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MINI REVIEW

Influence of photoinhibition on nitrification by ammonia-oxidizing microorganisms in aquatic ecosystems

Shimin Lu · Xingguo Liu · Chong Liu · Guofeng Cheng · Hongye Shen

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Abstract Photoinhibition of ammonia oxidation occurs widely in aquatic environments and could suppress the nitrification rate, lead to the composition variation of inorganic nitrogen and influence the stability of aquatic ecosystems. Both ammonia-oxidizing bacteria (AOB) and archaea are sensitive to light. The extent of photoinhibition and the time required for recovery depend on light wavelength, intensity, photon quantity and strains. Strong evidence indicates that photoinhibition in AOB by visible light is mainly caused by irreversible damage to ammonia monooxygenase (AMO) and the degradation of AMO is beneficial to AOB recovery. This review discusses photoinhibition in metabolic pathways used by ammonia oxidizers.

Keywords Photoinhibition · Nitrification · Ammonia-oxidizing bacteria · Ammonia-oxidizing archaea · Ammonia monooxygenase

S. Lu (✉) · X. Liu (✉) · C. Liu · G. Cheng · H. Shen
Fishery Machinery and Instrument Research Institute, Chinese Academy of Fishery Sciences, Shanghai 200092, China
e-mail: lushimin@fmiri.ac.cn

X. Liu
e-mail: liuxingguo@fmiri.ac.cn

1 Introduction

Nitrification is a crucial process in aquatic ecosystems, oxidizing ammonia (NH_3) to nitrate (NO_3^-) via intermediate nitrite (NO_2^-). The oxidation of NH_3 to NO_2^- is the first step and also the speed-limiting step of nitrification (Adair and Schwartz 2011) mediated by ammonia-oxidizing bacteria (AOB) and archaea (AOA) (Shafiee et al. 2019). The oxidation of NH_3 to NO_2^- is attained in two steps (Moomen and Ahmed 2018). First, the NH_3 is oxidized to NH_2OH by ammonia monooxygenase (AMO), and then further oxidized to NO_2^- by hydroxylamine (NH_2OH) reductase (Moomen and Ahmed 2018). AMO is a membrane-bound protein that consists of three subunits encoded by *amoC*, *amoA* and *amoB*, respectively (Fisher et al. 2018). The *amoA* gene is the most commonly used marker for tracking AOA or AOB in environmental samples (Lehtovirta-Morley 2018).

Light plays a key role in stimulating the uptake and excretion of inorganic nitrogen in the aquatic environment (Merbt et al. 2012; Wu et al. 2020). In 1962, the inhibition of light on ammonia oxidation was reported in laboratory cultures of AOB (Schoen and Engel 1962). Subsequently, the photoinhibition phenomenon was found in many aquatic environments such as oceans (Guerrero and Jones 1996a; Liu et al. 2018; Peng et al. 2018; Shiozaki et al. 2019), rivers (Lipschultz et al. 1985; Merbt et al. 2017) and fishponds (Wu et al. 2020). On their discovery, it was reported that AOA were also sensitive to light and more photosensitive than AOB (Merbt et al. 2012). AOA abundance and ammonia oxidation rates are usually consistent with light intensity in ocean waters (Beman et al. 2012; Horak et al. 2013; Newell et al. 2013). Photoinhibition is now used widely as an explanation for nitrite maxima near the base of the euphotic zone in oceanic waters (Olson 1981; Ward 1985; Vanzella and Guerrero 1989; Beman et al. 2012; Peng et al. 2015; Horak et al. 2018). Photoinhibition can suppress the nitrification rate, lead to the composition variation of inorganic nitrogen and influence the stability of the marine aquatic ecosystem (Shiozaki et al. 2019). However, a comprehensive summary and understanding of the photoinhibition phenomena in ammonia oxidizers is still lacking.

To understand fully the effects of photoinhibition on ammonia oxidizers, in this review, we have summarized the knowledge currently available on the photoinhibition phenomena found in laboratory and aquatic environments and discuss the cognitive progress in our understanding and the possible photobiological mechanisms involved.

2 Photoinhibition in aquatic environments

The photoinhibition of NH_3 oxidation is a widespread phenomenon in oceans. ^{15}N-tracer experiments using marine nitrifying bacteria have revealed that NH_3 oxidation activity was inhibited at a light intensity of less than 1% sunlight (Olson 1981). Ammonium oxidation rates were negatively correlated with light in the photic zone of the Washington coast and Southern California Bight; light has an important control over the depth distribution of ammonium oxidation activity (Ward 1985). Subsequently, it was reported that ammonia oxidation was performed mainly by marine Crenarchaeota via molecular and biogeochemical methods in the Gulf of California (Beman et al. 2008). This implicated that light plays a role in the depth distribution of AOA in the Gulf of California. A similar phenomenon was found in the Pacific Ocean (Church et al. 2010), the abundance of AOA *amoA* genes increased with decreasing light intensity between the upper waters and dimly lit waters of the mesopelagic zone. Data analyzed by Liu et al. showed that AOA distribution was controlled primarily by photoinhibition and secondarily by water temperature in the South Atlantic Bight (Liu et al. 2018). In late spring and late summer, in the surface waters of subarctic North Atlantic, isotope tracer experiments showed that, due to photoinhibition, ammonium and nitrite oxidation rates represented only 5.2% and 2.5% of total euphotic zone nitrate uptake, respectively (Peng et al. 2018). Satellite data analyses indicated that the euphotic zone has increased throughout the Arctic Ocean due to ice reduction, which may lead to a declining trend in nitrification and alter the composition of inorganic nitrogen, with implications for the structure of ecosystems (Shiozaki et al. 2019). In the NE subarctic Pacific, it was suggested that both light and NH_4^+ concentration played a role in regulating NH_3 oxidation rates, with rates increasing as light decreased and NH_4^+ concentrations increased (Grundle et al. 2013). The view that light is a main environmental factor of nitrification activity in the oxygenated water columns of oceans has been gradually accepted.

