolerate light radiation at 200 μmol $m^{-2}{\cdot}s^{-1}$ in microalgal–bacterial systems, whereas NOB are almost completely suppressed, which can result in partial nitrification in the bioreactor. An appropriate light level can stimulate AOB growth in microalgal–bacterial granular reactors and may improve algae metabolic activity. Granular sludges or artificial "light-shielding hydrogel" could effectively protect nitrifying bacteria from light intensities up to 1600 μmol $m^{-2}{\cdot}s^{-1}$ in wastewater treatment reactors. Microalgal–bacterial systems along with the associated "algal shading effect" have been widely used in pond aquaculture. This approach minimizes the need for costly mechanical aeration through photo-oxygenation and facilitates nutrient recovery by filter-feeding fish.

Keywords: photoinhibition; light resistance; ammonia-oxidizing bacteria (AOB); nitrite-oxidizing bacteria (NOB); nitrifying granular

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1. Introduction

The global discharge of nitrogen into wastewater is expected to increase from 6.4 Tg-N yr^{-1} in 2000 to 12.0–15.5 Tg-N yr^{-1} in 2050 [1], and nitrogen levels in water have become one of the most important pollution problems facing humanity today. Currently, biological nitrification and denitrification processes mainly remove nitrogen from wastewater. Biological nitrification is an aerobic process. However, aeration, which is required for this process, is an energy-intensive and costly process, potentially accounting for 45–75% of energy consumption in mechanized wastewater treatment plants [2]. The use of microalgal–bacterial systems to remove nitrogen from wastewater has gained attention over the past decade as an alternative to conventional nitrification, owing to their potential to reduce the energy consumption associated with mechanical oxygenation [3,4]. In addition to reducing the energy requirements associated with mechanical oxygenation, the system also offers several advantages, such as excellent settleability, high biomass production, and the ability to withstand toxicity and organic loading [5].

Biological nitrification is a crucial process in microalgal–bacterial systems. It oxidizes ammonia (NH_3) to nitrate (NO_3^-) via intermediate nitrite (NO_2^-), which is mainly

conducted by ammonia-oxidizing bacteria (AOB) and nitrite-oxidizing bacteria (NOB). Ammonia-oxidizing bacteria participate in the carbon (C) and nitrogen (N) cycles and are thus involved in environmental processes. AOB assimilate carbon dioxide (CO_2) via the Calvin–Benson–Bassham (CBB) cycle. The enzyme that catalyzes CO_2 fixation in AOB is encoded by the *cbb* genes [6]. The oxidation of NH_3 to NO_2^- requires two steps [7]. First, NH_3 is oxidized to hydroxylamine (NH_2OH) by ammonia monooxygenase (AMO), and then NH_2OH is further oxidized to NO_2^- by hydroxylamine reductase [7]. The key NOB enzyme, nitrite oxidoreductase (NXR), catalyzes the oxidation of nitrite to nitrate and can also facilitate the reduction of nitrate to nitrite. The *nxrA* and the *nxrB* genes are powerful functional and phylogenetic markers that can detect and identify uncultured NOB [8].

Light is an essential ecological factor for algae photosynthesis, yet the impact of light on nitrifying bacteria is also significant. Previous studies have shown that strong light radiation causes photo-oxidation damage to the AMO in *Nitrosomonas europaea* AOB, decreasing their ammonia oxidation activity [9]. In addition, light has also been shown to have a significantly negative effect on NOB in microalgal–bacterial systems [10]. In contrast, a recent study showed that appropriate light irradiation stimulated AOB growth [10]. Furthermore, previous research indicates that nitrification is closely related to light levels in algal–bacterial systems [10–12]. To save mechanical oxygenation and control the ammonia concentration of aquaculture water, the algal–bacterial symbiosis approach has been widely used in pond aquaculture [13–15]. With the development of anammox in recent years, the combined process of partial nitrification and anammox, utilizing light to suppress NOB, has garnered increasing interest [16,17]. Understanding the impact of light radiation on nitrification is crucial for the design and management of algal–bacterial systems. However, a comprehensive review of the effects of light irradiation on nitrification is still lacking.

Here, we summarize the current knowledge regarding the influence of light on AOB and NOB in microalgal–bacterial systems. Additionally, we explore its implementation and discuss the potential photobiological mechanisms involved. This study provides a theoretical foundation for the design, application, and management of microalgal–bacterial systems.

