

Review

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Review

Mitigating Greenhouse Gas Emissions in Agriculture: A Review

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Abstract: Agriculture (crop production, land use, and livestock) is the second most important greenhouse gas (GHG) emitting sector after the energy sector. Agriculture is also recognized as the source and sink of GHGs. Evidence demonstrates that the application of high amounts of nitrogen-rich fertilizers enhances methane (CH₄) and nitrous oxide (N₂O) emissions, which are potent GHGs with a high global warming potential (GWP). Considering its global contribution to the climate crisis, reducing GHG emissions in agriculture would considerably lower its share of the global GHG emission records, which may lead to enormous benefits for the environment and food production systems. Several diverging and controversial views questioning the actual role of plants in the current global GHG budget continue to nourish the debate globally. We must acknowledge that considering the beneficial roles of major GHGs to plants at a certain level of accumulation, implementing GHG mitigation measures from agriculture is indeed a complex task. This review seeks to provide key approaches for GHG mitigation in the literature (environmentally friendly crop cultivation and residue management practices, improvement of plants nutrients/fertilizer use efficiency, exploring the genetic diversity for low GHG emission, soil methane-producing bacteria, integrated soil fertility management, improved livestock feeding efficiency, and production, etc.). This work gathers key approaches from 275 peer-reviewed publications, including experimental research papers, review articles, and books, discussing greenhouse gas emissions mechanisms and mitigation to unravel effective strategies for GHG mitigation, proven to be effective or carry the potential to mitigate GHG generation from agriculture. This review also discusses in depth the significance and the dynamics of strategies regarded as game changers with a high potential to enhance, in a sustainable manner, the resilience of agricultural systems. Agricultural GHG mitigation approaches discussed in this work can serve as game changers in global efforts to reducing GHG emissions and alleviating the impact of climate change through sustainable agriculture and informed-decision making.

Keywords: nitrogen; livestock feeding; biochar; greenhouse gas; sustainability; agriculture; game changer; environment

1. Introduction

Climate change is one of the most life-threatening challenges humanity has ever faced, which puts at risk our common future [1]. The impact of climate change has been recorded on five dimensions known as the 5Ps: the people, planet, partnership, prosperity, and peace [2,3]. The major effects of climate change are persistent global warming and episodes of abiotic and biotic stresses that exacerbate the economic crisis [4], aggravate inequalities and social vulnerability [5,6], and increase food insecurity [7,8]. Empirical data reveals that the recorded gradual and persistent emission of greenhouse gases (GHGs: carbon dioxide (CO₂), methane (CH₄), nitrous oxide (N₂O), etc.) into the atmosphere are the major cause of the observed global warming events and climate crisis. GHGs are produced biologically or naturally (through the action of specific microorganisms in soil

or via chemical reactions) and by the action of humans (anthropogenic source: energy sector (73.2%), industry (5.2%), waste (3.2%)), and the remaining is attributed to agriculture (crop production, agricultural soils, livestock), land use and forests.

Agriculture, land use, and forests (herein referred to as ALF) are sinks and sources of GHGs. Sinks of GHGs are reservoirs of carbon removed from the atmosphere through biological carbon sequestration [9,10]. As sources, ALF account for about 18.4% of global GHG emissions. In the same way, agricultural soils and cultivation practices, especially due to the excessive applications of nitrogen (N)-rich fertilizers and livestock, are identified as leading sources of atmospheric GHG emissions that possess a high global warming potential (GWP) and the potential to exacerbate climate change effects [11]. Nevertheless, agriculture remains the economic sector that suffers the most from climate change. Of the well-identified GHGs emitted from agriculture (crop production and management, agricultural soils, agricultural practices and livestock), CH₄ ranks number one and accounts for nearly 67%, followed by N₂O and CO₂ with 32% and 1%, respectively.

Despite the observed historical preference for CH₄ to coal and oil, CH₄ has emerged as a leading GHG right behind CO₂ and before N₂O, with a GWP 28–34 times higher than that of CO₂ in a 30 year-period [12]. An estimated indicates that approximately 90% of CH₄ emitted during crop cultivation, especially in flooded-prone cultivation areas such as paddy fields (including rice production), are conveyed by crops through plant's gas exchange, majorly through micropores of leaf sheaths, not via stomata. Whereas, nearly 10% would be released to the atmosphere through ebullition or diffusion from the water surface or soil [13,14]. However, several diverging debates question on the actual role of plants in the current global GHG budget, especially CH₄ [15].

Some research groups argue that plants do not make CH₄, while supporting that plants do not contain a known biochemical pathway for CH₄ synthesis [16]. In contrast, plants only play a role of conveying gases produced by the action of specific soil microorganisms in the rhizosphere of roots and its immediate environment that move throughout the plant vessels and later released to the atmosphere [17-19]. Others think that this question remains open, while pointing to a strong relationship between CH₄ production and the ultraviolet radiation, and supporting that CH₄ would come from parts of plants that do not give off water [20-22]. A third voice nourishes the idea that, based on some lines of evidence, the production of CH₄ by plants would be part of a survival strategy during stress conditions [23,24]. According to the UNEP, reducing global GHG emissions from agriculture caused by linear food production systems, as part of the net zero carbon emissions targets, may help slow down the current global warming rate in the short term, reduce peak warming during this century, and bridge the GHGs emissions gap between current emission pathways or trajectories and those consistent with the 1.5 °C temperature goals [25].

Furthermore, agricultural practices such as stubble burning or crop residues burning is widely considered as another important source of atmospheric GHG emissions from agriculture. This farming practice was widely used by many farmers across the world to quickly get rid of crop residues after harvest is complete without employing an important work force. However, several reports have warned against serious damages of crop residues burning on the air quality and human health, in addition to GHGs carried (CO₂, CH₄, N₂O, etc.) in the smoke. Currently, there is strong consensus that farmers must abandon the burning of residues to adopt environmental friendly residues management practices.

Although studies question the net impact of N-rich fertilization regimes on the emission of CH₄ and N₂O from agriculture, a strong consensus exists on the fact that different rates of N applications differentially influence the activity of soil microorganisms, including methanogens and methanotrophs [26,27]. Like nitrogen, even if they do not belong to the class of mineral macronutrients, carbon, hydrogen, and oxygen are considered essential to the life of plants as they are required in large quantities to build the large organic molecules of the cell [28,29]. The O₂ level in the soil is essential for both plants and soil microorganisms [30]. In the flooded-prone or wetlands cultivation areas, the diffusion of O₂ is much lower compared to that of the upland, which conditions favor, in most cases, the formation of GHGs, including CH₄ [31]. During gas exchange, plants release O₂ through aerenchyma to the rhizosphere of the root system and the immediate environment. This

process called radial oxygen loss (ROL) helps reduce the accumulation of phytotoxins (sulfides and ferrous iron) but also helps in the reduction of CH₄ generation in the soil. ROL is regarded as a promising trait, which helps supply O₂ to hypoxic soil environments for efficient plant root growth and development [14]. In the same way, O₂ level in the rhizosphere is proposed to influence the activity of methanogens and methanotrophs [31], while O₂ deficiency, especially in waterlogging conditions, has long been suggested to cause injury to plants [32]. A recent study conducted by Duyen, *et al.* [33], aiming at exploring the genetic basis for ROL suggested a set of genes with the potential to regulate ROL in plants.

Like certain crop management practices, livestock production and management are an important source of atmospheric GHGs. Livestock (ruminants: cattle and sheep, etc.) contributes significantly to GHG emissions, especially CH₄, throughout their life (feeding process: digestion, burps, flatulence). At the latest COP26 and COP27 in Glasgow in 2021 and in Sharm el-Shekh in November 2022, global leaders expressed their concern over the impact of livestock-mediated CH₄ emissions to the atmosphere and their contribution to the global GHG emissions record and climate crisis (<https://www.zurich.com/en/media/magazine/2022/is-there-more-to-methane-than-cow-farts>, accessed on February 1, 2023). Because of its high GWP 30 times than CO₂ in a relatively short period, CH₄ is considered one of the most potent GHGs. Given the GWP of CH₄ and its contribution to global warming events, countries have signed a Global Methane Pledge (https://ec.europa.eu/commission/presscorner/detail/en/statement_21_5766, accessed on February 1, 2023) to keep 1.5 °C within reach.

This review seeks to increase global awareness of the necessity to rethink agriculture and food production systems while highlighting key approaches that can effectively play the role of game-changers or carry the potential needed to support global efforts to reduce GHG emissions from agriculture, which offer multiple beneficial outcomes for plants, the environment, and the people.

2. Major sources of greenhouse gases in agriculture

2.1. Agricultural Land Use and Management of Crop Residues

Crop production involves several land preparatory activities prior to cultivation. Economists have identified factors of production resources or inputs commonly used in the production process to produce goods and services. The production function is largely determined by the utilized amounts of the various inputs. Reports indicate that there are four basic resources or factors of production, which are land, labor, capital and enterprise. Labor, capital, and land are considered primary factors of production. Land includes not only the site of production but natural resources as well.