The photoinhibition phenomenon also occurs in freshwater environments. Lipschultz et al. found in *situ* nitrification photoinhibition occurred at about 100 $\mu Em^{-2} s^{-1}$ and maximal inhibition of nitrification at about 300 $\mu Em^{-2} s^{-1}$ in the eutrophic Delaware River (Lipschultz et al. 1985). There was a higher accumulation of AOA and AOB in general in the dark-side than on the light-side biofilm of cobbles in a wastewater treatment plant-influenced river (Merbt et al. 2011). Light manipulation experiments showed strong photoinhibition in dark-side biofilms of cobbles, whereas inhibition seemed to be buffered in biofilms developed under light conditions (Merbt et al. 2017). Algae growth and light exposure are responsible for the observed ineffectiveness of AOB and nitrite-oxidizing bacteria in natural aquaculture environments (Wu et al. 2020). Light was identified to be a major factor inhibiting nitrification in a wastewater reservoir in Israel (Kaplan et al. 2000). The aforementioned indicated that light is a major factor influencing the biological nitrogen circle and these findings help to elucidate the factors controlling the response of eutrophic systems to nutrient loading.

3 Photoinhibition dependent on wavelength, intensity, quantity of light and strains

The photoinhibition of AOB and AOA are closely related to the wavelength and intensity of light. As detailed in Table 1, so far, it has been found that monochromatic (narrowband) light in the range of 300–623 nm can affect the NH_3 oxidizing activity of AOB or AOA. Photoinhibition of *Nitrosomonas europaea* was first reported by Schon and Engel in 1962; they found that inhibition was caused by blue light (wavelengths below 480 nm) and that an intensity

Table 1 The influence of monochromatic (narrowband) light ranging from 300 nm to 623 nm on the NH_3 oxidizing activity of AOB or AOA

Wavelength (nm)	Microorganism	Findings	References
300	*Nitrosomonas cryotolerans*	After irradiation for 2 h still has 30.8%, 31.47%, 22.1% activity at 5, 15, 25 W m^{-2}, respectively	Guerrero and Jones (1996a)
		After 2 h irradiation cells took 20 h to regain 5 to 10% of NH_3 oxidizing activity	Guerrero and Jones (1996b)
350	*Nitrosomonas cryotolerans*	Still has 64.86%, 32.89%, 32% NH_3 oxidizing activity after irradiation for 2 h at 5, 15, 25 W m^{-2}, respectively	Guerrero and Jones (1996a)
	Nitrosococcus oceanus	After 2 h irradiation, took 1 h to regain 5 to 10% of NH_3 oxidizing activity	Guerrero and Jones (1996b)
400	*Nitrosomonas cryotolerans*	After 2 h irradiation, still has 79.2%, 34.61%, 47.12% NH_3 oxidizing activity at 5, 15, 25 W m^{-2}, respectively.	Guerrero and Jones (1996a)
	Nitrosococcus oceanus	After 2 h monochromatic irradiation, took 20 h to regain about 80% NH_3 oxidizing activity	Guerrero and Jones (1996b)
400–410	*Nitrosomonas europaea*	Ammonia oxidation was strongly inactivated	Hooper and Terry (1974)
> 430[a]	*Nitrosomonas europaea*	Caused little or no influence on ammonia oxidation	Hooper and Terry (1974)
450	*Nitrosomonas cryotolerans*	Took 1 h to restore up to 80% NH_3 oxidizing activity after 2 h irradiation	Guerrero and Jones (1996a)
	Nitrosococcus oceanus	After 2 h irradiation, took 1 h to restore up to 80% NH_3 oxidizing activity	Guerrero and Jones (1996b)
470 ± 5	AOB-G5-7 culture	Had strong effect on the growth at 30 μmol photons $m^{-2}s^{-1}$; while no influence at 3 μmol photons $m^{-2}s^{-1}$	French et al. (2012)
	AOA-DW culture	Did not recover after transfer from light at 30 μmol photons $m^{-2}s^{-1}$ to dark; and significantly lower growth at 3 μmol photons $m^{-2}s^{-1}$	French et al. (2012)
475	*Nitrosomonas cryotolerans*	After irradiation for 2 h, still has 87.91%, 52.11%, 39.28% activity at 5, 15, 25 W m^{-2}, respectively	Guerrero and Jones (1996a)
	Nitrosococcus oceanus	NH_3 oxidation activity was inhibited by 80% after 2 h irradiation	Guerrero and Jones (1996a)
500	*Nitrosomonas cryotolerans*	After exposure to light for 4 h at 25 W m^{-2}, there was no influence on NH_3 oxidation activity	Guerrero and Jones (1996a)
	Nitrosococcus oceanus	There was no influence on NH_3 oxidation activity after exposure to light for 4 h at 25 W m^{-2}	Guerrero and Jones (1996a)
600	*Nitrosomonas cryotolerans*	After exposure to light for 4 h at 25 W m^{-2}, there was no influence on NH_3 oxidation activity	Guerrero and Jones (1996a)
623 ± 3	AOB-G5-7 culture	No influence on NH_3 oxidation activity at 30 μmol photons $m^{-2}s^{-1}$	French et al. (2012)
	AOA-DW culture	Growth was significantly lower at 30 μmol photons $m^{-2}s^{-1}$	French et al. (2012)

