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Environmental factors militating against the activities of ammonia oxidizing archaea and ammonia oxidizing bacteria in soil

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Abstract

This review aims to scrutinize the effect of ammonia concentration, temperature, pH, drought and inhibitors on activity of AOA and AOB in soil. Ammonia concentration in soil increases during drought due to the reduced soil water content and, with desiccation stress or a combination of both factors result in greater inhibition of AOA than AOB during drought. AOA were more susceptible to increased desiccation stress than AOB, irrespective of initial soil ammonium concentration and AOA cultures were more sensitive than AOB to osmotic stress which represent an additional niche differentiating factor between AOA and AOB in soil. Activity and growth of AOA and AOB observed in soil amended with high ammonium concentration at different temperature, suggesting that AOA can contribute to nitrification in highly fertilized soil. The selective inhibition of AOA by simvastatin in culture and in soil provides evidence for oxidation of ammonia by AOB at low ammonium concentration. The findings advance our understanding of the influence of ammonium supply, temperature and osmotic stress on soil nitrification and its role in controlling the availability of ammonium-based fertilizers for plant uptake.

Keywords: Inhibition; Ammonia; Drought; Osmotic-stress; Niche

1. Introduction

Soil nitrification results in high commercial loss of ammonium-based fertilizers in soil (Raun and Johnson, 1999; Prosser, 2011; Subbarao *et al.,* 2015), with associated atmospheric and groundwater pollution by nitrous oxide (N_2O) and nitrate (NO^{3-}), respectively (Wrage *et al.,* 2001; Prosser, 2011; Hink *et al.,* 2016; Kozlowski *et al.,* 2014; 2016c). The nitrification process is usually limited by ammonia oxidation to nitrite (Prosser, 2011), which was thought to be driven only by ammonia oxidizing bacteria (AOB) (Prosser, 2011). Metagenomic studies (Venter *et al.,* 2004; Treusch *et al.,* 2005), cultivation of a marine ammonia oxidizing archaea (AOA) (*Candidatus. Nitrosopumilus maritimus*) (Konneke *et al.,* 2005) and the discovery of complete ammonia oxidizers (comammox) (Ca. *Nitrospira inopinata*) (Daims *et al*., 2015, van Kessel *et al.,* 2015) suggested a role for AOA and comammox in ammonia oxidation process in soil. The ammonia monooxygenase A gene (*amoA*) abundance of AOA and AOB, quantified determined using molecular method (quantitative polymerase chain reaction (qPCR)) indicate that AOA are more abundant, with a potentially greater role in soil ammonia oxidation compared to AOB (Leininger, *et al.,* 2006; Prosser and Nicol, 2008). These findings called for the reassessment of soil ammonia oxidizer (AO) community ecology and its significance for ammonia oxidation activity in soil. This raised questions for physiological features distinguishing between AOA and AOB, indicating their evolution and adaptation to certain sets of abiotic and biotic characteristics within the soil (i.e., niche specialisation) and consequently diverse patterns of utilizing resources (i.e., niche differentiation) (Erguder, *et al.,* 2009; Valentine, 2007). Several main distinguishing characteristics have been suggested: ammonia affinity (Martens-Habbena *et al.,* 2009), ammonia inhibition (Di *et al.,* 2009; 2010), ammonia source preference (Stopnišek *et al.,* 2010; Levičnik-Höfferle *et al.,* 2012), pH growth optimum (Prosser, 2011; Nicol *et al*., 2011), optimum growth temperature (Gubry-Rangin *et al.,* 2017; Jones and Morita, 1985; Koops and Harms, 1985; Lehtovirta-Morley *et al*., 2016; Jung *et al.,* 2016; Sauder *et al.,* 2017;

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Tourna *et al.,* 2011), sensitivity to drought (Thion and Prosser, 2014), requirement of salt concentration for growth (Koops and Harms, 1985) and inhibitors of ammonia oxidation activity (Martens-Habbena *et al.,* 2009; 2015; Taylor *et al.,* 2013; Vajrala *et al.,* 2014; Sauder *et al.,* 2016; Subbarao *et al.,* 2013; Lehtovirta-Morley *et al.,* 2013; Zhau *et al.,* 2019).