In agriculture (crop production, fisheries and livestock), these factors of production are essential resources and components of the production system to achieve a desired productivity and profitability. Practicing agriculture involves opening new cultivation lands or utilizing already existing and exploited cultivation fields. In many parts of the world, farmers set fire to agricultural lands to clear stubble, weeds and wastes, after harvest is complete and before sowing a new crop or when opening newly acquired agricultural land that is to be cultivated for the first time. On the one hand, voices claim that this practice appears to be the easiest and most economical way to open a new cultivation land or get rid of wastes and crop residues [34]. On the other hand, another trend of thought highlights that the environmental and human cost of agricultural open burning of crop residues far outweigh the near-term economic benefits for farmers. Burning of crop residues after harvest is used by many farmers as an alibi to quickly prepare the land for other crops in a crop rotation scheme for instance or is considered as a low-cost straw-disposal practice to reduce the turnaround time between harvesting and sowing for the next season. However, this practice is more and more castigated or even prohibited because of its negative impact on the environment (by degrading air quality in producing black carbon and reducing the fertility of soil) [35] and one of the largest causes of air pollution-associated illnesses and deaths after cookstoves (<https://www.ccacoalition.org/en/activity/open-agricultural-burning>, accessed on January 13, 2023).

In turn, black carbon would be responsible for about a third of all black carbon emissions globally, and constitute a short-lived climate pollutant that causes air pollution, climate change, and increase melting in the cryosphere (regions of snow and ice). In the same perspective, Singh, *et al.* [36] highlights that burning of crop residues is regarded as a serious threat to the environment and human health and wellbeing, induces loss of nutrients (nitrogen, phosphorus, potassium, sulfur, organic carbon, etc.) essential for soil fertility, plant growth and productivity. Crop burning is also counted among the major causes of air pollution in several parts of the world, therefore contributing to enhance mortality rates and slumping agricultural productivity.

Reports suggest that burning of crop residues produces heat that elevates soil temperature, which causes death of beneficial soil microorganisms. Successive burning of crop residues on an agricultural field may lead to a complete loss of the microbial population and reduces the level of nutrients such as nitrogen, destroy the organic matter and carbon in the top soil layer (0–15 cm) profile that makes soil fertile, causing yields to decrease over time and increasing the need for costly fertilizers. This soil layer is important for crop root development. Consequently, there could be a slow and steady reduction in soil health, which will eventually result in decreased productivity. Figure 1 displays a map of crop stubble burning globally.

On the one hand, Andini, *et al.* [37] assessed the impact of open burning of crop residues on air pollution and climate change. The authors observed that on average, 90% CO₂ and 8% CO were the most abundantly emitted GHGs over a period of one year, while nearly 2% included CH₄, SO₂, NO_x, NH₃, N₂O, and others. At the global scale, the assessment of climate charging emissions suggests that crop residue burning to contribute to 12–14% toward global warming potential. On the other hand, Romasanta, *et al.* [38] employed various rice straw management practices (SRt-straw retained including stubbles and incorporated, PSRm-partial straw removal only stubbles incorporated, CSRm-complete straw removal including removal of stubbles, and SB-straw burned followed by incorporation) to study their effects on GHG emissions and GWP contributions. The authors argued that despite the fact that open burning of straw residues emits, through smoke, high amounts of CO₂, the latter is not considered as net GHG emissions. Rather, CO₂ from smoke concludes the annual carbon cycle that started with photosynthesis. This could justify the observed focus in favoring investigations of burning residues-mediated CH₄ and N₂O emissions over other GHGs. In addition, the above study found that SRt recorded the highest GWP value per unit area. In contrast, CRSm yielded the lowest GWP, which eventually depends on the ensuing utilization of straw and the off-field emissions involved.

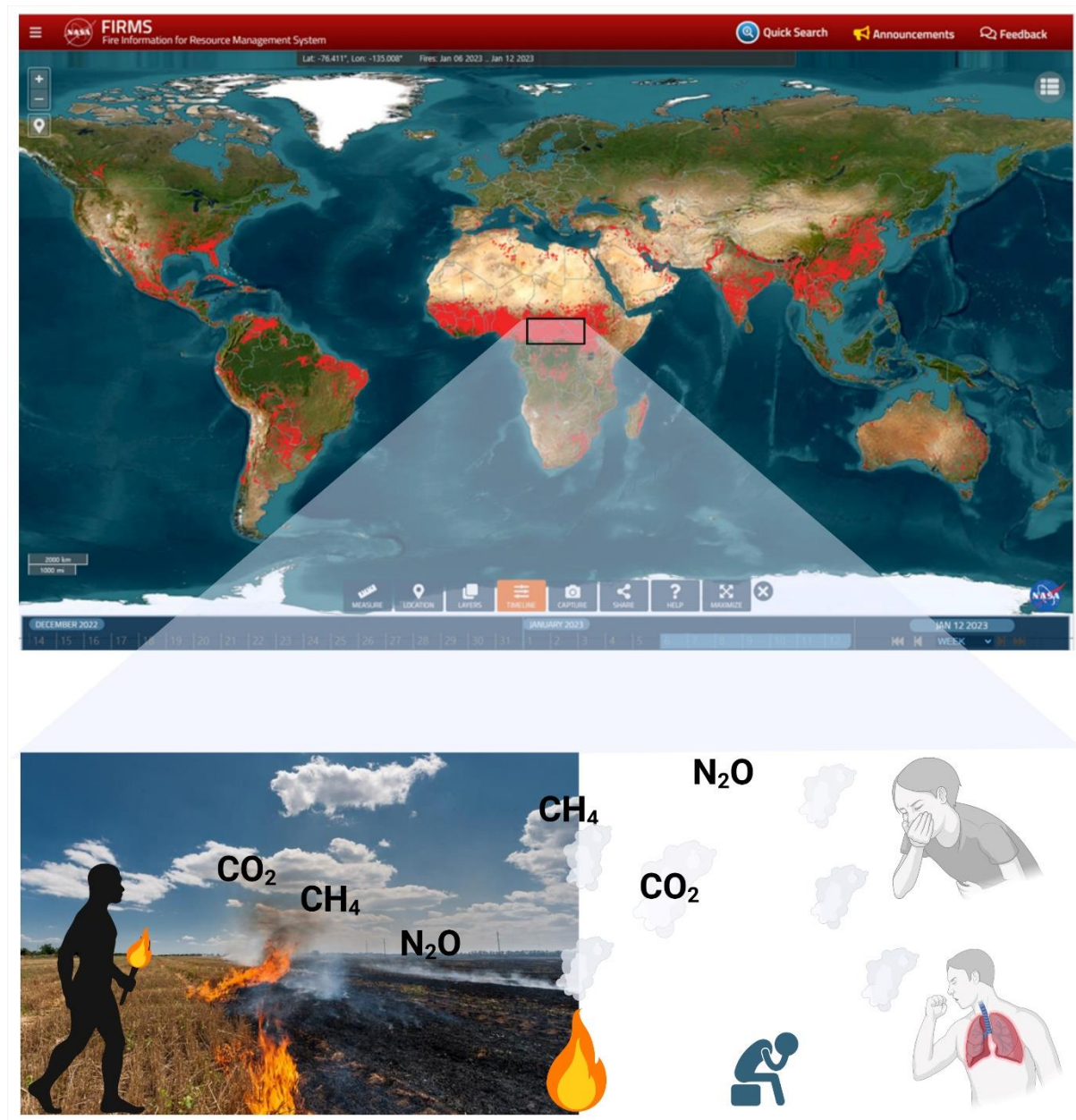


Figure 1. Illustration of the fire map in the world. Each dot (not to scale) represents a crop-stubble fire detected in a single day by a NASA (National Aeronautics and Space Administration) infrared imaging satellite (Fire Information for Resource Management System, FIRMS: <https://firms.modaps.eosdis.nasa.gov/map/#d:24hrs;@0.0,0.0,3z>, accessed on January 12, 2023).

2.2. Farming Practices and Fertilizers

Agriculture (farming practices/crop production and livestock production) is the second biggest GHG emitting sector after the Energy sector. An increasing trend in developing innovative agricultural practices and tools for more food production and animal feeding has long been at the core center of several agricultural-related research globally. Until before the last two decades, less attention was given to the environmental aspects of these farming practices, until the last few decades. The damages caused to the environment, health, and people's lives drew the attention of many when the situation became alarming and when consequences became evident and life-threatening (<https://agriculture.vic.gov.au/climate-and-weather/understanding-carbon-and-emissions/greenhouse-gas-cycles-in-agriculture>).

Figures 2A,B (adapted from Baggs and Philippot [39]) and S1 illustrate the share of agriculture in the global GHG budget in agriculture, including crops production and livestock and manure, land

use, and forestry are responsible for about 18.4% of global GHGs emissions. Based on their release amounts, CO₂, CH₄, and N₂O are considered as the major GHGs contributing the most to the global warming. However, in agriculture, CH₄ is the most abundant, followed by N₂O, and CO₂ (Figure 2B). With regard to their respective GWP, N₂O and CH₄ have higher GWP compared to CO₂. Concerning crop production systems, synthetic or mineral N-rich application regimes are reported as major factors enhancing GHGs emissions from agriculture [40]. Figures 3A,B and Figure S2 provides insights into the generation and emissions of GHGs from agriculture (crop production), such as N₂O, CH₄, and CO₂.