[a]Multiple monochromatic light was selected with a Bausch and Lomb 500-mm model grating monochromator

of light as low as 1000 lx were effective (Schoen and Engel 1962; Olson 1981). Hooper and Terry demonstrated light inhibition of NH_3 oxidation in suspended cells of *N. europaea*, with a maximum inhibition at short near-UV wavelength (410 nm) compared with other visible light (Hooper and Terry 1973, 1974). Guerrero and Jones reported that AOB subjected to longer wavelengths can regain activity faster than if exposed to shorter wavelengths. For instance, *Nitrosomonas cryotolerans* will take as long as 20 h to regain 5 to 10% of their ammonia-oxidizing activity when illuminated with 300 nm light, as opposed to 1 h to restore up to 80% when exposed to 450 nm (Guerrero and Jones 1996b). French et al. provided further evidence that blue light (470 ± 5 nm) at 30 μmol photons m^{-2} s^{-1} had a strong effect on the growth of AOB strains, while it was not influenced by red light (623 ± 3 nm) (French et al. 2012). With the discovery of AOA, the influence of light has attracted more attention. Evidence has shown that the growth and recovery rate of AOA was significantly lower in red light (623 ± 3 nm), whereas blue light (470 ± 5 nm) at 30 μmol photons m^{-2} s^{-1} could make AOA completely inactive (French et al. 2012). Overall, as shown in Fig. 1, results from the study support the conclusion that the degree of photoinhibition increases with the decrease of wavelength in the range of 300–623 nm for AOB and AOA.

The photon quantity is the product of irradiance and the length of exposure time. Photoinhibition relative to the quantity of photons depends on the conditions. For example, the NH_3 oxidizing activity in *N. cryotolerans* was not significantly different after 2 h exposure at cool-white light intensities of 15 W m^{-2} and 25 W m^{-2}. However, the quantity-dependent response was more dramatic at shorter wavelengths (300 to 400 nm) (Guerrero and Jones 1996a). For example, short-time/high-intensity (2 h at 20 to 25 W m^{-2}) experiments showed more photosensitivity than those with long-time/low-intensity (4 h at 10 to 12 W m^{-2}) (Guerrero and Jones 1996a).

At lower light intensities, AOA is more photosensitive than AOB. A study by Merbt et al. showed that AOA strains of *Nitrosospira multiformis* and *Nitrosotalea devanaterra* can be completely inhibited at 60 μE m^{-2} $s^{-1}$and 15 μE m^{-2} s^{-1} (white light), whereas AOB strains of *N. europaea* and *N. multiformis* were unaffected. When subjected to an illumination mode of 8-h light/16-h darkness at two light intensities (60 and 15 μE m^{-2} s^{-1}), unlike AOB, AOA showed no evidence of recovery during dark phases (Merbt et al. 2012). Qi et al. found that marine AOA strains cannot grow in white light (30 μmol photons m^{-2} s^{-1}) and did not begin to grow after being transferred from light to dark, while this white light intensity had no effect on AOB (Qin et al. 2014).

The extent of photoinhibition was associated with specific strains. With regard to AOA, Qin et al. found strain SCM1 significantly less photosensitive than two

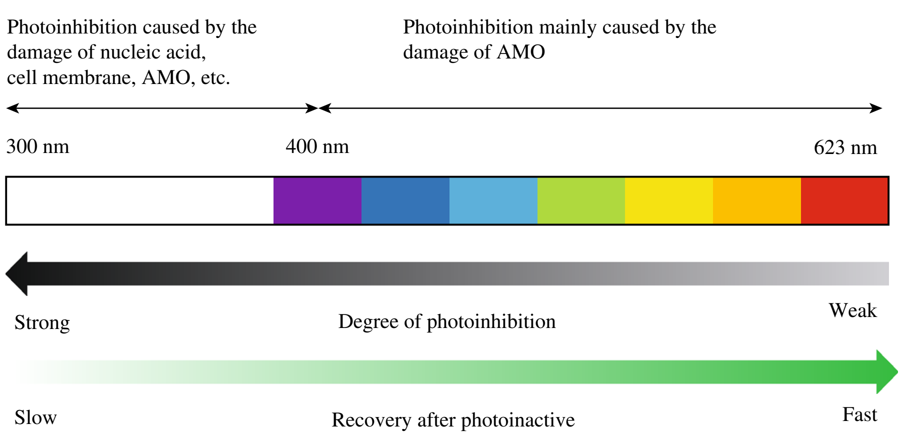

Fig. 1 It has been found that the light in the 300–623 nm wavelength has an impact on AOB and AOA. The degree of photoinhibition increases with decreasing wavelength, whereas, recovery after photoinactive is faster with increasing wavelength. The light in the 300–400 nm wavelength can cause damage to nucleic acid, cell membrane, etc., and is not limited to ammonia monooxygenase (AMO), whereas visible light mainly causes irreversible damage to AMO