2. Environmental factors affecting AOA and AOB in soil

2.1. Substrate (ammonia)

Ammonia oxidation is the major source of energy for AOA and AOB, and the only known energy source under aerobic conditions. There are several studies indicating that soil AOA prefer ammonia derived from mineralized organic rather than inorganic sources of ammonia. For example, growth of AOA was stimulated by ammonia from the mineralization of natural soil organic matter (Gubry-Rangin *et al.,* 2010) and in studies of acidic forest soil samples with high levels of nitrification activity, AOA but not AOB were strongly linked to ammonia oxidation activity in the presence of organic sources of ammonia (Stopnišek *et al.,* 2010; Levičnik-Höfferle *et al.,* 2012). Only AOA were detected in the soil and different levels of inorganic ammonia amendment had no effect on the rates of ammonia oxidation. However, nitrification rates were stimulated by addition of the organic nitrogen sources such as glutamate, urea and yeast extract (Stopnišek *et al.,* 2010; Levičnik-Höfferle *et al.,* 2012).

Further evidence suggests that ammonia concentration differentially affects AOA and AOB in soil, as high concentrations of ammonium from cow urine and inorganic sources (200 μg NH_4^+ N g-1 soil) stimulate the growth and ammonia oxidation activities of AOB but inhibit AOA, leading to decreases in AOA:AOB, while low ammonia concentration stimulates the growth of AOA but not AOB (Prosser, 2011; Nicol *et al.,* 2011). Also, cultivated AOA generally have higher affinity for ammonia when compared to AOB (Martens-Habbena *et al.,* 2009; Lehtovirta-Morley *et al.,* 2011). However, recent soil experimental studies detected the growth of both AOA and AOB in soil amended with high ammonia concentration (Lu *et al.,* 2012; Hink *et al.,* 2016; 2017). Isolated AOA species that belong to the genus Ca. *Nitrosocosmicus* can grow at high ammonia concentrations similar to those tolerated by AOB (Lehtovirta-Morley *et al.,* 2016). Moreso, the growth of Ca. *Nitrosocosmicus* is greater when AOB are inhibited under high ammonia concentration which indicates that Ca. *Nitrosocosmicus* is tolerant to high ammonia concentration in soils. This disputes the belief that there is inhibition of AOA growth in soil with high ammonia concentration. It also confirms the role of a Ca. *Nitrosocosmicus* in nitrification activity in soil with higher ammonia concentration (Bello *et al.,* 2021). This strongly suggests that not all AOA are inhibited by high ammonia concentration and there may be no difference between AOA and AOB in terms of ammonia affinity in soil.

2.2. Soil pH

pH plays a significant role in the ecological distribution of different phylotypes of microorganisms in the soil (Fierer and Jackson, 2006). Soil nitrification activity is also strongly linked with pH. pH is a vital environmental factor in the distribution of AOA and AOB through its effect on the availability and toxicity of ammonia. As the pH decreases by one unit, the ammonia availability for ammonia oxidisers is reduced by one order of magnitude as ammonia is converted to ammonium (NH_3 to NH_4^+; pKa = 9.25) (Nicol *et al.,* 2011; Prosser, 2011); Secondly, the potential toxic effect of free ammonia will reduce with decreasing pH. Thirdly, nitrite availability will decrease as pH decreases, a condition that favours AOA at the expense of AOB. AOB have been isolated from acidic soil, but their growth and isolation required culture medium at near neutral pH (Prosser, 2011; Hayatsu *et* al., 2017). Potential mechanisms that explain the growth and survival of AOB in low pH are existence of high pH microsites, aggregate or biofilm formation, surface attachment and ureolytic activity, as indicated by culture-based studies (Prosser, 2011). The existence of microsites which enable acid-sensitive nitrification in the upper layer (organic layer) of acid soils are attributed to the relatively high pH of rain water and the presence of hot-spots of mineralisation. Micro-sites might be as small as the immediate surroundings of mineralisers, where ammonia may diffuse directly into AOB cells (De Boer and Kowalchuk, 2001). This observation was based on the detection of nitrification in acid heathland soil suspensions only upon the onset of net N mineralization, even though in the presence of excess ammonium (Levičnik-Höfferle *et al*., 2012).