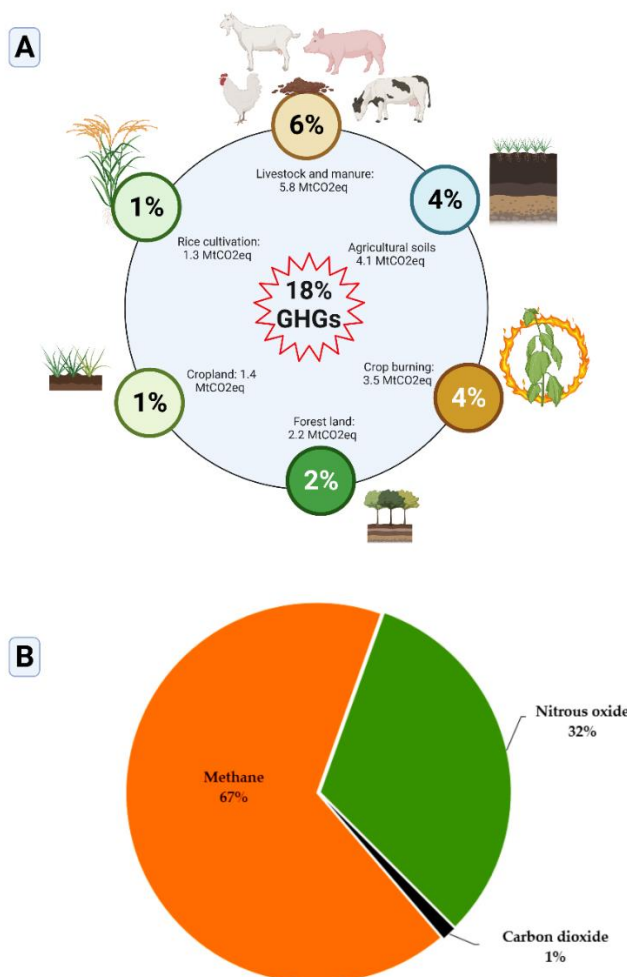


Figure 2. Sources of greenhouse gases from agriculture and the global share. (A) Cumulative greenhouse gases (GHGs) deriving from agriculture, land use and forestry globally (all GHGs considered), and (B) major GHGs emissions from agriculture by their importance. This illustration was created with BioRender.com.

A review on factors controlling N₂O and CH₄ emissions from soil indicated that nitrogen fertilizers, biological N fixation by associative free-living and mutualistic bacteria, organic N and the excreta of grazing animals are sources of N, which can lead to CH₄ and N₂O emissions from soil [41,42]. In essence, factors having a great potential to influence agriculture N₂O and CH₄ emissions are fertilizer type, N application rate, crop type, soil organic carbon content, soil pH and texture. On the one hand, production of GHG in agriculture is expected to increase with the increase in food demands (including animal products) following the relatively high population growth, the intensification of agricultural activities and the expansion of agricultural land coverage globally. On the other hand, monitoring and quantification of GHGs from agriculture under open field conditions has been a challenging task. Nevertheless, reducing the emission of GHGs is gaining momentum and

is at the center of global initiatives aiming at establishing effective strategies to lower the contribution of agriculture to the global warming.

2.3. Livestock production

The share of livestock alone in the agricultural GHG emission record surpasses that of crop production, agricultural soils, crop burning taken individually [43]. An estimate from various sources (foodandagricultureorganization.shinyapps.io/GLEAMV3_Public/, accessed on June 13, 2023) suggest that livestock would be responsible for nearly 11.1–19.6% of global GHG emissions. Other sources indicate that agriculture produces and emits nearly 18.4% of total GHG emissions recorded globally, including 6.2% is attributed to livestock and manure (Figure S1, <https://www.climatewatchdata.org>, accessed on February 24, 2022). A lot of critics point out animals, especially ruminants, for the part they play in climate change, and most often cattle and sheep are mostly indexed. Nevertheless, reducing GHG emissions from livestock remains the most important target.

3. Mechanisms of greenhouse gases production and emission from crop cultivation

3.1. Methanogenesis and Methanotrophy

Methane (CH_4) was first identified by the Italian physicist Alessandro Volta in the late 18th century [11]. Methanogenesis is an anaerobic respiration that generates CH_4 as the final product of this metabolism, through the exclusive action of methanogens, from substrates such as H_2/CO_2 , acetate, formate, methanol, and methylamines [44]. These bacteria are strictly anaerobic and are common in wetland environments. Several reports indicate that plant-mediated transport is the primary mechanism for CH_4 emission from agriculture, especially in flooded-prone crop cultivation areas such as rice paddy fields, which accounts for about 90% of CH_4 emitted to the atmosphere [14]. As the diffusivity of O_2 of gases is much slower in water than in air, direct exchange of gases between submerged tissues and the environment is impeded in flooded fields. Under these conditions, the aerenchyma play a dual role; one is the supply of O_2 to the roots and rhizosphere, while the other is the transport of gases such as CO_2 , ethylene, and CH_4 from the soil to the shoots and release to the atmosphere [14]. Under anaerobic conditions, organic matter such as glucose is oxidized to CO_2 , while the molecular oxygen (O_2) is reduced to water.

Three major pathways for CH_4 generation have been reported, including acetoclastic, methylotrophic, and hydrogenotrophic methanogenesis [45]. Acetoclastic methanogenesis is assumed to be the major pathway through which CH_4 is generated (acetoclastic methanogenesis). Acetoclastic Methanosaeta are dominant methanogens in organic-rich Antarctic marine sediments. In addition, two genes required for acetoclastic methanogenesis, *ackA* and *pta*, were identified and functionally characterized [46]. During hydrogenotrophic methanogenesis, hydrogen (H_2) is oxidized to hydrogen proton or ion (H^+), formic acid (CH_2O_2) or other simple alcohols are also oxidized in the process, and CO_2 is reduced to CH_4 .

Studies have shown that the most effective, if not the only biological option of degrading CH_4 is by microbial oxidation [47,48]. Kirschke, *et al.* [49] indicated that due to their characteristics (tight-aquatic terrestrial coupling and large organic matter accumulation), wetland or flood-prone cultivation environments are hotspots of biogeochemical processing. The authors supported that the high methanogenic activity in their anoxic, carbon-rich soils make wetlands or flood-prone cultivation areas source of global atmospheric CH_4 , emitting about 142–284 Tg CH_4 per year.

Methane is oxidized by methane oxidizing bacteria (MOB) or methanotrophs, in the presence of O_2 through methanotrophy. This process is restricted to prokaryotes (Methylosinus, Methylocystis, Methanomonas, Methylomonas, Methanobacter, and Methylococcus). Eukaryotic microorganisms, such as algae and fungi do not oxidize CH_4 . Methanotrophs require CH_4 as their sole source of carbon majorly through a process called “nitrifier denitrification” or from abiotic and biotic transformations of their metabolic intermediates, with the nitrifier denitrification being predominant and more favored in soils containing a high NH_4 supply [50,51]. In the process, they unlock the energy of

oxygen, nitrate, sulfate, or other oxidized species [52,53]. These bacteria occur mostly in soils, rice paddies, mud, landfills, among other places where CH_4 is available. In aerobic environments, MOB use O_2 and CH_4 to form formaldehyde. Reim, *et al.* [54] supported that anaerobic MOB found in paddy soils act as a bio-filter in mitigating emissions of CH_4 to the atmosphere, as O_2 is available in soils the atmospheric CH_4 is corroded. Aerobic methanotrophs has the ability to oxidize CH_4 via the MMO enzyme [55]. As per some evidence, there is strong linkage between the consumption of CH_4 and the composition of MOB communities. According to Walkiewicz, *et al.* [56], methanotrophy of arable soils may be affected by N fertilization. The authors observed that CH_4 oxidation was complete concomitant to the reduction of O_2 level in soil without NH_4 application; therefore supporting that methanotrophs would be favored under hypoxia in ammonium-fertilized soils.

Stein, Roy and Dunfield [55] supported that methanotrophs and ammonia (NH_3) oxidizers or nitrifiers share many similarities, such as having in common key enzymes including ammonia monooxygenase or particulate methane monooxygenase; they occupy similar ecological niches, and compete for nitrogen. Both CH_4 and NH_3 are highly reduced molecules and are suitable growth substrates for microbes, and they can be oxidized (aerobically or anaerobically) to yield energy. The authors further indicated that ammonia oxidizers are enzymatically capable of oxidizing CH_4 . In the same way, methanotrophs are capable of nitrification.

3.2. Nitrous Oxide generation and emission

Nitrous oxide (N_2O) is the third most important GHG behind CO_2 and CH_4 . Although it is less abundant and present at a concentration of about 320 parts per billion (ppb) in the atmosphere, N_2O is said to have a GWP nearly 300 folds greater than that of CO_2 and is regarded as the dominant stratospheric ozone-depleting substance [57]. Thomson, *et al.* [58] argued that N_2O emissions are difficult to estimate due to their predominant biogenic origin, and the N_2O -production and –consumption pathways occurring simultaneously in different microenvironments in the same soil (Figure 3A). N_2O is formed predominantly in soils and oceans [59], and is mediated by microbial processes [39]. The production of N_2O is the result of multiple biological pathways, including nitrification using the reactive N compound NH_4 [60,61], and denitrification, where NO_3 is converted back to N_2 in the biological N fixation [40,62-65] in the presence of O_2 [66], dissimilatory NO_3 reduction to NH_4 , nitrifier denitrification, and non-biological chemodenitrification. However, this event is particularly dominated by nitrification and denitrification [67,68]. Agricultural practices, climatic conditions, and soil properties have been recognized as the major source of N_2O emissions, driven by the soil moisture and temperature [69], aeration NH_4 , and NO_3 concentrations [70], and pH [71]. Other sources of agricultural N_2O and other nitrogen oxides (NO_x) release into the atmosphere are biomass burning and NH_3 from livestock manure accounting for about 65% of global N_2O emissions [72], land use and management [73], and leaching of agricultural N fields [74].