other isolates (HCA1 and SP0) when exposed to a diurnal light cycle, no apparent inhibition occurred in SCM1 at low light density (15 and 40 μE m^{-2} s^{-1}) and it retained about 20% growth rate at 180 μE m^{-2} s^{-1}. The response of strain HCA1 was similar to SCM1, which showed reduced specific growth rates of 11% and 22% at 15 and 40 μE m^{-2} s^{-1}, respectively, and complete inhibition at 180 μE m^{-2} s^{-1}. Strain PS0 was the most light sensitive of the three AOA isolates, showing reduced specific growth rates of 19% and 39% at 15 and 40 μE m^{-2} s^{-1}, respectively, and was completely inhibited at 80 μE m^{-2} s^{-1} (Qin et al. 2014). A similar phenomenon was observed in AOB by Merbt et al., *N. europaea* was more sensitive than *N. multiformis*, with decreases in the specific growth rate of 91% and 41% at 60 μE m^{-2} s^{-1} (Merbt et al. 2012). The photoinhibition for *N. cryotolerans* was 55% or 32% at 450 nm or 475 nm, respectively, while there was a steady inhibition (80% inhibition) for *N. oceanus* at the same radiation (Guerrero and Jones 1996a). The tolerance of the strains to light is different, maybe a better explanation was that there were consistent phylogenetic changes observed in AOA in shallow and deep ocean water (Beman et al. 2008; Luo et al. 2014).

4 Physiological mechanism of ammonia-oxidizing microorganisms to light

As shown in Table 1, it has been known for more than half of a century that Near-UV radiation and visible light can affect the NH_3 oxidizing activity of AOB or AOA. Near-UV radiation (300–400 nm) can cause damage to nucleic acid, cell membranes, inhibit growth, and can even kill *Escherichia coli* cells completely (Berney et al. 2006). Functional analysis has shown that photolyase and catalase genes exist exclusively in the epipelagic clade of AOA, rather than in the mesopelagic waters of oceans, which are responsible for damage to nucleic acid (Luo et al. 2014). This suggests that surface water AOA have evolved effective mechanisms to cope with ultraviolet-induced DNA damage. In addition, cells of AOB can recover ammonia-oxidizing activity shortly after exposure to near-UV radiation (300–400 nm) (Guerrero and Jones 1996b), this implicates that photoinhibition by near-UV radiation may involve the damage and new synthesis of AMO, which will be discussed in detail below.

Hooper and Terry found that malonaldehyde or lipid peroxides cannot be detected in photoinactivated cells, but new protein synthesis was necessary for recovery after photoinactivation by light (400–430 nm), indicating that a protein rather than the cell membrane had been damaged during the process of photoinhibition (Hooper and Terry 1974). Subsequently, it was documented that the damaged protein in the process of photoinhibition in *N. europaea* cells was AMO, but not NH_2OH reductase (Hyman and Arp 1992; Stein et al. 2000), which suggested that the photoinsensitive target is on AMO (Fig. 2). Allylthiourea, a reversible noncompetitive AMO inhibitor, can protect AOB from photoinactivation at concentrations which cause 100% inhibition of NH_3 oxidation (Hooper and Terry 1974; Juliette et al. 1993), indicating that static AMO is not damaged by visible light. Dynamic AMO is damaged in the conversion of NH_3 to NH_2OH. Therefore, it can be deduced that the conformational turn of AMO probably involves the NH_3 to NH_2OH reaction, as shown in Figs. 3 and 4. In the process of the conformational turn, the photosensitive sites will be exposed instantaneously, and the AMO will be inactivated. Allylthiourea can prevent the conformational turn of AMO and therefore protect AOB from photoinactivation.

Subsequently, Shears and Wood via a spectroscopic method documented the photosensitive oxygenated state of AMO in the NH_3 oxidation pathway (Shears and Wood 1985), and it was suggested that AMO was a copper enzyme, with changes in the valence state of copper ions involved in the process of photoinhibition. Further evidence from genetic analyses strongly supports a copper center in AMO (Fisher et al. 2018). Additionally, anaerobic conditions can protect AMO from photoinactivation in *N. europaea* cells (Hooper and Terry 1973; Juliette et al. 1993); it has been further reported that there are photosensitive oxygenated states of AMO in the NH_3 to NH_2OH process. Anaerobic conditions can prevent the change in the valence state of copper ions in AMO, so they can protect AMO from light inactivation. Therefore, it can be deduced that O_2 is a necessary substrate for the conformational turn of AMO.

