

Impact of Climate Change on Soil N₂O Emission

Subjects: Ecology

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Microbial-driven processes, including nitrification and denitrification closely related to soil nitrous oxide (N₂O) production, are orchestrated by a network of enzymes and genes such as *amoA* genes from ammonia-oxidizing bacteria (AOB) and archaea (AOA), *narG* (nitrate reductase), *nirS* and *nirK* (nitrite reductase), and *nosZ* (N₂O reductase). However, how climatic factors could influence these genes and processes and, consequently, soil N₂O emissions remain unclear.

Keywords: denitrification ; global warming ; greenhouse gas emission ; mega-analysis ; nitrogen fertilizer ; N₂O ; precipitation

1. Introduction

In the face of a growing global population, a paramount challenge is to increase production levels of food, feed, fiber, and fuel crops while simultaneously mitigating associated environmental impacts [1][2][3]. To meet the ever-increasing demands for food and energy, substantial quantities of chemical fertilizers, notably inorganic nitrogen (N) fertilizers, are routinely applied to agricultural lands each year. Although essential for production, this practice has created a serious problem: the release of soil greenhouse gases, most notably nitrous oxide (N₂O), into the atmosphere [4][5]. The repeated and excessive use of N fertilizers, coupled with N deposition and climate change, has amplified challenges related to nitrate leaching and N₂O emissions. Agricultural soils contribute up to 80% of anthropogenic N₂O emissions [6][7][8]. Remarkably, N₂O is a potent, long-lived powerful greenhouse gas with a global warming potential 265 times greater than CO₂ [2][9]. In addition to its impact on global warming, N₂O plays a significant role in stratospheric O₃ depletion [10]. Through photolysis and oxidation to nitric oxide, N₂O can contribute to O₃ depletion in the stratosphere, further accelerating global climate change with diverse effects on human health [11][12].

In recent years, the atmospheric N₂O concentration has risen from 270 ppb during the preindustrial era to 330 ppb, with an average increase of 0.73 ppb year⁻¹ [2][13]. Global N₂O emissions stemming from N inputs have surged by more than 30% in the past four decades [7][14]. Projections suggest that by 2030, N₂O emissions from croplands could make up 59% of global N₂O emissions [5][15]. This heightened N₂O emission disrupts greenhouse gas balances, offsetting the climate benefits gained from CO₂ removal and other climate mitigation strategies [2][16]. To address this escalating N₂O issue, a comprehensive understanding of the mechanisms and mitigation strategies for soil N₂O emission is not just valuable but indeed imperative.

Soil N₂O production and soil N cycling are intricately influenced by a diverse array of functional soil microorganisms [5][17][18]. Key players in this context include *amoA* genes of ammonia-oxidizing archaea (AOA) and ammonia-oxidizing bacteria (AOB), along with crucial functional genes such as *narG* (encoding nitrate reductase), *nirK* and *nirS* (encoding nitrite reductase), and *norB* and *nosZ* (encoding nitrous oxide reductase) genes [5][8][19]. These genes are significant actors in soil nitrification and denitrification processes. It is important to note that these nitrifying and denitrifying genes can be influenced by many factors, including climate change and various agricultural practices, leading to modifications in soil N transformation rates [5][20][21]. Consequently, evaluating the impacts of global climate change and agricultural practices on N cycling, especially concerning nitrification and denitrification, holds significant importance, as their effects on these microbial processes can induce positive feedback on climate change [7][22].

Numerous investigations have been undertaken in recent decades to explore the repercussions of climate change and agricultural practices on soil N₂O emissions in terrestrial ecosystems [2][23][24]. Due to the inconsistency among different individual studies, meta-analysis has been utilized to synthesize the results from these studies. Recently, a surge in meta-analyses has sought to quantify the impacts of these factors and practices [5][8][14][22]. However, these meta-analyses have, at times, produced varying results, promoting the need for a comprehensive evaluation [25]. This review aims to fill this gap by synthesizing the results of these meta-analyses on the impacts of climate change on soil N₂O emissions. It also delves into potential mechanisms underlying these effects on enzyme activities and genes associated with nitrification and denitrification processes. This review begins with a brief overview of N cycling and the role of N₂O

emissions in climate change, laying the groundwork for an in-depth discussion on the process and key genes governing soil emissions. Special emphasis is placed on recent meta-analysis studies, quantifying the impacts of climate change, such as global warming, elevated CO₂, and precipitation changes on soil N₂O emissions, utilizing mega-analysis (i.e., meta-meta-analysis) techniques.