2. Influence of Light Irradiation on AOB

2.1. Photoinhibition of AOB

The photoinhibition of AOB was discovered under laboratory cultivation conditions in 1962 [18]. Subsequently, the photoinhibition of nitrification has been found in many natural aquatic environments, such as oceans [19–21] and rivers [22,23]. Furthermore, in the past decade, it has been shown that the photoinhibition of AOB also widely occurs in microalgal–bacterial systems for treating artificial wastewater (Table 1). For example, batch experiments by Wang et al. [10] clearly showed that the light suppression of AOB was positively correlated with the light exposure period (200 μmol $m^{-2}{\cdot}s^{-1}$ for 10−16 h, 600 μmol $m^{-2}{\cdot}s^{-1}$ for 4−5 h, and 2000 μmol $m^{-2}{\cdot}s^{-1}$ for 2−4 h). Akizuki et al. [24] demonstrated that nitrification activity decreased significantly and linearly with increasing light level in dispersed sludge reactors and that the effect of light on dispersed nitrifying particles is expressed by the formula $y = -0.246\ \exp^{(283 \div (x+230))}$ ($r = 0.770$, $p < 0.01$), where x represents the light level, and y represents the nitrification activity. Vergara et al. [25] assessed the effect of a wide range of light intensities (0–1250 μmol $m^{-2}\ s^{-1}$) on dispersed nitrifying sludge, finding that nitrification activity at 250 μmol $m^{-2}\ s^{-1}$ matched that under dark conditions, but when the light level was above 500 μmol $m^{-2}\ s^{-1}$, it significantly decreased. An integrated model framework assessed by Peng et al. [12] showed that light radiation at 105 μmol $m^{-2}{\cdot}s^{-1}$ suppressed NOB activity, but not AOB. However, 63 and 74 μmol $m^{-2}{\cdot}s^{-1}$ light levels did not impact AOB or NOB. The light shading effects produced by microalgal–bacterial granular material may explain why AOB exhibits a slightly higher light stress tolerance in a microalgal–bacterial system than under pure culture conditions. As shown in Table 1, the shading effect of algae may allow the dispersed AOB to tolerate light radiation at around 200 μmol $m^{-2}{\cdot}s^{-1}$ in algal–bacterial

systems, whereas AOB activity constantly decreases, even at white light irradiances below 60 μmol $m^{-2}·s^{-1}$ under pure culture conditions [26].

As shown in Figure 1, previous research indicated that the photoinhibition of AOB by visible light was mainly caused by irreversible damage to copper-containing AMO [27,28]. Subsequently, Lu et al. deduced that the conformational change in AMO was likely involved in converting NH_3 to NH_2OH. During this conformational change, if the photosensitive sites of AMO are exposed to visible light, AMO becomes inactivated. Additionally, the synthesis of new AMO is necessary for recovery post-photoinactivation [29]. The extent of photoinhibition increases as the wavelength decreases in the 300–623 nm range, while recovery from photoinactivity accelerates with increasing wavelength [29]. Recent studies have shown that *amoA* gene expression is downregulated when AOB are exposed to white light radiation in a microalgal–bacterial system, shedding light on the mechanism of AOB photoinhibition at the genetic level [10]. In addition, light shock could lead to cellular metabolic disorders and membrane oxidation (Figure 1). After light shock, the activities of two antioxidant enzymes, superoxide dismutase (SOD) and catalase (CAT), increase, while the levels of reactive oxygen species (ROS) decrease. Near-UV radiation (300–400 nm) can damage nucleic acids, cell membranes, and more, affecting not just AMO [29,30]. It is possible that lactate dehydrogenase (LDH) is released following light shock due to the cell membrane damage caused by near-UV radiation [31]. AOB may secrete excessive extracellular polymeric substances (EPSs) under light stress to improve their resistance to external light stress. This secretion enhances adhesion and mutual interactions, facilitating the formation of a three-dimensional structure that helps avoid light radiation [22].

Besides directly damaging AOB cells, light can also indirectly inhibit AOB through microalgae [32–34]. This is because microalgae are more competitive for nitrogen than AOB in microalgal–bacterial systems with low ammonia concentrations [32–35]. In microalgal–bacterial systems for treating wastewater with a high ammonia content, the competitive advantage of microalgae in carbon sources offers the most plausible explanation for their inhibitory effect on AOB or NOB. It was reported that *Nitrosomonas europaea* grew poorly in Na_2CO_3-deficient media, where C was available only from the atmosphere, and when the cultures exhibited a long lag phase (~5 days, compared to 1 day in a carbonate-containing medium) [6]. Microalgae utilize CO_2 for photosynthesis, thereby lowering the concentration of carbonate ions and increasing the oxygen concentration in water. Evidence has suggested that the transcription of *cbb* genes is upregulated when the carbon source is limited, while the *amo*, *hao*, and other energy-harvesting-related genes are downregulated. Consequently, the ammonia oxidation ability of AOB becomes weak, leading to light suppression [6].