An alternative explanation for acid-sensitive AOB to be active in acid soil is by intracellular hydrolysis of urea and subsequent nitrification of the ammonia released (De Boer and Kowalchuk, 2001). After urea activation, Nitrosospira strain AHB1 was able to continue ammonia oxidation for several days in an acid medium (pH 5.0) containing only ammonium (De Boer and Laanbroek, 1989). The possession of urease activity seems to be common among Nitrosospira strains isolated from acid soils (Prosser, 2011). Nevertheless, it is unlikely that AOB's ability to hydrolyse urea is a specific adaptation to acid environments, as strains isolated from several other environments also possess this ability (De Boer and Kowalchuk, 2001)

Several studies have suggested that aggregation or biofilm formation of AOB enables their activity at low pH (De Boer *et al*., 1991; Spieck *et al*., 1992). It has also been shown that a *Nitrosomonas sp*. was able to nitrify at lower pH in biofilms than in cell suspensions (Prosser, 2011). Therefore, aggregates and biofilms may provide the required cell density for activity at low pH. Extracellular substances in which the bacteria appear to be embedded may provide the suitable conditions for nitrification in acidic pH (Prosser, 2011). It is, however, not yet clear how aggregation or high cell densities stimulate nitrification in acid environments (de Boer *et al*., 1991, 1995). The most interesting problem is how cells can supply their ammonia monooxygenase with NH_3. It seems likely that they possess an ammonium transport system and that they can keep their cytoplasmic pH sufficiently high for NH_3 generation (de Boer and Kowalchuk, 2001). Under low pH conditions, nitrite is predominantly present in its free-acid form, nitric acid, which is either toxic or can create toxic products. Hence, for ammonia oxidation to continue at low pH, nitrite must be removed by acid-tolerant NOB of the genus Nitrobacter (de Boer and Kowalchuk, 2001). Electron micrographs of forest soil suspensions nitrifying at low pH (pH 4) have been shown to contain aggregates of Nitrosospira-like cells surrounded by Nitrobacter-like cells. Such an intimate association between the AOB and the NOB may facilitate the transfer of nitrite, thus preventing the accumulation of toxic compounds. However, the close association of AOB and NOB has also been confirmed in pH-neutral environments, and it remains to be seen exactly how interactions between AOB and NOB may contribute to microbial strategies for nitrification in acid environments (de Boer and Kowalchuk, 2001).

The role of pH as a strong environmental factor for AO distributions in soil is well known. Several AO clades prefer specific soil pH which reflects their evolutionary histories (Nicol *et al*., 2011; Oton *et al*., 2016). Nitrosospira clusters 2, 3 and 4 are common soil AOB. Representatives of Nitrosospira cluster 2 prefer acidic soil because they are the predominant AOB in acidic agricultural soil (pH 4.5), acidic grassland pasture soil and acidic forest soils (Prosser, 2011; Nicol *et al*., 2011). The adaptation of Nitrosospira cluster 2 species to low pH may be linked to uerolytic ability (de Boer and Laanbroek, 1989), and other mechanisms facilitating growth of Nitrosospira cluster 2 may also exist (Prosser and Embley 2002). Nitrosospira cluster 3 AOB are naturally found in neutral pH soils, while some phylotypes are present in acidic soils, whereas the abundance of cluster 4 is less affected by soil pH (Prosser, 2011; Nicol *et al*., 2011). The long-term effect of soil pH influences the ammonia oxidation activity of AOA and AOB. The transcriptional activity of AOA decreases, while that of AOB increases with increase in soil pH (Nicol *et al*., 2011). Lastly, the impact of soil pH on the distribution and community structure of AOA has been locally, regionally and globally observed with certain AOA clades showing preference to specific pH (Gubry-Rangin *et al*., 2011; Vico-Oton *et al*., 2016).

2.3. Temperature

Temperature is one of the major ecological factors that affect both the activity and abundance of all soil microorganisms and associated geochemical cycles in the ecosystem (Szukics *et al.,* 2010). Ammonia oxidation has been measured at high temperatures in hot spring environments (76 to 87 ^{o}C) in the USA (de la Torre *et al.,* 2008), China (Zhang *et al.,* 2008) and Russia (Pearson *et al.,* 2008). Soil nitrification has been measured also at temperatures as low as 2 ^{o}C in winter soil (Cookson *et al.,* 2002) and nitrification activity has been documented in arctic soils with low temperature from 4 to 12 ^{o}C (Alves *et al.,* 2013). Optimum nitrification activity in soil occurs between 20 and 35 ^{o}C (Nicol *et al.,* 2011; Prosser, 2011; Gubry-Rangin *et al.,* 2017).