2. Impacts of Climate Change on Gene, Enzyme, Nitrification and Denitrification Processes, and Soil N₂O Emissions

Climate change such as global warming, elevated CO₂ concentration, and precipitation change has the potential to exert significant influences on soil N processes and soil N₂O emissions [26][27][28]. Here, the researchers collected data from meta-analyses exploring the impacts of climate change and quantitatively evaluated the response ratios concerning the effects of global warming, elevated CO₂ levels, alterations in precipitation patterns on various aspects of soil N dynamics, including soil N pools, abundance of genes, and soil N₂O emissions.

2.1. Impacts of Global Warming

Global warming has the potential to significantly influence microbially mediated N cycling processes, including N mineralization, nitrification, and denitrification. These alternations can lead to notable changes in soil N pool sizes, N availability, and soil N₂O emissions in terrestrial ecosystems [29]. A range of studies has demonstrated that increases in temperature can modify microbial N immobilization and mineralization rates [30][31][32]. Ecosystems and climate zones may have significant impacts on soil N processes. For example, those in forest soils can have different responses from those in grasslands. Cold regions may show more sensitive responses to warming than warm regions [33]. Additionally, several studies have reported that increased temperatures stimulate soil microbial metabolism, enhance soil enzyme activities, and accelerate the decomposition of organic matter [28]. Furthermore, elevated temperatures have been found to increase the abundances of genes like *nirK* and *nosZ* [34][35], with *nirS*-containing denitrifiers being more sensitive to temperature increases than those containing *nirK* and *nosZ* genes [26]. However, it is worth noting that several other studies have reported that elevated temperatures do not change the abundance of *amoA* genes or have found inconsistent responses of AOA and AOB to elevated temperatures [36][37].

To assess the overall impact of global warming on N processes, meta-analyses have been conducted on the impacts of temperature on soil N processes, enzyme activities, and soil functional genes involved in N₂O emission. In an early meta-analysis examining the influence of warming on soil N₂O emission, Bai et al. [38] collected 528 observations from 51 papers, revealing a non-significant mean effect size of 0.128 of soil N₂O emission by warming, based on 26 studies. Dai et al. [29] synthesized a comprehensive dataset of 1270 observations from 134 papers and revealed that elevated temperature significantly amplifies soil nitrification and denitrification rates, leading to a notable surge of up to 227% in N₂O emissions. The prevalence of the *nirS* gene increases in the presence of plants, whereas the *nosZ* gene becomes more predominant in the absence of plants at elevated temperatures. Conversely, the AOA, AOB, and *nirK* genes remain unaffected by the elevated temperature. More recently, Li et al. [27] analyzed 72 case studies from 46 papers and found that increased temperatures do not significantly affect the abundance of archaeal *amoA*, bacterial *amoA*, and *nosZ* genes, but they significantly decrease the abundances of *nirK* and *nirS* genes by 26% and 31%, respectively. Temperature increases N₂O emissions by 33%. Additionally, Salazar et al. [39] found that warming leads to increased N mineralization rates and N₂O emissions in cold ecosystems due to heightened enzyme activity targeting relatively labile N sources rather than alternations in the abundance of N-relevant genes (e.g., *amoA* and *nosZ*). Liu et al. [40] synthesized 1845 measurements from 164 publications and found that warming significantly enhances soil N₂O emission. About 1.5 °C of experimental warming significantly stimulates N₂O emissions by 35.2%.

The researchers quantified the impacts of warming on nitrification and denitrification genes and soil N₂O emission based on four meta-analyses (Table 1 and Table 2). The results of this mega-analysis showed that warming did not influence AOA or AOB (Table 2), but reduced MBN (−15.1%), and stimulated soil N₂O emissions (147.9%) (Table 1). Warming did not change *nirK*, *nirS*, and *nosZ* (Table 2). It enhanced the mineralization rate by 153.0%, nitrification rate by 62.0%, and denitrification rate by 159.7% (Table 1). It also increased Protease by 38.7% and Urease by 216.5% (Table 1). While there was no significant impact on the abundance of AOA and AOB, warming led to a decrease in MBN, increased soil N₂O emissions, and stimulated rates of N cycling processes such as mineralization, nitrification, and denitrification. The increased enzyme activities further highlight the accelerated decomposition of organic matter and nutrient cycling under warming conditions.