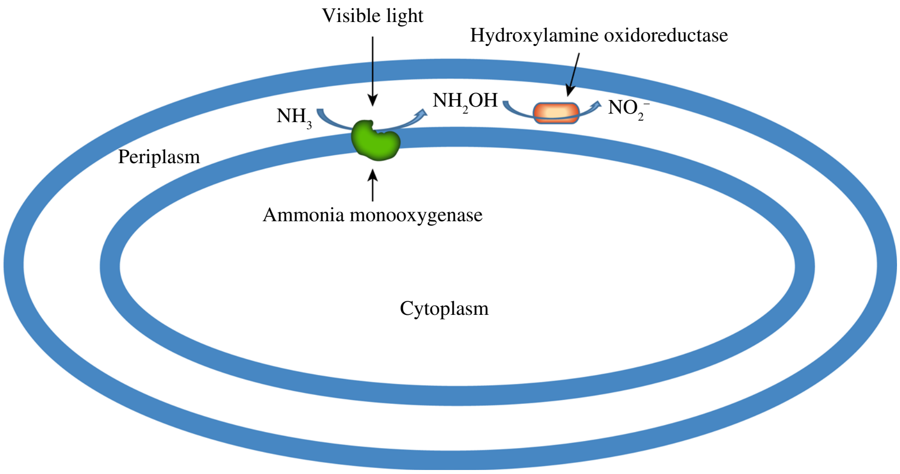

Fig. 2 The oxidation of NH_3 to NO_2^- involves two steps. First, NH_3 is oxidized into hydroxylamine (NH_2OH) via the membrane-bound protein ammonia monooxygenase (AMO), and then it is oxidized into NO_2^- in the cell periplasm via NH_2OH reductase. Visible light can cause inactivation of AMO but does not affect the conversion of NH_2OH to NO_2^-

NH_3 is a substrate for AOB, consequently, it is easy to surmise that NH_3 is also necessary to induce the conformational turn in AMO. Therefore, as with anaerobic conditions providing a protective mechanism for photoinhibition, the absence of NH_3, theoretically, could also protect AMO from photoinactivation. However, this is hard to prove, because AOB are chemoautotrophic microorganisms and the oxidation of NH_3 is the sole source of power for energy transduction and biosynthesis (Hooper et al. 1997). A lower level of mRNA involved in AMO can be detected in NH_3-deprived cells (Wei et al. 2004, 2006). In the complete absence of external NH_3, to survive, AOB must mobilize its own reserve of NH_3 or amino acids. The present understanding is that this will occur through the AMO oxidation pathway, involving the conformation turn of AMO and a photosensitive state. Therefore, in the complete absence of external NH_3, AOB will appear to be photoinactive, which was well documented by Hooper and Terry, and a small amount of nitrite production was observed in the absence of ammonia (Hooper and Terry 1974).

The above speculation was also supported by the phenomenon that an increase in ammonia concentration can buffer the photoinhibition of AOB (Hooper and Terry 1974; Takahito and Yatsuka 1984). Increasing the ammonia concentration (for instance, 2 mg to 10 mg/L) could significantly increase the expression level of AOB *amoA* mRNA (Fukushima et al. 2012), implicating a high level of AMO synthesis and high concentrations of AMO in AOB cells at high NH_3 concentrations. The photoinactivation of NH_3 oxidation was a rate constant proportional to some light intensity (Hooper and Terry 1974). Therefore, increasing the NH_3 concentration can buffer AOB from photoinhibition to a certain extent and a low NH_3 concentration can accelerate AMO photoinactivation. However, it is not clear whether the detailed response mechanism of the *amo* operon is prompted by high or low concentrations of ammonia. Similarly, it is thought that decreasing temperature can accelerate the degree of photoinhibition of AOB (Hooper and Terry 1974) because lowering the temperature can downregulate the expression level of *amo* mRNA and the nitrification rate (Che et al. 2017).

Interestingly, allylthiourea can accelerate AOB photoinactivation at concentrations which cause less than 100% inhibition of NH_3 oxidation, rather than buffer the photoinhibition to AOB (Hooper and Terry 1974). The phenomenon provides evidence to help us further understand the mechanism of photoinhibition. Less than 100% inhibition of NH_3 oxidation indicates that part of the NH_3 oxidation activity could be carried out and there is some energy and an ATP supply in cells, so ATP-dependent enzymes can still work. Transcriptional analysis showed that there are two ATP-dependent enzymes in *N. europaea* cells, ClpB (ATPase-dependent protease) and HflB (ATP-dependent zinc metallopeptidase (cell division FtsH)