Nitrification, a major component of the global nitrogen cycle, is initiated with the oxidation of ammonia (NH_3), governed by two specialized groups of ammonia oxidizers named ammonia-oxidizing bacteria (AOB) and ammonia-oxidizing archaea (AOA) [75]. Stein [76] highlighted that ammonia-oxidizers contribute to the generation of N_2O , with AOB prevailing over AOA that produces lower yields of N_2O than bacteria during aerobic NH_4 oxidation in soil [77,78]. Hink, Nicol and Prosser [50] supported that nitrogen fertilization during crops cultivation increases significantly N_2O emissions in the presence of O_2 . For several decades, until recent reports showed evidence of AOA being active in the nitrification process [79-83], it was believed that AOB were the only microbes responsible for the oxidation of NH_3 to NO_2 . Then, the conversion of NO_2 to NO_3 is regulated by nitrite oxidoreductase [84]. As per to some evidence, a complete oxidation of NH_3 to NO_3 (complete NH_3 oxidation, camammox) is mediated by a single organism [85,86].

Microbial production in soils is the prevalent source of N_2O , which is enhanced with the application of N-rich fertilizers [87,88]. Nevertheless, fertilizers alone cannot account for the historical global trends of atmospheric N_2O concentrations [89]. Soils account for 56%–70% of total global annual N_2O budget, while anthropogenic N_2O sources, especially due to N-rich fertilization, is responsible for nearly 40% of global N_2O emissions [89-91]. Cost-effective inhibitors, which have the

potential to regulate nitrogen processes in soils, are highly recommended. Sufficient knowledge of sources of GHGs production via various microbial processes in the soil is a prerequisite.

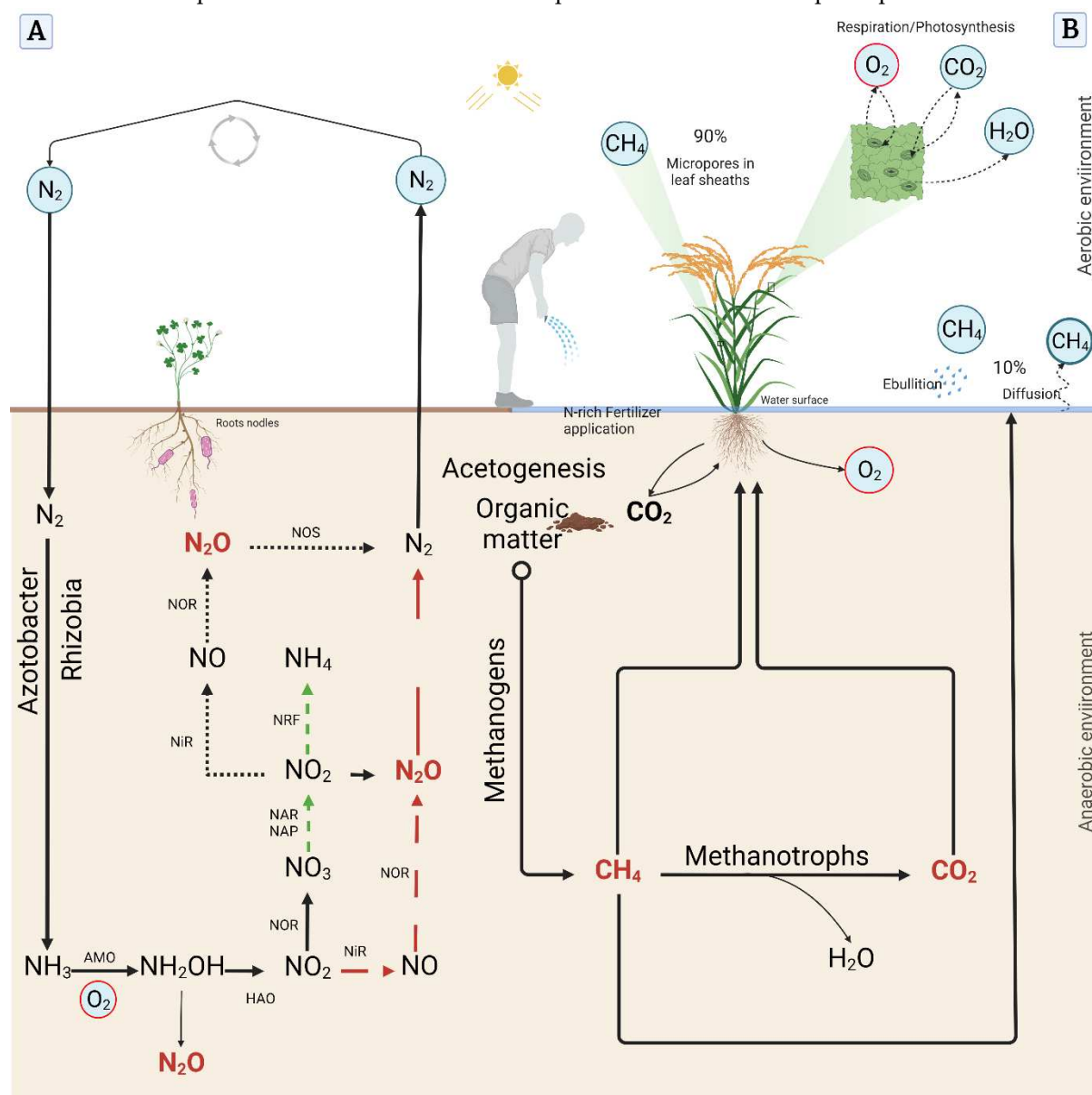


Figure 3. Simplified illustration of the nitrogen biological cycle and greenhouse gases emissions in plants. (A) Nitrogen gas N_2 fixation and nitrous oxide (N_2O) generation during nitrification and denitrification. Black continuous lines with an arrow represent the nitrification process. Black dotted lines with an arrow indicate the denitrification process. Green medium dash lines show the nitrate ammonification process. Red long dash lines with an arrow denote the nitrifier denitrification. (B) Methane (CH_4) generation and emission from nitrogen-rich fertilizers and organic matter decomposition under the action of methanogens, and CH_4 oxidation mediated by methanotrophs. Greenhouse gases have a red font. This model was created using biorender design platform (<https://app.biorender.com/>, accessed on 2023.03.25).

3.3. Carbon dioxide emission and sequestration

Carbon dioxide (CO_2) is the best-known anthropogenic GHG. High throughput scientific data suggest that the increased emissions of CO_2 resulting from various sources (majorly from fossil fuel burning and much less from agriculture) have the potential to affect global temperatures, considering the radiative effects of CO_2 and water vapor on the surface temperature of the earth. Likewise, based on theoretical scientific predictions, an increase of CO_2 by 250–300% over time would cause an

increase in temperatures in the Arctic by 8–9% [92]. Agricultural soils and cultivation activities are identified as leading sources of atmospheric GHG emissions, which have a high GWP and the potential to exacerbate climate change effects. Agriculture is both as sink and as source for GHG. Agriculture sinks of GHG are reservoirs of carbon removed from the atmosphere through biological carbon sequestration. Carbon sequestration here refers to the capacity of agricultural lands and forests to capture and long-term storage of atmospheric CO₂ in the soil. Data indicate that the curve of CO₂ increase over time has a zigzag pattern rather than an increasing as steady rate, which suggests a signal of a sink (the massive uptake of CO₂ by terrestrial and oceanic plants in specific seasons). These data provide evidence of the importance of sinks in the control of atmospheric GHGs concentrations, while showing at the same time that this control might be limited and underlying upward trend that the sinks are no longer balancing the sources [92]. In this regard, CO₂ sequestration currently presents the best solution to counterbalance the increase of GHGs. This includes enhancing biomass production, application of low-cost plant growth regulators and bio-fertilizers, agricultural conservation practices (no-till, use of biochar, no crop residue burning, etc.). CO₂ is removed from the atmosphere by plants and converted to organic carbon through the photosynthesis process. During the decomposition of organic carbon, it is converted back to CO₂ through the respiration process.

4. Mechanisms of GHG production and emission from livestock

Livestock-mediated GHG emissions occur at different levels, including (i) enteric fermentation, (ii) manure, (iii) feed production, (iv) land use change, (v) energy, and (vi) processing. During the enteric fermentation (a regular digestive process of ruminants), ruminants such as cattle and sheep produce CH₄ within the rumen (fore-stomach) during digestion, through a reaction between carbon and hydrogen. Reports suggest that nearly 90–95% of CH₄ produced during enteric fermentation (a digestive process that convert sugars into simple molecules for absorption into the bloodstream, which in turn produces CH₄ as a by-product) and released to the atmosphere, occurs through burps (burping). In essence, cow belching due to enteric fermentation is the largest CH₄ source in livestock as illustrated in Figure 4. Another portion of CH₄ is produced in the intestine and later expelled. The latter accounts for about 5–10% of CH₄ emissions, which occur during farting. In addition, setting ponds and lagoons for processing manure produce a significant amount of CH₄ as well (<https://climate.nasa.gov/faq/33/which-is-a-bigger-methane-source-cow-belching-or-cow-flatulence/>, accessed on February 1, 2023). In this case, solid waste produces both CH₄ and N₂O, when manure is tore in liquid systems such manure lagoons. Likewise, feed production is another source of GHG gas emissions. A small amount is associated to manufacturing fertilizers and other farm inputs (CO₂), and fertilizing crops (N₂O) [93]. GHG are also emitted during feed transportation and processing. Furthermore, expansion of pasture for grazing animals and cropland for growing feed crops (land use change) results in conversion of forest, grassland, and other land, causing emissions of CO₂ stored in biomass and soils [94]. Although several studies assumed that GHG emissions balances out by carbon sequestration, Xu, Sharma, Shu, Lin, Ciais, Tubiello, Smith, Campbell and Jain [43] found that, in addition to CH₄ and N₂O, CO₂ is release from livestock production than it is sequestered in vegetation and soil via pasture, rangeland, and feed crops. The authors indicated that soil and livestock respiration, tillage, and manure among others are important sources of CO₂. In the same way, energy used to produce farm inputs and feed serves in animal production for ventilation, cooling, and other activities, and constitutes a source of GHGs. Although GHG emissions related to processing (slaughtering of livestock, processing and packing the meat for consumers, which extends beyond the farm gate) is not a major component of raising livestock per se, it is included in most global estimates [95,96].