Table 1. Effects of climate change factors on the main microbial enzymes and nitrification and denitrification rates, based on results of meta- and mega-analyses. Values are effective size (RR, %) with 95% confidence intervals.

Climate Change Factor	Nitrogen Fixation		Mineralization			Nitrification			Denitrification		MBC	MBN	Soil N ₂ O Emission	Reference	
	Rate	Bacteria	Rate	Protease	Urease	NH ₄ ⁺ -N	Rate	Enzyme	NO ₃ ⁻ -N	Rate					Enzyme
Warming		-9.1% [-34.7%, 26.5%]	153.0% [106.9%, 209.4%]	38.7% [6.4%, 80.7%]	216.5% [59.5%, 528.0%]	-0.6% [-20.8%, 24.7%]	62.0% [33.2%, 97.1%]		8.6% [-14.0%, 37.4%]	159.7% [127.1%, 196.9%]		-15.1% [-27.4%, -0.7%]	147.9% [92.2%, 219.7%]	[27][28][29][39]	
Elevated CO ₂						-0.3% [-7.1%, 7.0%]	32.7% [7.4%, 63.9%]	-18.4% [-32.7%, -1.0%]	13.1% [4.7%, 22.1%]	5.3% [-7.7%, 20.1%]	-20.8% [-34.5%, -4.2%]	1.6% [-20.1%, 29.1%]	27.8% [16.4%, 40.3%]	40.6% [25.3%, 57.8%]	[12][22][28]
PPT+													54.2% [29.5%, 83.7%]	[27][28]	
PPT-													-45.9% [-55.9%, -33.6%]	[27][28]	

Table 2. Effects of climate change factors on the abundance of main genes involved in the processes of nitrification and

Table 2. Effects of climate change factors on the abundance of main genes involved in the processes of nitrification and denitrification based on the results of meta- and mega-analyses. Values are effective size (RR, %) with 95% confidence intervals.

Climate Change Factor	Nitrogen Fixation		Nitrification		Denitrification		Reference
	Rate	Bacteria	Rate	Enzyme	Rate	Enzyme	
Warming	-5.1% [-11.3%, 6.7%]		0.7% [-15.5%, 20.0%]		-1.34% [-22.0%, 24.7%]		[27][28][29][39]
Elevated CO ₂			5.7% [-9.8%, 23.9%]		12.8% [-9.5%, 40.6%]		[12][22][28]
PPT+			-5.1% [-29.9%, 28.4%]		-33.2% [-44.7%, 9.4%]		[27][28]
PPT-			28.5% [-20.0%, 106.6%]		23.4% [-4.1%, 58.8%]		[27][28]

Note: Bolded values indicate significant effects. MBC: microbial biomass carbon. MBN: microbial biomass nitrogen.

Note: Bolded values indicate significant effects. PPT+ indicates increased precipitation. PPT- indicates reduced precipitation. AOA: *amoA* genes from ammonia-oxidizing archaea. AOB: *amoA* genes from ammonia-oxidizing bacteria. *narG*: nitrate reductase. *nirS* and *nirK*: nitrite reductase. *nosZ*: N₂O reductase.

2.2. Impacts of Elevated CO₂

It is well documented that elevated CO₂ enhances plant growth and biomass production and increases ecosystem carbon sequestration [13][27][41]. Elevated CO₂ can also have several other impacts, such as promoting organic C decomposition, enhancing microbial activity, and stimulating soil extracellular enzyme activity [28][42]. However, the impacts of elevated CO₂ on nitrification, denitrification, and associated functional genes are still a topic of ongoing research, and the results are not consistent. Various studies have reported diverse responses to elevated CO₂ in the nitrification and denitrification rates, with some showing negative, positive, or neutral effects of elevated CO₂ on these processes [13][43]. Variations also exist in the responses of nitrifying and denitrifying functional genes to elevated CO₂ conditions. Different studies have reported divergent outcomes, indicating that the amounts of AOA, AOB, *nirK*, *nirS*, and *nosZ* functional genes may exhibit increases, decreases, or remain unaffected under elevated CO₂ levels [43][44][45].