Table 1. Effect of light level on nitrification activities reported by different studies.

Nitrifying Microorganism	Light Level	Light Source	Irradiance Time	Finding	References
AOB and NOB	63, 74 μmol $m^{-2}·s^{-1}$	White fluorescent tubes	Continuous illumination for 40 days	AOB and NOB were not inhibited by 63 or 74 μmol $m^{-2}·s^{-1}$ light level	[12]
AOB and NOB	105 μmol $m^{-2}·s^{-1}$	White fluorescent tubes	Continuous illumination for 30 days	NOB, but not AOB, were inhibited	
Nitrosomonadaceae AOB and *Nitrospiraceae* NOB	≥180 μmol $m^{-2}·s^{-1}$	Cool white LED tubes	With a dark/light cycle of 12 h/12 h	NOB were significantly inhibited in the batch reactors	[36]
Nitrosomonadaceae AOB and *Nitrospiraceae* NOB	At 225 μmol $m^{-2}·s^{-1}$	Cool white LED tubes	With a dark/light cycle of 12 h/12 h	NO_2^--N accumulated in batch reactors	

Table 1. *Cont.*

Nitrifying Microorganism	Light Level	Light Source	Irradiance Time	Finding	References
Nitrosomonadaceae AOB and *Nitrospiraceae* NOB	The average visible and UV light intensities were 42 and 3 mW cm^{-2}	Sunlight	Exposed to sunlight for 61 days	Nitrifying bacteria were substantially inhibited in algal–bacterial symbiosis	[32]
Nitrosomonadaceae AOB and *Nitrospiraceae* NOB	200 μmol m^{-2}·s^{-1}	The light panel was 80% similar to solar light	10−16 h	The suppression of light on AOB and NOB positively correlated with the light exposure period	[10]
Nitrosomonadaceae AOB and *Nitrospiraceae* NOB	600 μmol m^{-2}·s^{-1}	The light panel was 80% similar to solar light	4−5 h	The suppression of light on AOB and NOB positively correlated with the light exposure period	
Nitrosomonadaceae AOB and *Nitrospiraceae* NOB	2000 μmol m^{-2}·s^{-1}	The light panel was 80% similar to solar light	2−4 h	The suppression of light on AOB and NOB positively correlated with the light exposure period	
Nitrifying granular sludge	450 μmol m^{-2}·s^{-1}	LED light devices	12 h	The activity significantly decreased by 50% compared to the dark condition	[24]
Nitrifying granular sludge	1600 μmol m^{-2}·s^{-1}	LED light devices	12 h	The activity significantly decreased by 70% compared to the dark condition, while in the granular sludge reactors, the activity barely changed	
Nitrosomonadaceae AOB and *Nitrospiraceae* NOB	The average light level was 1531 μmol m^{-2}·s^{-1}	Sunlight	63 days	Sunlight, algae growth, and free nitrous acid decreased the activity of AOB by 25.7% and completely inhibited NOB activity	[37]
Nitrosomonas-related AOB and *Nitrospira*-related NOB	200 μmol m^{-2}·s^{-1}	Cool white light-emitting diodes	In continuous dark/light (12 h/12 h) cycles	AOB abundance increased from 0.2% to 2.1%, whereas NOB abundance reduced gradually from 0.07% to below 0.01%	[38]
Nitrifying bacterial	Below 250 μmol m^{-2}·s^{-1}	LED lamps	Continuous illumination for 15 days	No significant effect on nitrification activity	[25]
Nitrifying bacterial	At 500 μmol m^{-2}·s^{-1}	LED lamps	Continuous illumination for 15 days	It decreased NH_4^+-N removal by 20% and NO_3^--N production by 26%	
Nitrifying bacterial	At 1250 μmol m^{-2}·s^{-1}	LED lamps	Continuous illumination for 15 days	It decreased NH_4^+-N removal by 60% and NO_3^--N production by 71%	
Nitrosomonas AOB and *Nitrospira* NOB	From 100 to 50 μmol m^{-2}·s^{-1}		Continuous illumination for 105 days	A syntrophic algal/partial nitrification/anammox granular sludge process was developed	[39]