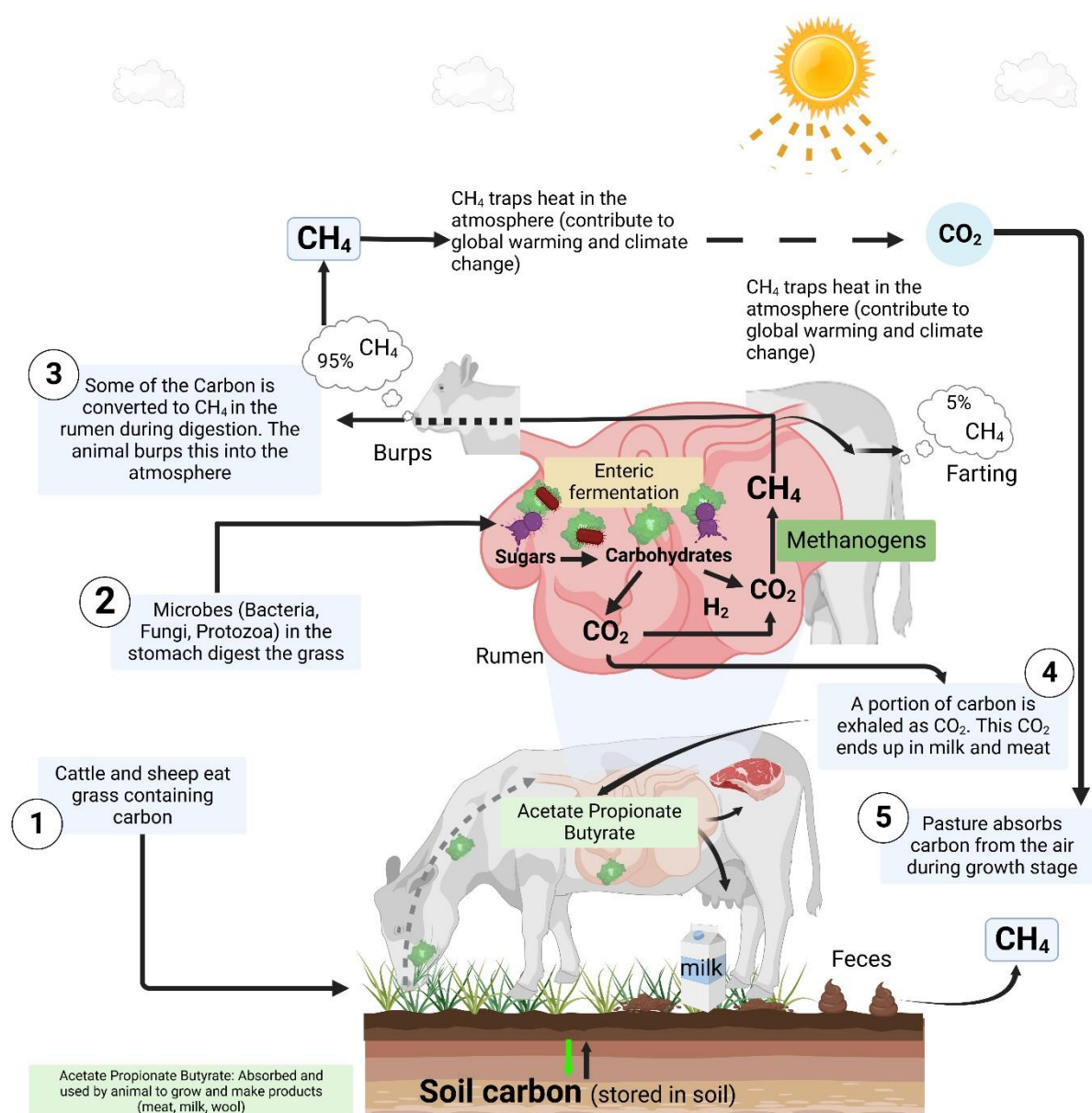


Figure 4. Illustration of greenhouse gas production and emissions from livestock (ruminant animals).

Unlike the forest, environmental sciences, and the energy sector, measuring and quantifying GHG emissions from crop cultivation in the field remains a challenge, due to the complexity of sampling procedures and data collection, design of effective and convenient chamber size and plant growth, the variation in weather conditions during the day, among other factors. Although some progress has been recorded in recent years, GHG emissions measurement tools and technology is not yet accessible to all. In crop production, scientists and environmentalists commonly use customized PVC chambers various shapes and dimensions (square, cubic, cylindrical, etc.) for field applications used for grass plant species, cereal crop species, or livestock (cow, sheep, etc.) to condition the gas and syringe for gas samples collection, thermometer temperature data acquisition, etc. For the laboratory analysis, GC MS is commonly used.

5. Approaches to Reduce GHG Emissions in Agriculture

Farming practices are not always the same around the world, although there are some common practices and similarities shared among certain regions of the world. The possible reasons explaining in part this situation may include the diversity of soils properties and characteristics, rainfall patterns

and climates varying from one region to another as well as cultural and social dimensions. In addition, different farming practices or methods may work better in a given environment but perform differently in other places. Furthermore, different areas of the world are better for growing certain types of crops, and some farms are huge, while others are small. Besides, there are also cases where farms are operated by large corporates or companies, middle-scale or small-scale farmers, with modern technologies or secular practices with limited resources [97]. In essence, agriculture is the process of producing food, including grains, fiber, fruits, and vegetables, raising livestock producing feed for animals, among others. Since the invention of agriculture (about 10,000 BCE), humans took control of their environment to produce their own food. As of today, modern agriculture, characterized by a linear production system, is a subject of controversies because of its contribution to global GHG emissions. Given the importance of the subject, and considering the necessity to address the agricultural-associated GHG emissions (about 18.4% of global GHG emissions), we could think of several potential solutions that may be regarded as game changers. Scientists and agricultural practitioners have come up with suggestions that may have a greater impact on lowering GHG emission records over time. In the below paragraphs, we attempted to collect and propose diverse approaches, not to be considered in the order of importance, which may exert transversal effects on GHG emissions and economical aspects of food production, while targeting agricultural practices, crop management habits and fertilizer application regimes or plant nutrition schemes, plant breeding methods and technology, livestock management and feeding, etc. Below are some of the areas identified with the potential to contribute to the reduction of GHG emissions from agriculture. A summary of most promising approaches is provided in Table 1.

5.1. Enhancing Nitrogen Use Efficiency in Plants

Nitrogen use efficiency (NUE), also referred to as N uptake, transport, translocation, assimilation, and remobilization, is regarded as a way of understanding the relationships between the total nitrogen inputs compared to the nitrogen output (Figure 5). Breeding for enhanced NUE in plants is essential but a challenging task regarding the complexity surrounding N acquisition and assimilation by plants. Improving NUE would imply targeting genetic loci controlling various aspects of the NUE using a forward genetic approach, targeting specific genes or transcription factors encoding genes associated with N acquisition, transport, and assimilation events. These could be identified through quantitative trait locus (QTL) analysis and fine mapping of detected QTLs or genome-wide association studies. In addition, the application of reverse genetics that employ molecular techniques to elucidate the function of genes through genetic engineering, coupled with sequencing technologies have gained momentum in the scientific community [98-100]. These techniques offer a wide range of opportunities and open new paths to investigating genetic factors controlling important traits in plants under various environmental conditions. Nevertheless, developing crop varieties with a high NUE is a promising approach to reducing application rates of synthetic fertilizers especially in wetlands cultivation areas.

Although the mechanism of N acquisition, uptake, and assimilation by plants is well described [101,102], the molecular basis of NUE in plants have not been fully elucidated, and continue to be investigated. Studies aiming at investigating mechanisms underlying NUE identified key protein families with a high potential to controlling NUE in plants under various cultivation conditions [103,104], while others suggested methods for assessing and estimating NUE in plant crops [105-107]. NO_3^- and NH_4^+ are the major forms of N taken up by plants, with NO_3^- being the most abundant. N is acquired from soil through a combined action of low- and high-affinity NO_3^- and NH_4^+ transporters. The latter are found within five protein families, including NO_3^- transporter 1 (NRT1) and 2 (NRT2), chloride channel (CLC), and slow anion channel-associated/slow anion channel-associated homologs (SLAC/SLAH), while assimilation primarily involves glutamine and glutamate synthase encoding genes but not limited to [103,108,109]. The enzyme glutamate dehydrogenase (GDH), which protects the mitochondrial functions during episodes of high N metabolism takes part in N remobilization [110].