The researchers found that four meta-analyses have been published on the impacts of elevated CO₂ on genes involved in N processes and N₂O emissions. Barnard et al. [46] reviewed the impacts of elevated CO₂, N, and temperature on nitrification, denitrification, and soil N₂O emission and found that elevated CO₂ enhanced net nitrification, reduced potential denitrification (-18%), increased net nitrification (33%), and did not significantly alter soil N₂O emissions. Li et al. [28] analyzed the impacts of multiple climate factors on N-cycling genes and found that elevated CO₂ increased N-cycling functional gene abundances (19.5%). In particular, elevated CO₂ increased *nirK* but did not change AOB. Du et al. [42] collected data from 50 publications and reported that elevated CO₂ enhanced N₂O emissions by 44%. Elevated CO₂ increases the abundance of AOB (21%), *nirK* (15%), and *nirS* (15%) but does not change AOA and *nosZ*. Gineyts and Niboyet [22] used 879 observations from 58 papers and found that elevated CO₂ increased AOA (62%), *nirK* (32%), and *nirS* (27%), leading to 26% increases in soil N₂O emission.

Synthesizing these meta-analyses, the results showed that elevated CO₂ increased the abundance of *nirS* (18.0%) and soil N₂O emission by 40.6% but did not significantly change AOA, AOB, *nirK*, and *nosZ* (**Table 1** and **Table 2**). Elevated CO₂ also increased MBN (27.8%), net nitrification rate (32.7%), and NO₃⁻-N (13.1%) but reduced nitrifying enzymes by 18.4% [12][22][28][46] (**Table 1**). While there was an increase in soil N₂O emissions, possibly associated with changes in denitrification (as indicated by increased *nirS* abundance), there were mixed effects on nitrification-related parameters. The increased MBN, net nitrification rate, and NO₃⁻-N levels indicate the stimulation of N cycling processes, but the reduction in nitrifying enzymes suggests a potential deceleration of ammonia oxidation. These findings highlight the need to consider multiple factors influencing soil N dynamics in the context of elevated CO₂.

2.3. Impacts of Precipitation

In terrestrial ecosystems, precipitation change can have multifaceted effects. These alterations influence soil microclimate and impact the soil water balance, soil aeration, nutrient availability, and microbial ecology [27][38]. Consequently, they play a role in shaping soil N₂O emissions. For example, Štoviček et al. [47] found that soil microbial diversity tends to be high under dry conditions due to the fragmentation of niches in dry soils. However, drought can also reduce the genetic potential and stability of soil microbiomes [28]. Homyak et al. [48] investigated the effects of reduced precipitation on soil N₂O emissions and found that a reduction in precipitation significantly lowers soil N₂O emissions, suggesting that denitrification is more sensitive to drought than processes controlling N supply. Decreased precipitation appears to have minimal effects on the abundances of archaeal *amoA*, bacterial *amoA*, *nirK*, and *nosZ*, but it shows positive effects on the abundances of *nirS* [27]. Conversely, increased precipitation has little effect on the abundances of archaeal *amoA*, *nirK*, *nirS*, and *nosZ* while exhibiting negative effects on the abundances of bacterial *amoA* [27].

Several meta-analyses have been conducted to further understand the impacts of precipitation on soil N₂O emissions [27][49]. For example, Yan et al. [49] performed a meta-analysis incorporating 84 published studies and found that increased precipitation significantly increases N₂O emissions (+154.0%), whereas decreased precipitation significantly decreases N₂O emissions (-64.7%). They also found that precipitation increases enhanced soil N₂O emissions by 128.3% in temperate forests and by 179.6% in boreal forests but did not influence soil N₂O emissions in grasslands. The impacts of decreased precipitation also varied in different ecosystems, ranging from no effect in subtropical forests to -24.3% in temperate forests and -92.6% in grasslands. However, only two papers have synthesized the impacts of precipitation on N-cycling genes and soil N₂O emission. Li et al. [27] explored the effect of global climate change on N₂O emissions and the related N functional genes in terrestrial ecosystems. Their findings indicated that precipitation promoted N₂O emissions by 55%, while reduced precipitation inhibited N₂O emissions by 31%. Based on two meta-analyses, the results showed that increased precipitation did not influence AOA, AOB, *nirK*, *nirS*, or *nosZ* (**Table 2**) [27][28]. Reduced precipitation did not change AOA and AOB but increased *nirS* by 173.6% and reduced soil N₂O emission by 45.9% (**Table 1** and **Table 2**) [27][28]. It is worth noting that the sample sizes of two meta-analyses were also small (18 and 20 for soil N₂O emissions). More studies are needed to focus on the N-cycling genes. Nevertheless, the findings emphasize the importance of considering the direction and magnitude of precipitation changes when assessing its impact on soil N dynamics and greenhouse gas emissions.

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