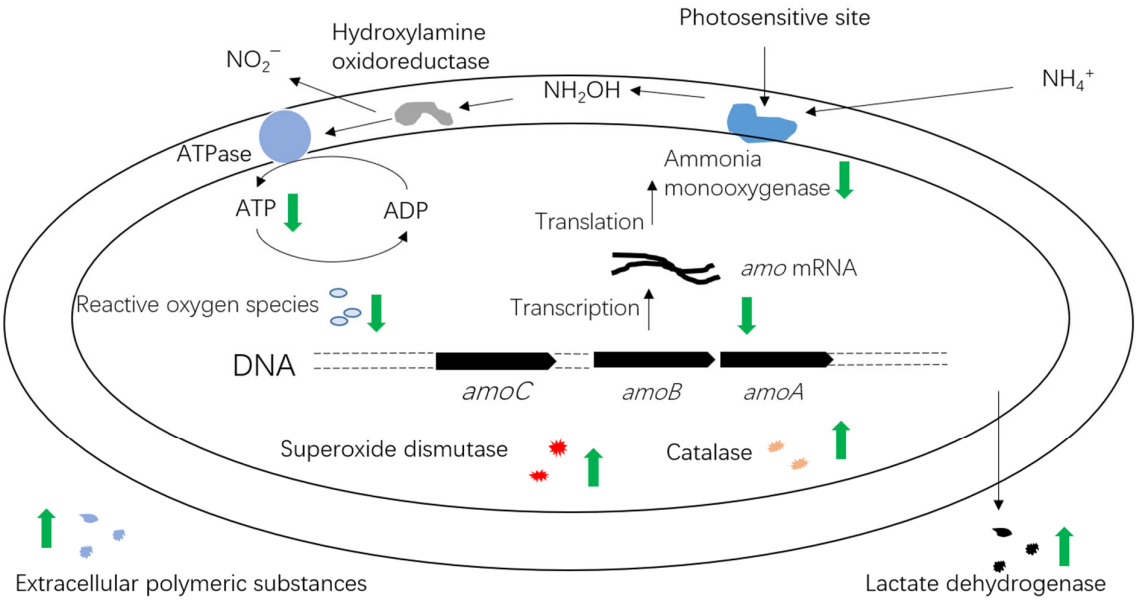

Figure 1. Possible mechanisms of photoinhibition of ammonia-oxidizing bacteria (AOB) include the location of photosensitive sites on ammonia monooxygenase (AMO) that are susceptible to visible light [29]. When exposed to intense light, AMO becomes irreversibly deactivated [40]. Light radiation can lead to cellular metabolic disorders and membrane oxidation. In this context, the activities of superoxide dismutase (SOD) and catalase (CAT) increase, while the levels of reactive oxygen species (ROS) decrease. Additionally, the release rate of lactate dehydrogenase (LDH) and the production of extracellular polymeric substances (EPSs) increase [31]. The expression of the *amoA* gene is downregulated [10], leading to a weakened ammonia oxidation ability in AOB. The green arrow in the blue box means the activities of two antioxidant enzymes, superoxide dismutase (SOD) and catalase (CAT) increase, after light shock.

2.2. Effect of Light on AOB Biodiversity

Previous studies have shown that photoinhibition is associated with specific AOB strains under pure culture conditions. For example, Merbt et al. reported that *Nitrosomonas europaea* ATCC19718 was more sensitive than *Nitrosospira multiformis* ATCC25196, with decreases in specific growth rates of 91% and 41%, respectively, at a light level of 60 μmol $m^{-2}{\cdot}s^{-1}$ [26]. It has also been suggested that light plays a selective role in AOB biodiversity in a microalgal–bacterial system. For example, after prolonged exposure to light in light-treated reactors, the population of the genus *Nitrosomonadaceae* Ellin6067 doubled, the number of AOBs in the other four genera reduced, and *Nitrosomonas* (a typical AOB) disappeared [10]. The percentage of *Nitrosomonadaceae* gradually increased from 2% to 4% under intense light illumination in photo-sequencing batch reactors, and no other AOB were detected [36]. Similarly, a study by Kim and Park [17] showed that the proportion of the family *Nitrosomonadaceae* increased from 0.126% to 0.379% after blue light illumination. Recently, it was reported that *Nitrosomonas* spp., when coupled with anammox bacteria, could adapt to long-term light irradiation in photogranules, successfully establishing a synthetic algal/partial discrimination/anammox gross sludge process [39]. As described in numerous studies, *Nitrosomonadaceae* AOB exhibit a flexible response to light irradiation, making it advantageous over other AOB types in the microalgal–bacterial system.