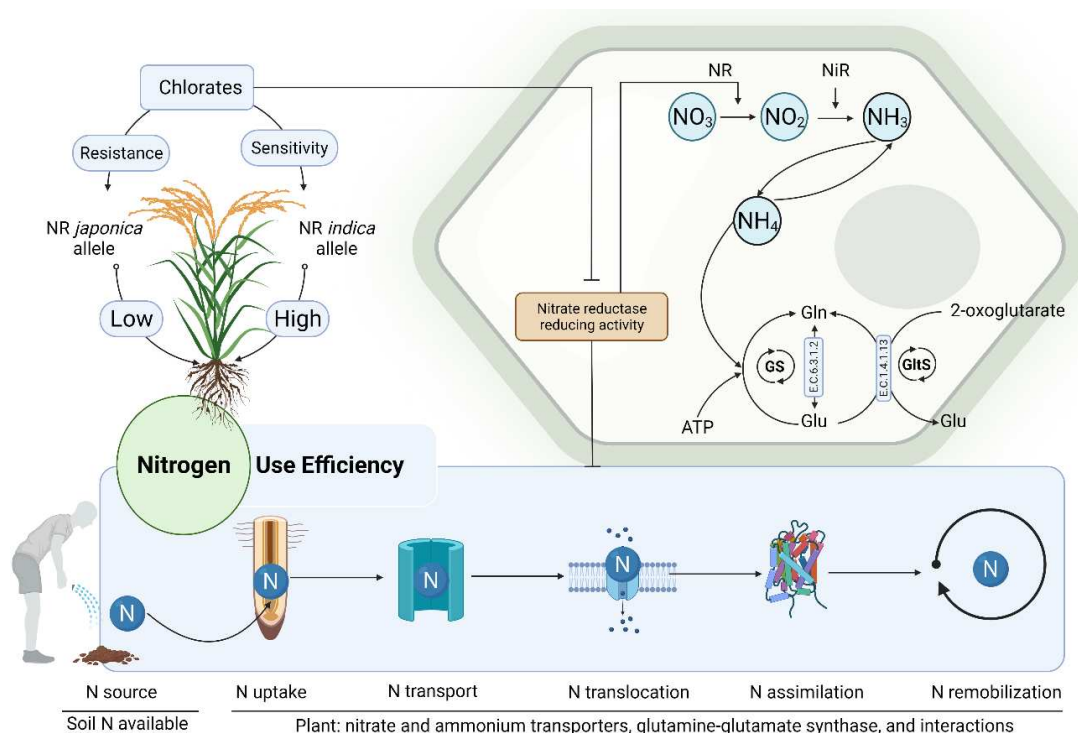


Figure 5. Schematic representation of nitrogen use efficiency in plants. This model was created using biorender design platform (<https://app.biorender.com/>, accessed on 2023.05.25).

Application of synthetic N-rich fertilizers during crops cultivation dramatically increased the last decades. This common agricultural practice has been shown to contribute to GHG emissions. In this regard, several strategies to reducing the emissions of GHGs from agriculture have been proposed. Number of methods employed to assess the NUE in different crop species are reported [111-113]. Of this number, various strategies aiming at improving NUE have been implemented, and their efficiency varies with crop species [114-120]. With the recent advances in plant breeding techniques and the advent of sequencing technologies, a wide range of opportunities are explored to identify high NUE in crop plants in various breeding populations. Screening for chlorates (ClO_3) sensitivity may also help identify rice varieties with an enhanced NUE [106].

Furthermore, in higher plants, phytohormones were originally known as a group of naturally occurring organic substances, which positively or negatively regulate plant growth and development. In addition to their basic roles, plant hormones are recognized as key players in coordinating multiple (both local and long-distance) signaling pathways at the whole-plant level [121]. As per some evidence, plant hormones interact with nitrogen (N) as well as other nutrients such as iron, sulphur, and phosphorus [122-126]. Among the well-studied phytohormones, abscisic acid (ABA), auxin, and cytokinin (CK) are closely associated with the N signaling. NO_3 availability differentially affects phytohormones accumulation. For instance, NO_3 signaling was proposed to interact with AtIPT3 in Arabidopsis and regulate N acquisition events, while inhibiting auxin (AUX) signaling and basipetal transport (translocation from shoot to root). Meanwhile, Vidal, *et al.* [127] suggested that NO_3 induces the activity of the auxin receptor gene AFB3, which in turn promotes lateral root, N acquisition and uptake. In contrast, NO_3 was observed to repress the transcript accumulation of the auxin response factor ARF8.

Moreover, several studies target key N transporters and assimilation related genes to attempt improving the NUE in plants. Nitrate reductase (NR), nitrite reductase (NiR), plastidic glutamate synthase (GS2), and Fd-GOGAT are involved in the primary NO_3 assimilation events. In contrast, the cytosolic glutamate synthase (GS1) and nicotinamide dinucleotide hydrogen (NADH)-GOGAT are involved in the secondary ammonia (NH_3) assimilation and remobilization. In this regard, Chen, *et al.* [128] suggested that genetic manipulation of NO_3 remobilization in plants, a key component of the N metabolism, would help improve NUE, while critically reducing N fertilizer demand and

alleviating environmental pollution. To date, genetic engineering techniques are used with the purpose of improving NUE in plants crops [129-131]. Figure 6 highlights some of the tools and methods employed to investigate the mechanisms and key players in the N metabolism with the purpose of improving NUE in plants, as well as its beneficial outcomes.

Heuermann, *et al.* [132] showed that NO_3 stimulates Cytokinin (CK) synthesis. However, elevated CK levels may delay plant senescence, while favoring a prolonged N uptake. Likewise, Ruffel, *et al.* [133] reported a NO_3 -CK relay and distinct systemic signaling for N supply and demand. Gu, *et al.* [134] supported that nitrogen and CK signaling play a role in root and shoot communication, which maximizes plant productivity. CK biosynthetic genes include IPTs, play a key role in root development, bud outgrowth and shoot branching, and plant development. CK activity occurs in two stages. During the initial stage, CK is produced in the outer layer of the roots and translocate inward. In the second stage, the inner part of the root pushes outward, and forms the nodule. This stage has been proposed to be controlled by IPT3. A study revealed that a knockout mutant plant lacking the IPT3 gene failed to form nodules in the roots [135], which suggests that IPT3 would play a key role in the formation of nodule and nitrogen fixation. Lin, *et al.* [136] recently observed that NO_3 restricted nodule organogenesis through CK biosynthesis inhibition. Similarly, Sasaki, *et al.* [137] supported that CK regulates root nodulation in plants. Moreover, growth-promoting microorganisms are widely used in agriculture for their roles in the promotion of plant growth and productivity. In their report, Singh, *et al.* [138] revealed that *Trichoderma* spp., known as plant growth promoter and biocontrol fungal agents, can enhance NO_3 acquisition events, and were shown to encompass the ability to regulate transcripts level of high-affinity NO_3 transporters, in a crosstalk with phytohormones.

Table 1. Summary key approaches for GHG reduction in agriculture.

Advantages	Prerequisite	Application	Outcomes
Nitrogen use efficiency			
<ul style="list-style-type: none">- Highly effective and helps mitigate the impact of excessive nitrogen-rich fertilizer applications- Helps optimize exogenous N applications and causes efficient utilization of N available by plants, including the assimilation and remobilization- Offers several environmental benefits, including reduced CH₄ and N₂O production and emissions- Reduces excess nutrients leaching of excess synthetic N application and groundwater pollution, nutrient runoff, and downstream water quality- Reduces production costs from N-rich fertilizers acquisition and application	<ul style="list-style-type: none">- Requires high-level skills and expertise in breeding and biotechnology- Requires a strong understanding of molecular mechanism underlying N metabolism in plants- NUE is genotype or species-specific- Identification of genetic resources adapted to specific cultivation environments- Knowledge about the nitrogen biological cycle and metabolism- Demanding in terms of resources, time, and adequate infrastructure	<p>Can be improved through:</p> <ul style="list-style-type: none">- Conventional or modern or molecular plant breeding techniques, associated with sequencing technologies and bioinformatics- Genetic engineering of targeting NO₃ or ammonium transporters (with a high-, low, or dual-affinity) or transcription factors regulating N acquisition and assimilation pathways.- Targeting transcription factors controlling N acquisition and assimilation, and remobilization- Targeting respiration versus nitrogen metabolism- Soil fertility management	<ul style="list-style-type: none">- Enhanced tolerance toward abiotic stress- Improved plant productivity, yield, and quality- Reduced production costs
Radial oxygen loss (ROL)			
<ul style="list-style-type: none">- ROL is the only biological way of degrading CH₄ and occurs through soil microbial activity-mediated oxidation.- Compensate the impeded direct exchange of O₂ between submerged tissue and the environment in wetlands cultivation areas.- Ensure a sustainable supply of O₂ and diffusion in water, known to be about 10,000× slower than in air.- Facilitates transport of O₂, and other gases, within plants is enhanced by tissues high in porosity enhanced by the formation of aerenchyma.	<ul style="list-style-type: none">- Strong knowledge of the mechanisms underlying the aerenchyma formation and oxygen fluxes in plant roots- Understanding factors inducing ROL barriers in roots, including suberin and lignin formation- Understanding genetic factors and physiological processes controlling the formation of ROL	<p>Can be improved using:</p> <ul style="list-style-type: none">- Existing panel of conventional or modern plant breeding techniques- Genetic engineering targeting genetic loci controlling oxygen fluxes and root development- Soil biology and management	<ul style="list-style-type: none">- Enhanced aeration of anaerobic flooded or submerged soils- Reduced methanogenesis through the control of methanogens activity- Promoted methane-oxidizing microorganisms

- Enhances the activity of methane-oxidizing bacteria (MOB)-mediating the CH ₄ oxidation process	barriers such as suberin and lignin
- Reduces the activity of methanogens involved in CH ₄ generation	Informed knowledge of soil biology

Application of biochar

- Improves soil fertility, carbon storage, and filtration of percolating soil water	- Requires acquisition of adequate technology, such as biochar reactors	- Improved soil fertility and water availability to plants
- Improves soil water holding capacity and other physical soil properties	- Do not require sophisticated technology and resources	- Reduces N-rich fertilizers applications and production costs
- Increases absorption of soil organic matter and controls absorption of toxic compounds by plants	- Sustainable availability and access to biomass and organic matter	- Enhanced nitrogen use efficiency
- Influences carbon and nitrogen transformation and retention in soil	- Affordable and applicable both at low and large scales	- Enhanced plant productivity
- Promotes growth of beneficial microorganisms		- Increased soil carbon sequestration
- Reduces N ₂ O production		- Reduced nitrogen leaching
- Draws CO ₂ from the atmosphere, providing a carbon sink on agricultural lands		- Have beneficial outcomes for the environment
- Prevents deforestation		