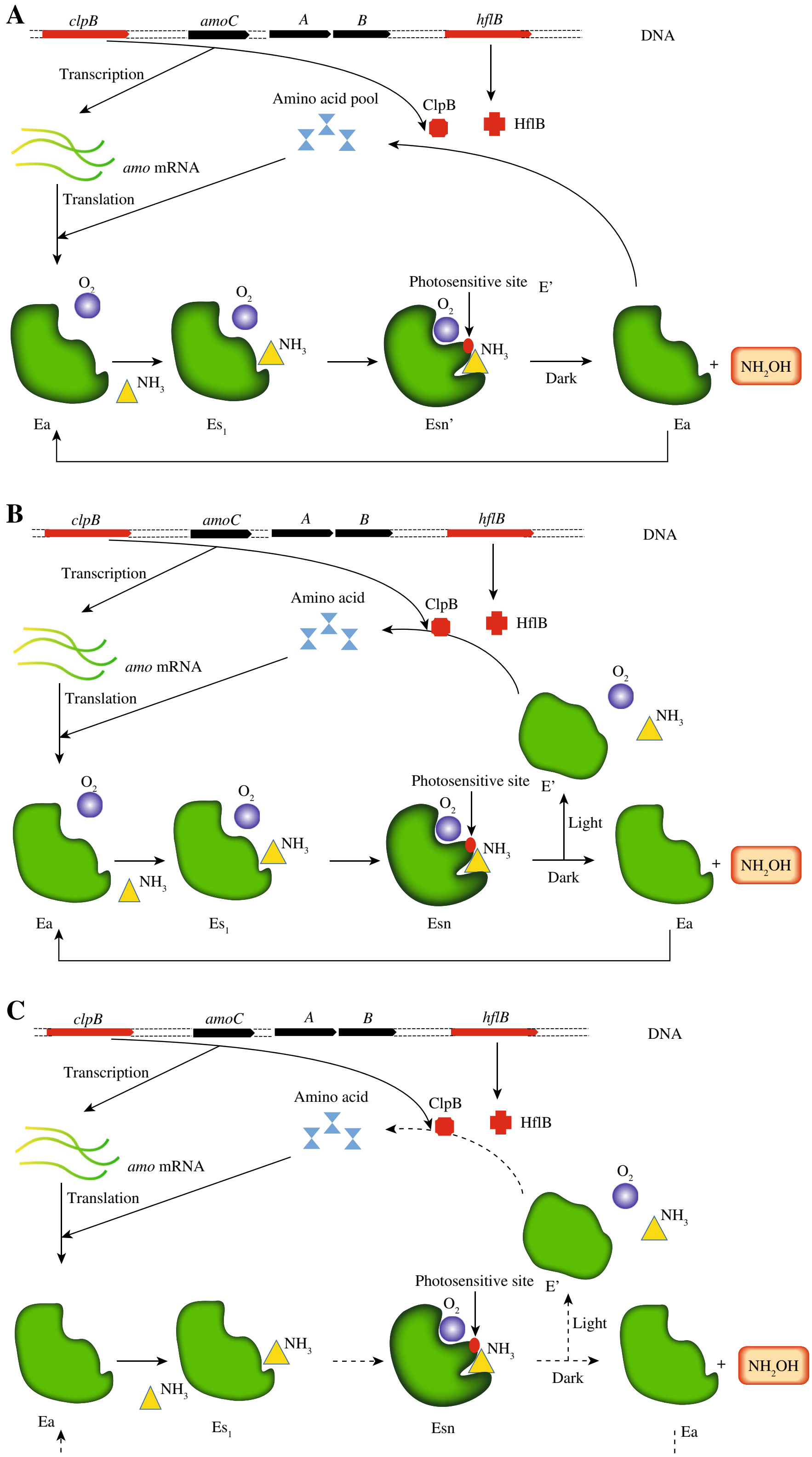

Fig. 3 Possible mechanisms of photoinhibition in AOB. Ea, Es_1, Esn and E' represent static, initially activated, photosensitive and photoinactive states of ammonia monooxygenase (AMO), respectively. Solid and dotted lines with arrows represent possible metabolic pathways and blocked metabolic pathways, respectively. In the NH_3 to NH_2OH process, there are many transitional intermediates of AMO; only intermediate Esn has photosensitive sites. If exposed to light, Esn can change into inactive E' or return to the static state Ea again. The relative position of genes *amoC*, *A*, *B*, *clpB* and *hflB* are based on the complete genome of *Nitrosomonas europaea ATCC* 19718. **a** When there is no light, the coordination of O_2 and NH_3 induces the conformation turn in AMO and NH_3 becomes NH_2OH. Inactivated AMO will be degraded by ATP-dependent proteases ClpB or HflB. **b** When there is light, the coordination of O_2 and NH_3 induce the conformation turn of AMO, NH_3 becomes NH_2OH. In the process, if photosensitive sites of intermediate Esn are exposed to light, the photo oxidated AMO E' will be degraded by ATP-dependent protease ClpB or HflB. **c** Under anaerobic conditions, because there is no O_2, the AMO cannot be induced into the photosensitive state, so anaerobic conditions can protect AOB from photoinactivation