2.3. Light Stimulation of AOB Growth

Recent studies have shown that an optimum light level could stimulate the growth of AOB in microalgal–bacterial granular reactors. Wang et al. [10] first reported the stimulatory effects of energy densities of 0.03−0.08 kJ mg^{-1} VSSs (volatile suspended solids), corresponding to 80–160 W and 400–1000 μmol $m^{-2}{\cdot}s^{-1}$ for 2.0–5.0 h at concentrations

of 2750–4250 mg L^{-1}, on AOB in sequencing batch reactors when treating real or synthetic municipal wastewater. Subsequently, Yang et al. [31] confirmed that light could increase AOB activity by 120% at a specific light energy density (Es) ranging from 0.0203 to 0.1571 kJ·mg^{-1} VSS. These stimulatory effects were supported by increased electron transport system activity, key enzyme activity (AMO), gene expression (*amoA*), and energy generation (ATP consumption) during light treatment. To date, few reports exist on the stimulation of AOB growth by light irradiation in pure cultures. It is possible that light itself does not stimulate AOB growth. It is likely that the appropriate light needed to promote AOB growth is closely related to algae metabolic activity. The nitrification process, as shown in stoichiometric Equation (1) [41], produces 4 mol of H^+ for 2 mol of ammonia consumed, which can result in a decrease in solution pH. The photosynthesis process in algae can be represented by stoichiometric Equation (2) [42], where, for every 106 mol of CO_2 assimilated, 18 mol of H^+ is consumed, generating 138 mol of O_2. Photosynthesis not only consumes the H^+ generated during nitrification but also provides substrate O_2 for nitrification. Furthermore, nitrification bacteria and algae generally coexist in the system as bioflocs [43], meaning that nitrification and photosynthesis simultaneously occur in a very small space, and the metabolites produced by the two reaction processes can be rapidly transported away. Therefore, appropriate light can stimulate the growth of AOB in microalgal–bacterial granular reactors more effectively than dark conditions.

$$2NH_4^+ + 3O_2 \rightarrow 2NO_2^- + 4H^+ + 2H_2O \quad (1)$$

$$106CO_2 + 16NO_3^- + HPO_4^{2-} + 18H^+ + 122H_2O = (CH_2O)_{106}(NH_3)_{16}H_3PO_4 + 138O_2 \quad (2)$$

3. Photoinhibition of NOBs

Similar to AOB, NOB are also sensitive to light radiation in microalgal–bacterial systems. Moreover, NOB are less resistant to strong radiation than AOB. Generally, dispersed NOB can tolerate light radiation of less than 200 μmol m^{-2}·s^{-1} in algal–bacterial systems (Figure 2). As previously mentioned, an integrated model framework developed by Peng et al. [12] showed that light radiation at 105 μmol m^{-2}·s^{-1} inhibited NOB activity but not AOB. Peng et al. [36] found that NOB was significantly inhibited in photo-sequencing batch reactors when the light level was up to 225 μmol m^{-2}·s^{-1}, and previous studies have shown obvious NO_2^--N accumulation in photo-sequencing batch reactors. Si et al. [38] found that the abundance of *Nitrospira*-related NOB gradually disappeared after 150 days of operation at a light level of 200 μmol m^{-2}·s^{-1}, whereas *Nitrosomonas*-related AOB increased from 0.2% to 2.1%, resulting in partial nitrification in the bioreactor.

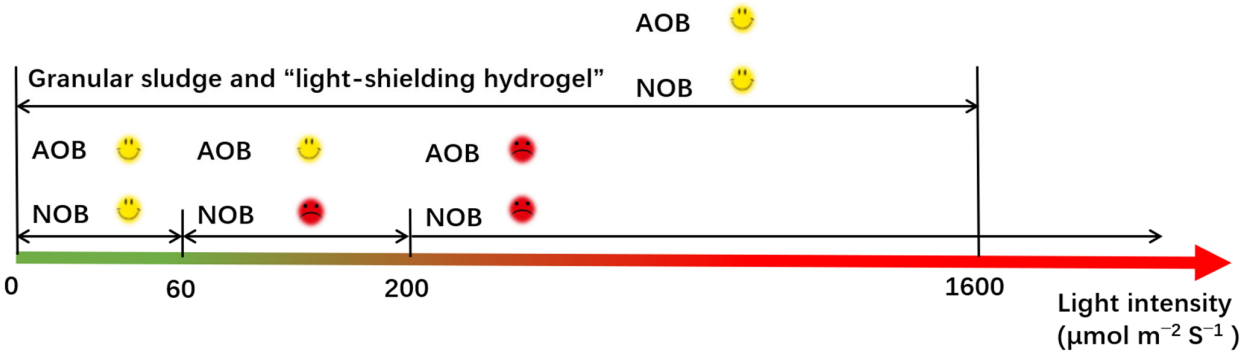

Figure 2. Influence of light level on ammonia-oxidizing bacteria (AOB) and nitrite-oxidizing bacteria (NOB) in a microalgal–bacterial system [12,36,38]. The AOB and NOB mainly belong to the genera *Nitrosomonadaceae* and *Nitrospiraceae*, respectively. "☺" suggests that AOB and NOB are safe, while "☹" suggests that the corresponding light radiation significantly inhibits AOB and NOB. The "light-shielding hydrogel" entraps nitrifiers in carbon black-added alginate hydrogel beads [11].