Best Agricultural Practices

- System of Rice Intensification (SRI)	- Irrigated or lowland rice cultivation system	- Improved crop, soil, and water management
- Improves nutrients (fertilizer), soil, and water management	- Involves the use of less amount of seeds	- Improved crop productivity
- Use of less amount of seeds due to greater planting spacing	- Raw material for making compost	- Enhanced fertilizer usage efficiency
- Optimizes production costs	- Used as an energy source when converted into pellets	
- Incorporation of crop residue (plant biomass) into the soil and stopping crop residue burning	- Source of livestock feed bedding when used as a straw	
- Use of high-quality seeds as starting materials		
- Requires intensive labor (force)		
- Requires a high level of knowledge, technicity, and skills in crop (rice) cultivation		
- Avoiding crop residue burning		

<ul style="list-style-type: none">- Preserves soil microbial community- Optimizes the use of plant biomass- Promotes conservation agriculture practices (maintaining the diversity of crop species and soil cover)- Improves soil fertility- Important source of energy for the industry and nutrition for animal feeding- Offers substantial environmental benefits- Use of animals' feces as manure- Improves soil fertility and other properties- Enhances integrated soil fertility management- Improves soil microbial life	<ul style="list-style-type: none">- Requires basic skills and knowledge in soil fertility and crop management- Requires basic knowledge of crop residue management and recycling- Requires minimum equipment for crop residue processing and recycling	<ul style="list-style-type: none">- Source of raw materials for the industry- Used as organic matter for plant nutrition- Important source of energy generation (gas)	<ul style="list-style-type: none">- Reduced GHG emissions- Improved crop and soil fertility management- Diversified use of plant biomass
	<ul style="list-style-type: none">- Requires a minimum space and resources for animal waste management- May require detoxification or drying process prior to the final use- Require essential skills and knowledge in animal waste processing and recycling		
Improving ruminant feeding efficiency and enhancing target-specific ruminal bacterial activity			
<ul style="list-style-type: none">- Improves nutrients use efficiency of ruminants- Enhances quality of meat and dairy products- Reduces enteric GHG production	<ul style="list-style-type: none">- Knowledge of ruminants' feeding behavior and digestive system- Understanding the mechanisms of CH₄ production in the rumen and biochemical reactions	<ul style="list-style-type: none">- Dietary manipulation- Breeding ruminants with low methane emission- Additive nutrients intake- Targeting specific digestive bacterial activity in the rumen	<ul style="list-style-type: none">- Reduced methane emissions- Improved feed use efficiency and nutrition- Improved productivity meat and milk)

- Understanding animal genetics and breeding	- Reduces environmental impact due to meat and milk production
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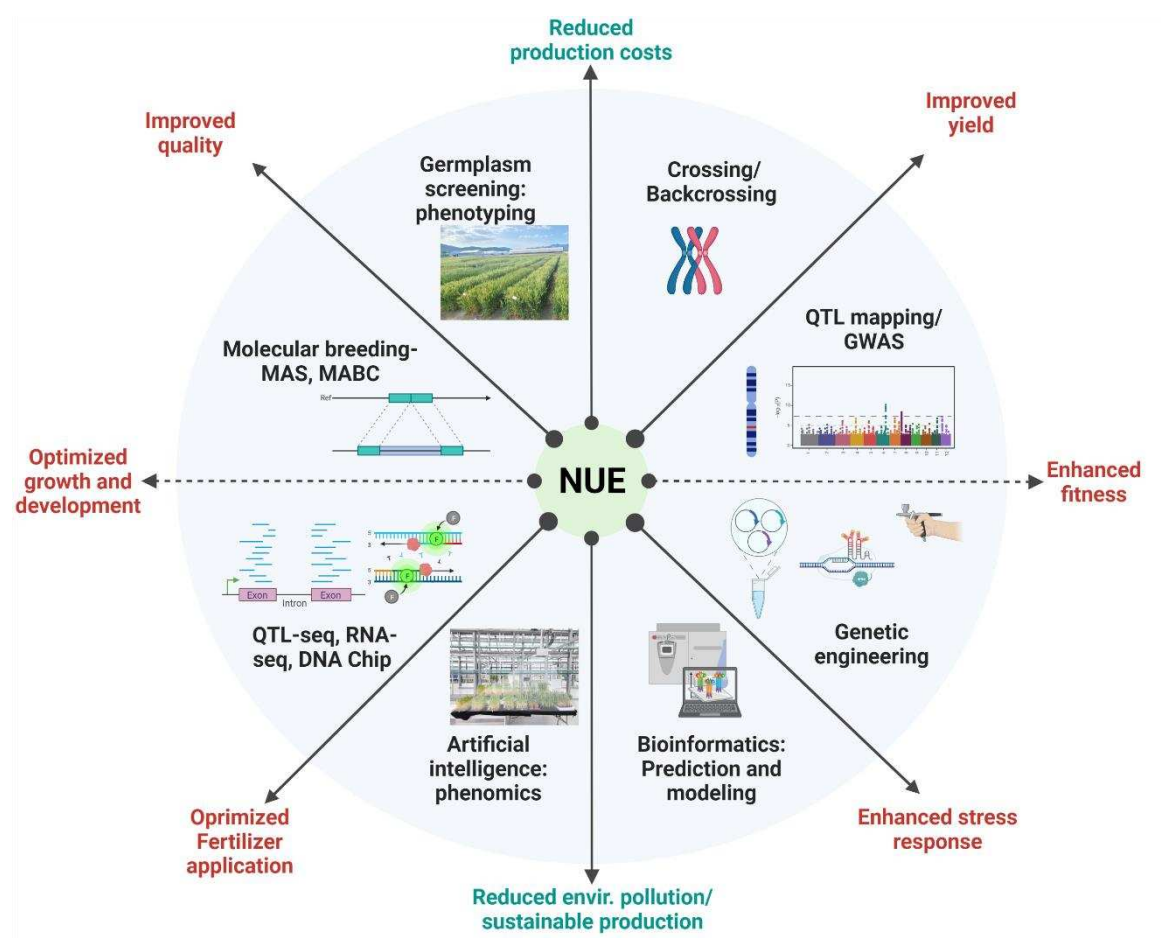


Figure 6. Illustration of different methods and tools employed to understand N metabolism and improve NUE in plants. Highlighted circular zone in different segments shows various methods, technologies and tools employed to enhance the understanding of N metabolism in order to improve NUE. Continuous lines with an arrow connected to the origin denotes the possible outcomes, but limited to, of an improved NUE for plants and the environment. This model was created using biorender design platform (<https://app.biorender.com/>, accessed on 2023.06.11).

5.2. Improving Abiotic Stress Tolerance in Plants

Nitrogen acquisition and uptake can be restricted under abiotic stress conditions, such as drought and salinity. External fluctuations of N supply to plants caused by abiotic stress occurrence have been shown to hinder NO_3 acquisition as well as other subsequent events due to water scarcity [139]. As per to some evidence, high- and low-affinity NO_3 transporters and glutamate synthase-encoding genes [140], and phytohormones biosynthetic and signaling pathway genes [141,142] (in addition to well-characterized abscisic acid (ABA), jasmonic acid (JA)), would play important roles in the adaptive response mechanism towards abiotic stress tolerance in plants. In addition, Zhong, *et al.* [143] revealed that over expression of a bZIP (basic leucine zipper) transcription factor encoding gene in Arabidopsis, *AtTGA4* conferred drought tolerance through the increase in NO_3 transport and assimilation mediated by high- and low-affinity NO_3 transporters and NO_3 encoding genes. Owing to the above, capitalizing on the recorded progress in terms of understanding plant nutrition and abiotic stress tolerance in plants, exploring the interplay between NUE and abiotic stress tolerance could serve as novel and exciting research direction. The outputs would give more insights that allow breeding for abiotic stress tolerance, such as drought, while addressing NUE using an integrated or system thinking approach.

5.3. Exploring Radial Oxygen Loss and Intermittent Drainage

The importance of oxygen (O_2) in the life of plants has been established. O_2 plays a fundamental role in plants metabolism. For instance, O_2 serves as a terminal electron acceptor of the electron transport, and its concentration plays an important role in regulating cellular respiration [144]. The internal transport of gases is said to be crucial for vascular plants inhabiting aquatic, wetland, or flood-prone environments [145]. O_2 is the rate-limiting substrate for the efficient production of energy in aerobic organisms. Therefore, they need to adjust their metabolism to the availability of O_2 .

Plants have the ability to produce oxygen in the presence of light. However, when the O_2 diffusion from the environment cannot satisfy the demand set by metabolic rates, plants can experience low O_2 availability [146]. Flooding or waterlogging induces hypoxic conditions in plants, which may lead to a reduced energy production. Under these conditions, the direct exchange of O_2 between the submerged tissues and the environment is strongly impeded and other programmed cell death (PCD) [147]. The diffusivity of O_2 in water is about 10,000 times slower than in the air. In addition, the transport of O_2 and other gases across the plant increases by tissues high porosity [148], which results from the intercellular gas-filled spaces formed as a constitute part of development [149-152], and may be enhanced further by the formation of aerenchyma [153]. The aerenchyma facilitate the flow of O_2 in and outside the plant, which provide roots with O_2 under flood-mediated hypoxia [14]. Colmer *et al.* [14] also indicated that aerenchyma provides a low-resistance internal pathway for gas transport between shoot and root extremities, and by this pathway O_2 is supplied to the roots and rhizosphere; whereas, CO_2 and CH_4 move from the soil to the shoot and atmosphere by the same means. The O_2 that is released to the rhizosphere of the root system and the immediate environment through the aerenchyma is known as radial oxygen loss (ROL) [154]. In the same perspective, Mohammed, *et al.* [155] revealed that rice overexpressing the EPIDERMAL PATTERNING FACTOR 1 (OsEPF1)-mediated reduction of stomatal conductance resulted in an increased formation of root cortical aerenchyma, which would be in part explained by reduced O_2 diffusion from shoot to the root where EPF signaling may be involved.