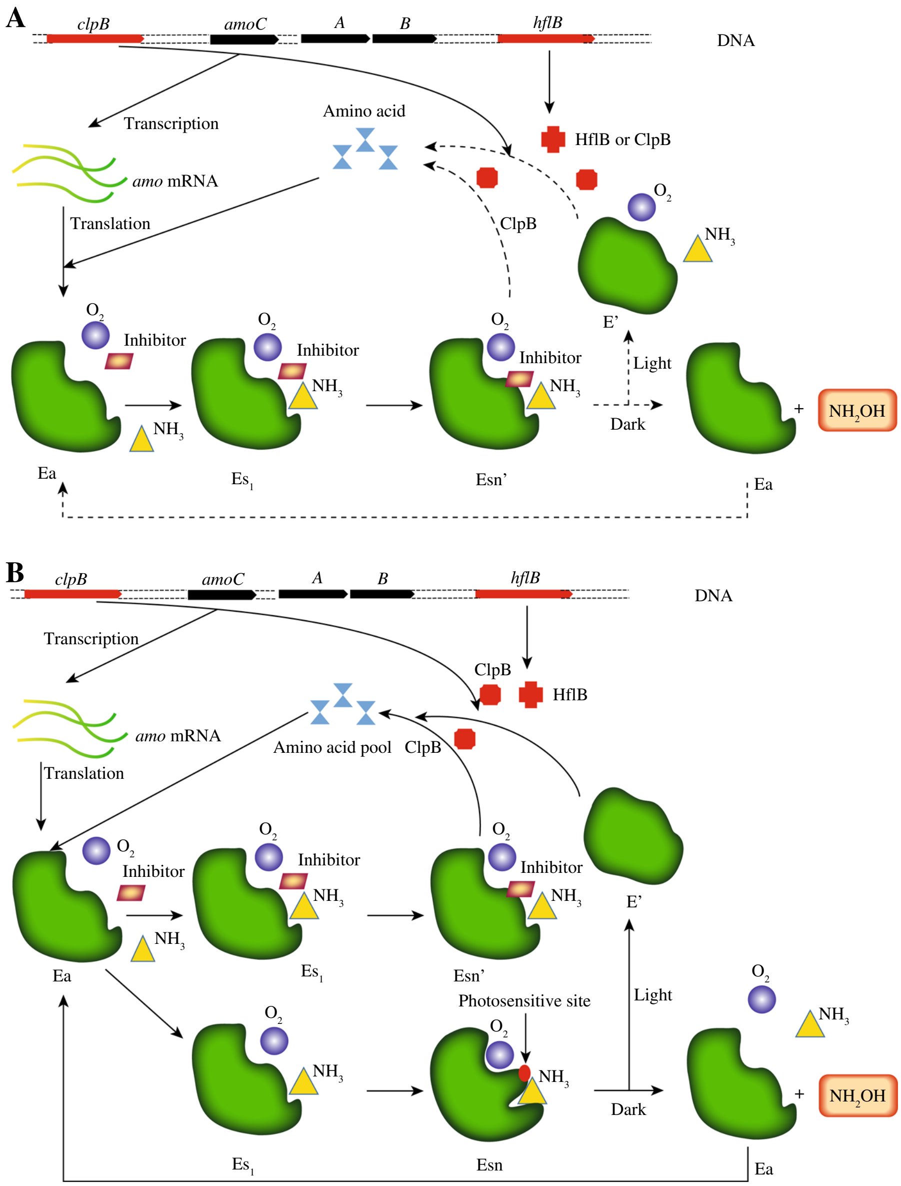

Fig. 4 Possible mechanisms of photoinhibition in AOB involving allylthiourea. Ea, Es_1, Esn and E' represent static, initially activated, photosensitive and photoinactive states of ammonia monooxygenase (AMO), respectively. Esn' represents AMO inactivated by allylthiourea. Solid and dotted lines with arrows represent possible metabolic pathways and blocked metabolic pathways, respectively. In the NH_3 to NH_2OH process, there are many transitional intermediates of AMO; only intermediate Esn has photosensitive sites. If exposed to light, Esn can change into inactive E' or return to the static state Ea again. **a** In allylthiourea at concentrations that caused 100% inhibition of ammonia oxidation. All AMO adopts inactive state Esn', NH_3 oxidation pathway stops completely, no ATP is produced and ATP-dependent protease ClpB or HflB cannot function. The inactive AMO Esn' cannot be depredated. Allylthiourea leads to a reversible loss of AMO activity, the AMO can regain NH_3 oxidation activity after illumination. **b** In allylthiourea concentrations causing less than 100% inhibition of ammonia oxidation. Part of AMO can translate NH_3 into NH_2OH, and it will be gradually inactivated by light, which is depredated by ClpB or HflB. Another part of inactive AMO Esn' by allylthiourea can be depredated by ClpB. The inhibition of allylthiourea to AMO is transient, but photoinactivation of ammonia oxidation follow first-order kinetics with a rate constant proportional to incident light intensity. Therefore, allylthiourea can accelerate AOB photoinhibition at this concentration

Table 2 A general timeline of representative research on the photoinhibition of ammonia-oxidizing microorganisms