At present, at least seven NOB genera have been identified: *Nitrobacter*, *Nitrotoga*, *Nitrococcus*, *Nitrospira*, *Nitrospina*, *Nitrolancea*, and *Candidatus nitromaritima* [8,44]. The current understanding of NOB photosensitivity is relatively limited, especially regarding microalgal–bacterial systems [29]. As shown in Table 1, to date, mainly *Nitrospira-related* NOB and *Nitrosomonas-related* AOB have been found in microalgal–bacterial systems, and *Nitrospira-related* NOB seem to be more photosensitive to light than *Nitrosomonas-related* AOB. Previous studies have attributed the greater sensitivity of NOB to the relatively low cytochrome c contents in *Nitrobacter* NOB [45]. Barak et al. [46] suggested the possibility of light impeding electron transfer from cytochrome c to nitrite reductase. Likewise, Wang et al. [10] confirmed that the downregulated expression of *nxrB* was the main reason for *Nitrospira* NOB suppression. Similar to AOB, when NOB are exposed to light radiation, they also exhibit metabolic disorders and cell membrane damage (Figure 3). When exposed to light stress, the activities of SOD antioxidant enzymes increased, ROS decreased, while the LDH release rate and EPS significantly increased [31].

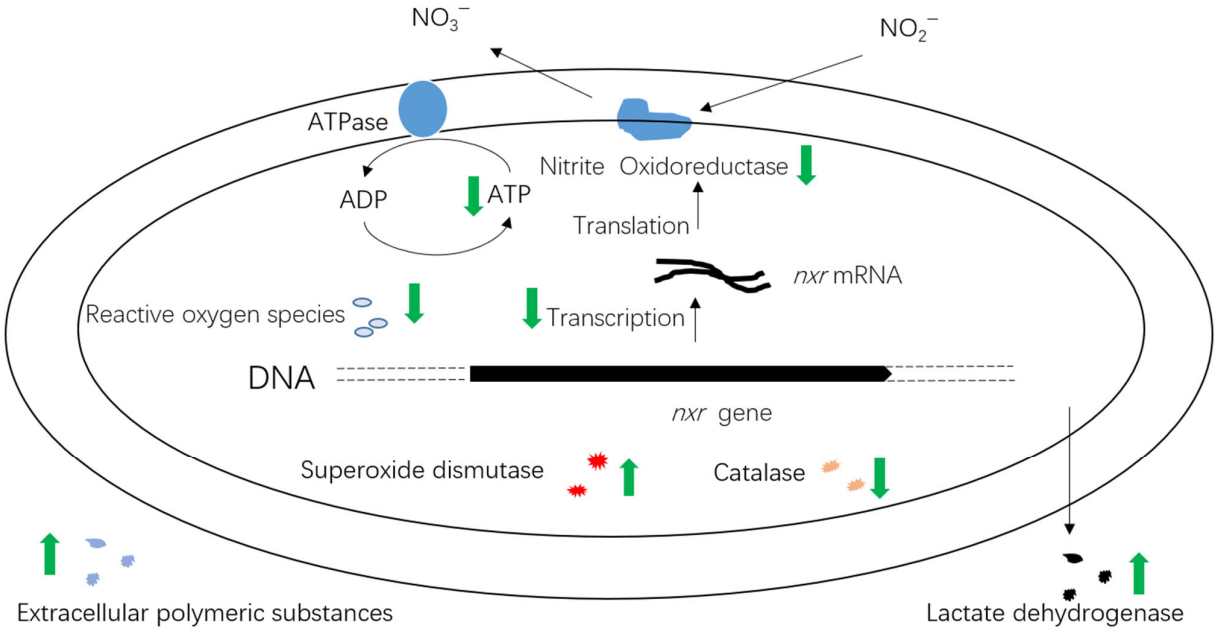

Figure 3. Possible mechanisms of photoinhibition of nitrite oxidation bacteria (NOB). The *nxr* gene of NOB expression is downregulated [10], and the nitrite oxidation ability of NOB becomes weak, even completely lost. Light irradiation can lead to cellular metabolic disorders and membrane oxidation. Superoxide dismutase (SOD) increases, and reactive oxygen species (ROS) decreases [31]. Additionally, the release rate of lactate dehydrogenase (LDH) and the production of extracellular polymeric substances (EPSs) are observed to increase under these conditions [31]. The green arrow in the blue box means the activities of two antioxidant enzymes, superoxide dismutase (SOD) and catalase (CAT) increase, after light shock.