Nitrification activity and amoA abundance of AO increase while the community structure of AO changes with increase in temperature from 10 to 35 ^{o}C (Nicol *et al.,* 2011; Prosser, 2011). Another line of evidence also linked soil pH to temperature response of AOA (amoA abundance) in soil at low ammonia concentration. This is due to the detection of different optimum growth temperatures for AOA in acidic soils (pH 3.9 to 4.7) and acido-neutral soils (pH 5.0 to 7.5) (20 ^{o}C and 30 ^{o}C, respectively) (Gubry-Rangin *et al.,* 2017). Soil ammonia oxidation activity and AOA amoA abundance decrease at temperatures above 30 ^{o}C (Gubry-Rangin *et al.,* 2017). For cultured isolates, AOB growth and nitrite production increased from 0 ^{o}C (in *N. cryotolerans*) and 5 ^{o}C (in other *Nitrosomonas spp*.) to 28 ^{o}C with optimum growth at 28 ^{o}C (Jones and Morita, 1985; Koops and Harms, 1985), while Comammox (*N. inopinata*) grow optimally at 46 ^{o}C (Daims *et al.,* 2015). Studies also indicate that nitrite production and amoA abundance of AOA isolates (e.g., *Ca. N. franklandus, Ca. N. oleophilus, Ca. N. exaquare and N. vienniensis*) increases with increase in temperature and with optima at 40, 30, 33 and 42 ^{o}C, respectively (Lehtovirta-Morley *et al*., 2016; Jung *et al.,* 2016; Sauder *et al.,* 2017; Tourna *et al.,* 2011). However, nitrification by ammonia oxidizersin soil decreases in a near neutral soil after temperature of 30^{o}C (Bello *et al.,* 2021).

2.4. Drought

Drought as a natural phenomenon is an abnormal dry weather condition that lasts long enough to cause a reduction in water content, changes in biogeochemical cycles mediated by microorganisms in the soil and damage to plants due to inability of both microbes and plants to absorb water from soil as a result of the decrease in matric potential (Wilhite and Glantz, 1985). It is a major factor which affects microorganisms and biogeochemical processes in the soil. It causes

a reduction in the thickness of water films on the surface of the soil particles leading to shortage in supply of substrate to microorganisms, reduction in microbial movement, change in structure of the microbial communities and activities in the soil including nitrification (Schimel *et al.,* 2007). The decrease in matric potential and osmotic potential increases desiccation and osmotic stress. Water potential is defined as the work done in moving one molecule of water from some point in the system at a constant temperature and pressure to a pool of pure water at atmospheric pressure and at the same temperature as the system (Griffin, 1981; Campbell, 1985). Matric water potential generally applies to water interactions at surfaces and interfaces (Potts, 1994). Once water molecules are associated with interfaces such as the surfaces of solid particles e.g. soil, proteins, ribosomes, bacteria, and viruses in an aqueous solution, they have less affinity to react chemically in solutions or to escape to the surrounding vapour phase. Interfaces thus decrease the thermodynamic activity of water, especially near the solid surface (Potts, 1994). Interfaces, together with solutes, lower water activity (aw) so that there is an additive effect in solutions which contain solutes and solid particles. The removal of a considerable fraction of water from microbial cells through a drying stress is called desiccation, which can be achieved either by rapid or slow drying process. One major contrast between matric stress and osmotic systems is that under desiccation the surface of microbial cell walls that are exposed to a gas phase, which is referred to as matric stress, whereas under osmotic stress microbial cells are constantly covered in an aqueous solution, even though water activity is reduced (Potts, 1994).

A decrease in matric potential reduces the movement of bacteria within the soil matrix (Schimel *et al.,* 2007; Or *et al.,* 2007). The reduction in the thickness of water films on the surface of the soil particles reduces the supply of substrate, such as ammonia for ammonia oxidizers (AO) (Stark and Firestone, 1995). The physiological costs caused by drought on soil microorganisms leads to great changes in essential minerals (carbon and nitrogen) distribution in soil. Hence, matric potential plays a vital role in structuring the microbial communities and biogeochemical cycles they control in the soil (Griffin, 1981; Schimel *et al.,* 2007; Wagner, 2017). A decrease in soil matric potential leads to the acquisition of osmolytes and/or production of compatible solutes by microorganisms (Csonka, 1989; Roeßler and Müller, 2001).