Year	Research	Reference
1962	The first report of photoinhibition in pure cultures of *Nitrosomonas europaea*	Schoen and Engel (1962)
1973	Light as a specific inhibitor of ammonia oxidation in *Nitrosomonas*	Hooper and Terry (1973)
1974	Photoinactivation of ammonia oxidation in *Nitrosomonas*	Hooper and Terry (1974)
1981	Differential photoinhibition of marine nitrifying bacteria: a possible mechanism for the formation of the primary nitrite maximum	Olson (1981)
1984	Photoinhibition and recovery of NH_4^+-oxidizing bacteria and NO_2^- oxidizing bacteria	Takahito and Yatsuka (1984)
1985	Spectroscopic evidence for a photosensitive oxygenated state of ammonia mono-oxygenase	Shears and Wood (1985)
	Light and substrate concentration relationships with marine ammonium assimilation and oxidation rates	Ward (1985)
	The effects of light and nutrients on rates of ammonium transformation in a eutrophic river	Lipschultz et al. (1985)
1988	Effect of light on the activity and survival of *Nitrosomonas* sp. and *Nitrobacter* sp. isolates from fish ponds	Diab and Shilo (1988)
1989	Effect of CO and light on ammonium and nitrite oxidation by chemolithotrophic bacteria	Vanzella and Guerrero (1989)
1990	Oceanic and estuarine ammonium oxidation: Effects of light	Horrigan and Springer (1990)
1992	$^{14}C_2H_2$- and $^{14}CO_2$- 1abeling studies of *de novo* synthesis of polypeptides by *Nitrosomonas europaea* during recovery from acetylene and light inactivation of ammonia monooxygenase	Hyman and Arp (1992)
1996	Photoinhibition of marine nitrifying bacteria. I. Wavelength-dependent response	Guerrero and Jones (1996a)
	Photoinhibition of marine nitrifying bacteria. II. Dark recovery after monochromatic or polychromatic irradiation	Guerrero and Jones (1996b)
2000	Differential regulation of *amoA* and *amoB* gene copies in *Nitrosomonas europaea* upon exposure to acetylene or light	Stein et al. (2000)
2011	Spatial segregation of AOA and AOB in the dark-side and the light-side biofilm of a river cobbles	Merbt et al. (2011)
2012	Differential photoinhibition of bacterial and archaeal ammonia oxidation	Merbt et al. (2012)
	Differential photoinhibition of AOA and AOB from freshwater	French et al. (2012)
2014	Marine ammonia-oxidizing archaeal isolates display differential photoinhibition	Qin et al. (2014)
2018	Light and temperature control the seasonal distribution of Thaumarchaeota in the South Atlantic bight	Liu et al. (2018)
	The nitrogen and oxygen isotopes of nitrate confirmed that nitrification was not significant within the euphotic zone of North Atlantic Ocean	Peng et al. (2018)
2019	Stronger light levels in the future Arctic Ocean could further suppress nitrification and alter the composition of inorganic nitrogen, with implications for the structure of ecosystems	Shiozaki et al. (2019)
2020	Light exposure is responsible for the observed ineffectiveness of nitrifying bacteria in natural aquaculture environments	Wu et al. (2020)
2020	Nitrification or microalgal uptake is regulated more strongly by daily average light intensity than by instantaneous light intensity in batch reactors	Akizuki et al. (2020)

transmembrane protein), and their expression is upregulated when exposed to chloroform (Gvakharia et al. 2007). ClpB gene expression upregulates on exposure to chloromethane, a noncompetitive inhibitor of ammonia oxidation like allylthiourea, which prevents the irreversible loss of AMO activity

(Gvakharia et al. 2007). Moreover, it was documented that protease FtsH was responsible for the degradation and protective removal of the photooxidation protein in the thylakoid membranes of plant cells (Lindahl et al. 2000). Therefore, it can be speculated that the enzymes ClpB or HflB will recognize inactivated AMO caused by photooxidation and allylthiourea as a damaged protein and degrade and remove it over time. The inhibition of AMO by allylthiourea is transient, but photoinactivation of ammonia oxidation was shown to follow a rate constant proportional (Hooper and Terry 1974). It is implicated that AMO damaged by photoinactivation and inhibition by allylthiourea can be degraded simultaneously. Therefore, the experimental phenomenon presented is that allylthiourea can accelerate AOB photoinhibition at concentrations that do not cause less than 100% occupation of NH_3 oxidation (Fig. 4b).

To summarize, as shown in Figs. 3 and 4 the aforementioned can explain the photoinhibition phenomenon in AOB. (1) Ammonia oxidizers will be exposed to photoinhibition by visible light and can regain ammonia activity when moved from light to dark. (2) Anaerobic conditions can protect AOB from photoinhibition. (3) AOB showed very significant photosensitivity at low NH_3 concentrations, when NH_3-deprived or at low temperatures, whereas increasing NH_3 concentration can buffer AOB from significant photoinhibition. (4) Allylthiourea can protect AOB from photoinhibition at concentrations that cause 100% inhibition of ammonia oxidation. (5) Allylthiourea can accelerate AOB photoinactive at concentrations that cause less than 100% inhibition of ammonia oxidation.

To fully understand the cognition process behind the photoinhibition of ammonia oxidizers, a general timeline of representative research is available, as shown in Table 2. Early exploration mainly focuses on the physiological mechanism of photoinhibition in AOB. With the discovery of AOA, researching the ecological mechanism has been prioritized, especially the niche differentiation of AOA and AOB caused by light in aquatic environments. So far, there is still little direct evidence of the regulatory pathways involved in photoinhibition in AOA.

5 Conclusions

The photoinhibition phenomenon is widespread in oceans and freshwater environments. When the monochromatic (narrowband) light wavelength is longer than or equal to 500 nm, there was no influence on the NH_3 oxidation activity of AOB, while AOA cultures were still significantly lower in growth at 30 μmol photons $m^{-2}s^{-1}$ of 623 ± 3 nm light. The degree of photoinhibition increases with decreasing wavelength in the range of 300–623 nm, whereas, recovery after photoinactive is faster with increasing wavelength. The photoinhibition in AOB by visible light is mainly caused by irreversible damage to the copper-containing enzyme AMO, but not NH_2OH reductase, the new AMO synthesis was necessary for recovery after photoinactivation. Enhancing the ammonia-oxidizing activity of AOB, such as by increasing ammonia concentration, can buffer them from photoinhibition. An anaerobic and noncompetitive inhibitor like allylthiourea can protect AOB from photoinhibition at concentrations that cause 100% inhibition of ammonia oxidation.

AOA are more sensitive to light than AOB, the low availability of laboratory cultures in AOA has restricted physiological studies of photoinhibition, there is still a lack of comprehensive knowledge in this field about AOA. Therefore, further research about photoinhibition, especially in metabolic pathways of AOA, is urgently needed because it involves the composition of inorganic nitrogen and the stability of the oceans' ecosystem.

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