4. Resistance to Light Radiation

From an economic perspective, sunlight is undoubtedly the best choice for microalgal–nitrifying bacterial systems. However, sunlight intensity often exceeds 2000 μmol $m^{-2} \cdot s^{-1}$ [24,47], which can severely inhibit AOB and NOB activities [48]. To harness strong light, such as sunlight, new techniques have been developed to mitigate the photoinhibition of nitrifying bacteria under strong light exposure. For example, Akizuki et al. [24] suggested that a nitrifying granular sludge produced stable ammonium oxidation under intensive light, and they confirmed that the activity in granular sludge (average granule diameter of around 300 μm) was not significantly inhibited by sunlight exposure. In contrast, compared to dark conditions, within a dispersed sludge reactor, the nitrification activity significantly decreased by 50% and 70% at light intensities of 450 and 1600 μmol $m^{-2} \cdot s^{-1}$,

respectively [48]. A possible reason for the light stress tolerance observed in granular sludge could be that the thick aggregate layer prevents light penetration into the granule interior. It was reported that the transmission of incident light clearly decreased with increasing thickness of the layer [49]. For example, around 50% of the incident light was obscured at 250 μm from the surface [49]. Based on this "shading effect", Nishi et al. [11] developed a "light-shielding hydrogel" in which nitrifying bacteria were trapped in carbon black alginate hydrogel beads and confirmed that they could protect the nitrifying bacteria from intense light up to 1600 μmol $m^{-2} \cdot s^{-1}$ in microalgal–nitrifying bacterial consortia. To some extent, these results show that the "shading effect" can effectively protect nitrifying bacteria from strong light suppression.

5. Influence of Light-Induced Nitrification Changes on Microalgae

In a mature microalgal–bacterial system, ammonia removal occurs through two mechanisms: nitrification by microorganisms and assimilation by microalgae. Nitrifying bacteria and microalgae work synergistically; once nitrification is suppressed by light, algae growth can also be severely affected. At high light intensities (such as 1250 μmol $m^{-2} \cdot s^{-1}$), AOB and NOB were both inhibited to a certain extent, and ammonia removal depended primarily on assimilation by microalgae [25]. Under this condition, high concentrations of microalgae could cause a CO_2/O_2 imbalance and a pH increase. CO_2 is the substrate for algae photosynthesis, so a shortage of CO_2 can reduce or halt algal photosynthesis. Due to the lack of nitrification ability, the pH of the microalgal–bacterial system may reach > 12, which is detrimental to algae growth [50]. Furthermore, a high pH would increase the free ammonia (NH_3) concentration [51], which can significantly inhibit microalgae growth [52]. For example, NH_3 concentrations of 34 and 51 mg/L at pH 9.5 (20–25 °C) could reduce the algal photosynthesis of *Scenedesmus obliquus* by 50% and 90%, respectively [52]. Furthermore, as photosynthesis increases and nitrification weakens, the microalgal–bacterial system's dissolved oxygen may become supersaturated. Under this condition, more oxygen radicals would develop during the respiratory gas exchange, damaging the microalgae membrane [53,54].

6. Implementation

As shown in Table 1, *Nitrosomonadaceae* AOB and *Nitrospiraceae* NOB often coexist in a microalgal–bacterial system, and the activities of *Nitrospira*-related NOB are more photosensitive than those of *Nitrosomonas*-related AOB [10,17,38]. This characteristic has been successfully used to establish partial nitrification systems [10,38,39]. Using light to inhibit the growth of NOB could avoid secondary pollution and further reduce operational costs [10,38] compared to other control methods, such as low dissolved oxygen, high temperature, a short sludge retention time, suitable free ammonia, and free nitrous acid [55]. Partial nitrification could substantially increase nitrite accumulation and could potentially be combined with heterotrophic denitrification or anammox to make wastewater treatment more efficient. It has been estimated that a partial nitrification–denitrification microalgal system could save 18.3% oxygen and 26.6% carbon when combined with a conventional nitrification–denitrification microalgal system [10]. Perhaps this is because the chromaticity and turbidity of wastewater could significantly affect photoinhibition efficiency [31,56]; this method has only been tested at the laboratory scale and has not been used in practice [57].