Osmolytes are organic solutes or ions that are used by microorganisms to maintain cell volume and balance the cytoplasmic concentration with the outer environment to prevent cell lysis (microorganism) or plasmolysis (plant). Osmolytes are accumulated through the production of organic solute (compatible solutes) or the absorption of ions from the surrounding solutions (osmo-protectant) to maintain cellular integrity (Roeßler and Müller, 2001; Schimel *et al.,* 2007; Or *et al.,* 2007). Microbial response to a decrease in matric potential varies from one organism to the other. However, the preservation of stability of the entire microbial community is connected to the stimulation of protective or adaptive survival mechanisms (Schimel *et al.,* 2007; Roeßler and Müller, 2001; Allison and Martiny, 2008). The process by which microorganisms accumulate osmolytes for maintenance of cellular integrity during drought requires high energy, which may be detrimental to the activities of the intracellular enzymes, due to the inhibition of their activities by high concentration of solutes which decrease the water potential within the cell (Griffin, 1981; Roeßler and Müller, 2001).

Archaea and bacteria both respond to changes in the soil matric potential by producing osmolytes and/or acquiring compatible solutes. Archaeal compatible solutes are different from their bacterial counterparts. Archaea produce polyhydric alcohol phosphodiesters and the majority of archaeal osmolytes have carboxylate, phosphate or sulphate groups and are thus negatively charged ions (Roeßler and Müller, 2001). The negatively-charged ion helps to counteract the high intracellular concentration of common cation (K^+) found in archaea. The potassium ion (K^+) found in archaea is used for the maintenance of internal protein folding and hydrophobicity. By contrast, bacterial osmolytes mainly comprise of α-amino acids and their derivatives such as proline, alpha-glutamic acid and betaine (Roeßler and Müller, 2001).

Climate change, due to anthropogenic activity, has led to an increase in drought periods in many soils that were previously not affected by drought (IPCC, 2007). Several studies indicate that the nitrification activity in soil decreases during drought (Stark and Firestone, 1995; Gleeson *et al.,* 2010; Vasileiadis *et al.,* 2012; Thion and Prosser, 2014). Studies have also shown that AOA and AOB respond differently to changes in soil water potential. AOB *amoA* abundance increases while AOA amoA abundance decreases in the soil when soil water-filled pore spaces (WFPS) changes from dry to wet (Gleeson *et al.,* 2010). Other studies by Thion and Prosser, (2014) indicate that AOB are less sensitive to drought than AOA, and AOB are more resilient than AOA after rewetting. The sensitivity of AOA in the soil subjected to drought has been linked to the inhibition by high ammonium concentration observed after rewetting (Thion and Prosser, 2014). In contrast, there is evidence that a decrease in soil matric potential inhibits AOB but not AOA *amoA* transcriptional activity (Vasileiadis *et al.,* 2012). Comparison of *amoA* abundance dynamics and nitrite production suggests that AOA were more susceptible to reduced matric potential than AOB, irrespective of ammonia concentration in soil and culture, respectively (Bello *et al.,* 2019. These results provide evidence for greater sensitivity of AOA than

AOB to both components of water stress, matric and osmotic potential, which represents an additional niche differentiation between these two essential groups of ammonia oxidizers.

2.5. Salt concentration

Studies have linked the salt (NaCl) requirements by AOA and AOB for growth to the conditions in the natural environment of the organisms (Koops and Harms, 1985). For example, AOB isolated from marine and brackish waters have an obligate requirement for NaCl for growth with optimum NaCl requirement between 300 and 400 mM, while other species of AOB do not require NaCl for growth but can tolerate NaCl concentrations between 0 and 100 mM. However, AOB strains isolated from eutrophic environments generally tolerate higher levels of NaCl (between 400 and 500 mM) than species from other environments. AOB isolated from soil and freshwater environments only tolerate NaCl concentrations between 200 and 300 mM (Koop and Harms, 1985). Experimental studies of AOB (*N. europaea* NCIMB 11850) indicate that growth is stimulated in liquid culture by addition of ≤100 mM NaCl and further increase in NaCl concentration reduces its growth rate (Wood and SÖrensen, 1998). The recent study on the AOA, Ca. *Nitrosotenuis cloacae* shows that it has a low salt tolerance (≤ 0.27 mM) and its growth rate is reduced with increasing NaCl concentration (Li *et al.,* 2016). Other evidence indicates that some AOA are better adapted to a lower salinity environment (Mosier *et al.,* 2012) except for the marine AOA isolate Ca. *N. maritimus* which requires a high concentration of about 445 mM NaCl for optimum growth (Konneke *et al.,* 2005; Mosier and Francis, 2008).

2.6. Nitrification inhibitors

Table 1 Examples and characteristics of general and selective NIs

Nitrification inhibitors	Mechanisms of actions	Examples of organisms tested	References
Acetylene (C_2H_2)	It irreversibly inhibits AOA and AOB amo, (both in pure cultures and soil). It forms a covalent bond with the enzyme by blocking the binding of ammonia	*N. europaea, N. multiformis, N. maritimus*, *Ca.* N. devanaterra	Hyman and Wood, 1983; Hynes and Knowles, 1978; Lehtovirta-Morley *et al.,* 2011; Tourna *et al.,* 2011; Offre *et al.,* 2009
1-octyne	It inhibits AOB amo, (both in pure cultures and soil) by blocking the binding of ammonia	*N. europaea, N. multiformis, N. maritimus*	Taylor *et al.,* 2013; Hink *et al.,* 2016
Cycloheximide	It inhibits protein synthesis in eukaryotes and AOA.	*N. maritimus* and *N. europaea*	Vajrala *et al.,* 2014; Hayatsu *et al.,* 2008; De Boer and Kowalchuk, 2001
2-phenyl-4,4,5,5-tetramethylimidazoline-1-oxide-3-oxyl (PTIO)	Nitric oxide (NO) scavengers, it reacts with other nitrogen oxide compounds such as NO, NO_2 and HNO. It inhibits AOA in pure cultures only	*N. maritimus*, *N. viennensis, N. europaea, N. briensis, N. multiformis, N. cryotolerans, N. ureae, N. oligotropha, N. oceani*	Yan *et al.,* 2012; Goldstein *et al.,* 2003; Ellis *et al.,* 2001; Walker *et al.,* 2010; Shen *et al.,* 2013; Jung *et al.,* 2014; Martens-Habbena *et al.,* 2015
Trolox, Methylene blue hydrate, Caffeic acid and Curcumin	nitric oxide scavengers, it inhibits AOA in pure cultures only	*N. europaea, N. maritimus,* AOA-G6 and AOA-6f	Sauder *et al.,* 2016
Dicyandiamide	It prevents ammonia uptake, utilisation and act as a copper chelator in AOA	*Ca.* N. devanaterra	Subbarao *et al.,* 2013; Lehtovirta-Morley *et al.,* 2013
Nitrapyrin (2-chloro-6-(trichloromethyl) pyridine)	It chelates copper in AOA amo	*Ca.* N. devanaterra	Subbarao *et al.,* 2013; Lehtovirta-Morley *et al.,* 2013

Allylthiourea (ATU)	It chelates copper in AOA amo	*Ca.* N. devanaterra and *N. viennensis*	Martens-Habbena *et al.,* 2015; Lehtovirta-Morley *et al.,* 2013
Simvastatin	It irreversibly inhibits AOA but stimulates AOB in culture and soil	*N. europaea, N. multiformis, N. maritimus*, *Ca.* N. devanaterra	Bello *et al.,* 2020

Nitrification inhibitors (NIs) are substances that prevent ammonia oxidation to nitrite by AO. NIs prevent nitrogen loss in the soil and thus help promote plant growth. There are two main types of NI namely biological and chemical or synthetic nitrification inhibitors. Biological nitrification inhibition (BNI) refers to the natural ability of certain plants or other species of microorganisms to produce and release NIs to suppress the activity of nitrifying microorganisms and reduce or prevent nitrification and nitrous oxide emission in soil (Subbarao *et al*., 2013). Common examples of plants with potent BNIs are *Brachiaria sp*., *Pennisetum maximum* and feed-grain crops such as sorghum (Subbarao *et al.,* 2010). Numerous BNIs that belong to different chemical groups have been isolated, identified and purified from plant tissues or root exudates (Subbarao *et al*., 2013). Compounds with NI activity in the root and shoot systems of B. humidicola include Brachialactone, unsaturated free fatty acids (FFA), linoleic acid and alpha-linolenic acid (Subbarao *et al*., 2010). Brachialactone, linoleic acid and alpha-linolenic acid inhibit nitrification activity in both AOA and AOB by binding to the active sites of the two enzymes that are involved in the oxidation of ammonia to hydroxylamine and the conversion of hydroxylamine to nitrite (AMO and HDH) in *N. europaea* (Subbarao *et al*., 2010).