Although rare, reports do exist on the use of microalgal–bacterial systems in pond aquaculture practices. Nevertheless, they are widely and successfully used in pond aquaculture to minimize costly mechanical aeration via photo-oxygenation and nutrient recovery by filter-feeding fish, especially in China, where there are 3,030,151 ha aquaculture ponds. Annual production is 23.5 million tons of freshwater fish and 2.8 million tons of seawater fish [58]. Compared to a sewage treatment system, aquaculture ponds are a relatively complex microalgal–bacterial ecosystem (Figure 4). They require nitrifying bacteria to remove the ammonia and nitrite generated during the aquaculture process and algae to provide food for filter fish, such as silver carp. Algae photosynthesis provides oxygen for respira-

tion by nitrifying bacteria and aquaculture animals. On sunny days, the dissolved oxygen concentration in aquaculture water can reach a supersaturated state without mechanical aeration [59]. This may be due to the shading effect caused by the highly concentrated algae in the pond water. Although aquaculture ponds are directly exposed to sunlight every day, they are still rich in AOB (10^2–10^4 cell mL^{-1}) [15]. During the breeding season, aquaculture ponds receive large amounts of bait daily, but the pond water ammonia concentrations are generally less than 0.21 mmol L^{-1} [60]. This result suggests that AOB in pond water can continuously remove the ammonia produced by aquatic animals and residual bait under sunlight irradiation. To date, there have been few studies on the photosensitivity of AOB and NOB in pond aquaculture water, and it is not clear how these nitrifying bacteria avoid light irradiation. It is also not clear how ecological compensation mechanisms associated with other environmental factors affect the photoinhibition process and the self-repair ecological mechanisms in AOB damaged by light irradiation. The lack of information on these issues has restricted the continued development of pond aquaculture. Therefore, future research should concentrate on the mechanism associated with nitrifying bacteria's escape from photoinhibition.

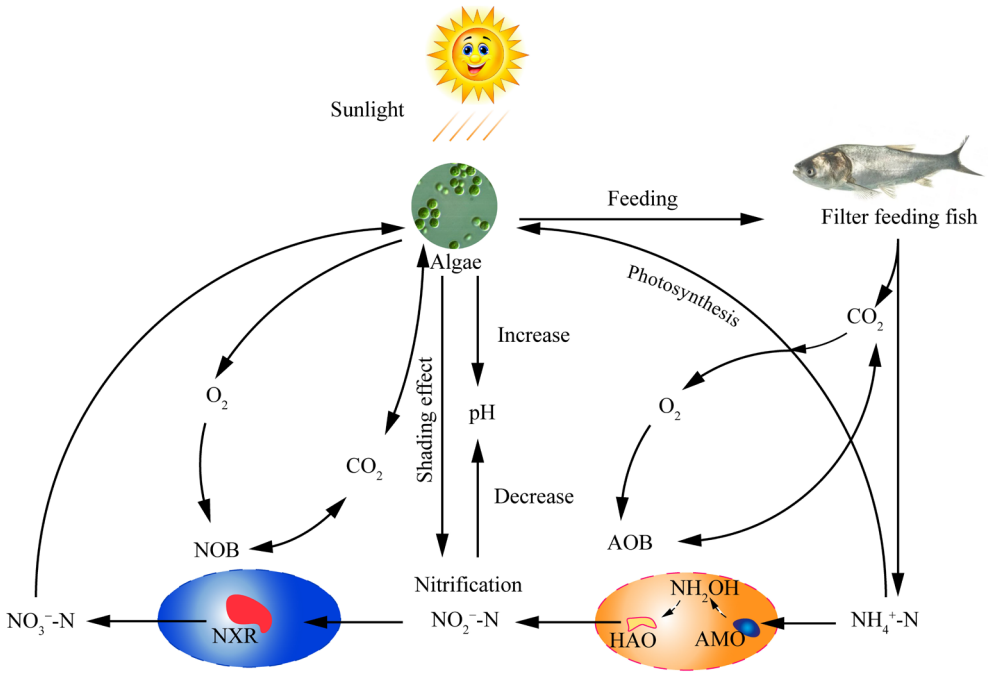

Figure 4. Possible co-working mechanism for algae and nitrifying bacteria in an aquaculture pond system. High concentrations of algae protect nitrifying bacteria from light inhibition, while algae and nitrifying bacteria work together to maintain a neutral pH in the aquaculture water. Algae use CO_2 to generate O_2 for nitrifying bacteria and fish, while CO_2 produced by bacteria and fish provides a substrate for algae photosynthesis [59].

7. Conclusions

In a microalgal–bacterial system, *Nitrosomonadaceae* AOB and *Nitrospiraceae* NOB often coexist. Generally, NOB are less resistant to light irradiation than AOB, which can result in partial nitrification in the bioreactor. Optimum light conditions can stimulate the growth of AOB in microalgal–bacterial granular reactors, and techniques such as granular sludges or artificial "light-shielding hydrogel" could effectively protect nitrifying bacteria from strong light suppression. Within a microalgal–bacterial system, algae growth could also be severely affected once nitrification is suppressed by light. The microalgal–bacterial process has been widely and successfully implemented in pond aquaculture practice to minimize costly mechanical aeration. This review provides a theoretical basis for designing and managing the microalgal–bacterial ecosystem.

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