A phenyl propanoid root exudate from sorghum, methyl 3-(4-hydroxyphenyl) propionate (MHPP), is also a potent biological nitrification inhibitor. MHPP inhibits nitrification by blocking the active site of AMO, but it has no inhibitory effect on HAO. BNIs such as sorgoleone, a p-benzoquinone exudate from root of sorghum plant, are also capable of inhibiting AOB. Sorgoleone contributes immensely to the biological nitrification inhibition capacity in sorghum plant (Subbarao *et al.,* 2013). Other BNIs, such as methyl ferulate and methyl-p-coumarate found in the root tissues of *B. humidicola*, also inhibit nitrification activity in the soil (Subbarao *et al*., 2013). Chemical nitrification inhibitors (CNIs) have been used as metabolic blockers in several ecological studies (Prosser, 2011). Nitrification inhibitors were important to understand the type of interactions between AO and NOB and, after the discovery of AOA in 2005, to differentiate the relative contributions of AOA and AOB to nitrification in different ecosystems where AOA and AOB coexist (Taylor *et al.,* 2013). In summary, selective inhibitors are an important tool in studying nitrification, in addition to the possible application for increasing the efficiency of nitrogen-based fertilizers. Examples and characteristics of general and selective CNIs that have been used in studying nitrification activity and archaea inhibition are listed in Table 1. Simvastatin (8–100μM) selectively inhibits AOA in culture and in soil under low and high ammonia concentrations but stimulates AOB in both acidic (pH 4.5) and near-neutral (pH 6.5) soils (Bello *et al.,* 2020). This suggest simvastatin as a selective AOA inhibitor which can be used to investigate kinetic characteristics of AOB in soils and to study the competition between AOA and AOB in soil.

2.7. Potential future studies

This review reports several research on the effect of ammonium-based fertilizer application in commercial agricultural practice on soil nitrification. Several studies have been conducted to determine the effect of ammonia concentration on ammonia oxidation and nitrification rate in soil. Additional investigation of this would further our knowledge in understanding the effect of different ammonia concentrations on the rate of nitrification in soil. Simvastatin has been identified as a potent inhibitor of ammonia oxidation in AOA. Simvastatin is a general archaeal inhibitor, application of simvastatin with ammonium-based fertilizer will inhibit all archaea in soil with unknown ecological consequences. Therefore, further studies of ecological effect of simvastatin in soil is recommended before commercial use. This study also provided evidence that acidophilic and neutrophilic AOA respond differently to simvastatin in terms of the inhibitory concentrations. However, it is understood that few AOA and AOB representatives have been used to investigate ammonia oxidation inhibition by simvastatin. Therefore, additional screening of other AOA and AOB activity inhibition by simvastatin is recommended for further studies in order to generalize the recent findings. Also, evaluation of contributions of comammox to ammonia oxidation activity in soil is recommended for future studies

3. Conclusion

The discovery of AOA initiated research for important environmental factors causing niche differentiation between AOA and AOB. This review exploited the synergy of culture-dependent and soil microcosm techniques to determine and separate the effects of major environmental factors (i.e., drought, ammonia concentration, temperature and inhibitor of

ammonia oxidation) distinguishing AOB and AOA in soil ecosystems. Using both (culture-dependent and soil microcosms) approaches, it was demonstrated by the studies reported in this review, that the inhibition of growth and ammonia oxidation activity in AOA during drought had no link with the concentration of ammonia in soil during this period. Also, both AOA and AOB are able to oxidize ammonia and grow, irrespective of the ammonia concentration in soil. Hence, this fact that AOA and AOB oxidized ammonia at low and high ammonia concentrations disproves previous assumptions of niche separation of AOA and AOB by different ammonia concentrations. Therefore, the combination of the different approaches was more beneficial in advancing the knowledge of nitrification in soil ecology compared to a single approach.

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