Furthermore, flood-prone and wetland cultivation areas, where anaerobic conditions are prevailing and a relatively high amounts of N-rich fertilizers are often applied, have proven to be major sources of GHG gases emissions during crops cultivation [156,157]. The flood status produces anoxic environments that are conducive to the production and emissions of CH_4 . According to Bodelier, *et al.* [158], the only biological way of degrading CH_4 , the second most important GHG globally but the first in agriculture, is by microbial oxidation. In the same way, Reim, Lüke, Krause, Pratscher and Frenzel [54] studied methane-oxidizing bacteria (MOB) under oxic-anoxic conditions in a flooded paddy soil, and suggested that MOB act as a bio-filter in mitigating CH_4 emissions to the atmosphere. Biological emissions of CH_4 from wetlands are major uncertainty in CH_4 budgets. The MOB use CH_4 as their sole source of carbon and energy, as long as oxygen is available [159], contrasting with the methanogenesis by Archaea that is known as an anaerobic process accounting for most biological CH_4 production in nature. .

According to Dalal, Allen, Livesley, Richards and Soil [42], aerobic well-drained soils are generally a sink for CH_4 , due to the high CH_4 diffusion rate into such soils and subsequent oxidation by methanotrophs. The capacity of soils to uptake CH_4 varies with land use, management practices [160], and soil conditions [161]. In contrast, large CH_4 emissions are usually observed in anaerobic conditions, such as wetlands, rice paddy fields, and landfills. Warm temperatures and the presence of soluble carbon provide optimal conditions for CO_2 production and incompletely oxidized substrates, thus enhancing the activity of methanogens. Likewise, a close relationship between the increase in atmospheric CO_2 levels and the subsequent increase in CH_4 emissions has been proposed. In this regard, studies suggested intermittent drainage to reduce the activity of anaerobic methanogens in the soil, especially in flooded crop cultivation systems, which may have a direct impact on the amount of CH_4 produced and released by up to 80%. Although in-season or intermittent drainage can result in significant reduction in CH_4 production and emissions, this crop management technique aiming to mitigate CH_4 emissions can cause an increased N_2O emissions, even if the overall warming potential remains lowered [88,162].

As for Walkiewicz, Brzezińska, Bieganski and Soils [56], the activity of methanotrophs is favored under hypoxia in ammonium (NH_4) fertilized soils. In Figure 7, we illustrate the action of ROL on methanogens and methanotrophs activity, which influences CH_4 production through oxidation process to yield water and CO_2 . Studies revealed that there are factors that may cause the reduction of ROL with the formation of a ROL barrier. Colmer, *et al.* [163] reported that low concentrations of organic acids may help trigger a barrier to ROL in roots. Ejiri and Shiono [164] supported that the prevention of ROL would be associated with exodermal suberin along adventitious roots. Abiko, *et al.* [165] observed the formation of a ROL barrier on lateral roots, in addition to adventitious roots, and reported a major locus controlling the formation of ROL barrier in maize. The authors argued that the enhanced formation of aerenchyma and induction of a ROL barrier would confer waterlogging tolerance, which argument was supported by Ejiri, *et al.* [166] suggesting that a barrier to ROL helps the root system cope with waterlogging-induced hypoxia. In their study, Peralta Ogorek, *et al.* [167] reported a novel function of the root barrier to ROL in conferring diffusion resistance to H_2 and water vapor. In rice, the first genetic locus associated with ROL was recently identified, with a set of genes suggested to be involved in aerenchyma-mediated ROL in plants [33]. Therefore, with the growing concern about mitigating GHG emissions from agriculture, exacerbated by the application of excessive amounts of N-rich fertilizers, coupled with the hypoxic conditions and low diffusion of O_2 in waterlogged or flooded cultivation areas, breeding for high ROL in plants could serve as an alternative to conventional techniques such as intermittent drainage that are rarely employed in wetlands. This could be essential for areas such as paddy fields that require efficient water management and where drainage could not be applicable due to evident circumstances such as limited access to a water source. Moreover, it has been evidenced that respiration and nitrogen assimilation in plants are tightly linked. In this regard, studies exploring the interplay between the above factors supported that mitochondrial-associated metabolism can be used as a mean to enhance NUE in plants [168-170].

Carbon dioxide (CO_2) is the most abundantly emitted of all GHGs. However, CO_2 has a global warming potential 25 times less than that of CH_4 and 300 times less than that of N_2O . Global leaders and scientists, among other, stressed at the COP26 that CH_4 is a great threat to accelerate global warming over a 30-year period, which makes CH_4 much more potent than CO_2 and the greater climate change hazard. As indicated earlier, irrigated or flood-prone cultivation, systems are favorable environments for CH_4 production, which is by far the most abundantly emitted in agriculture. Rice (staple food for nearly half of the world's population) production occurs through irrigation/flooded or wet environments or upland/rainfed system. For instance, the use of system of rice intensification (SRI) [171], which focuses on changing the management of plants, soil water, and nutrients to create more productive and sustainable rice cultivation, while tending to reduce environmental impacts, could serve as a relevant alternative to reducing GHG emissions. Some of the fundamental concepts of SRI include the use of a smaller amount of seeds and greater planting distances, less use of inputs and intermittent irrigation instead of flood irrigation (savings in irrigation water and inputs) and reduced environmental footprint of rice farming. Regardless of the benefits of SRI, it is overly labor-intensive, requires a higher level of technical knowledge and skill than conventional methods or rice cultivation [172].

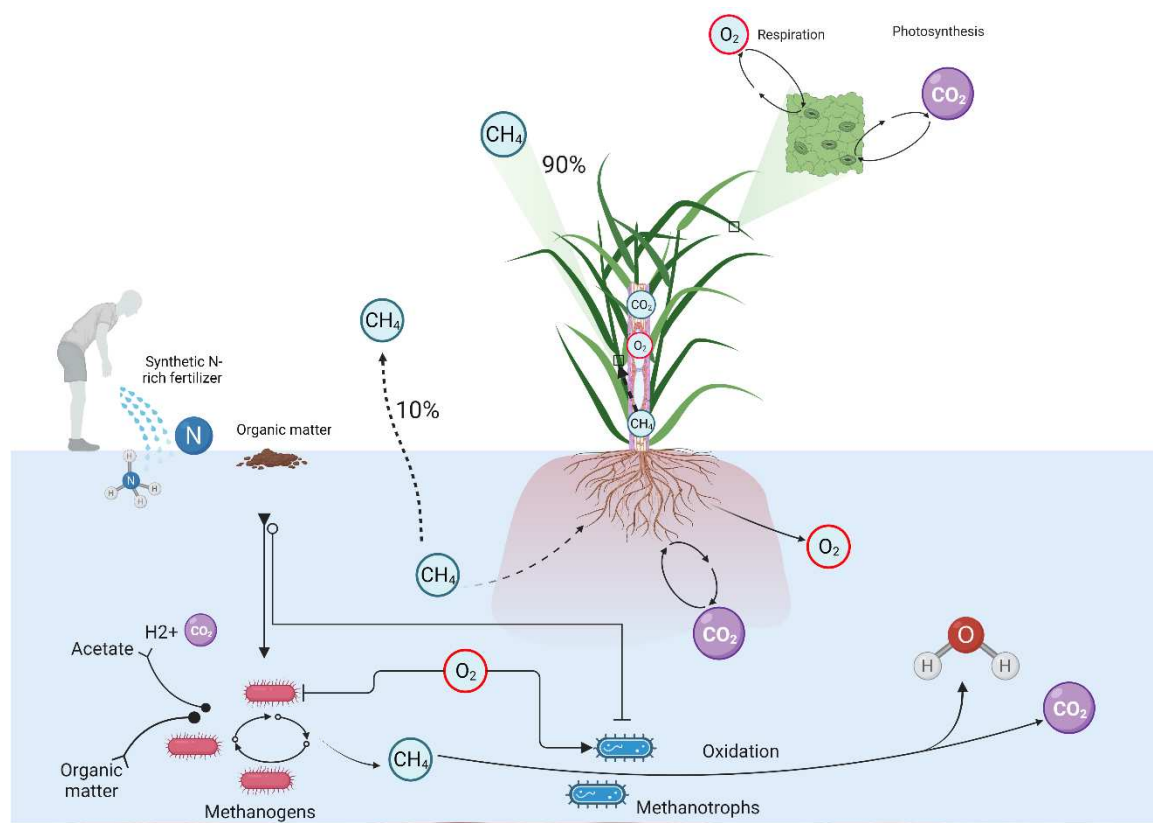


Figure 7. Illustration of ROL in plants and mitigation of GHG emissions. Internal transport of gases is crucial for vascular plants in wetland or flooded prone environments. The direct exchange of gases between submerged tissues and the environment is impeded due to the slow diffusivity of gases in water. Soil aeration can fluctuate and zones of low O_2 are widely spread in soil. In many wetland plants, aerenchyma is well developed even in drained conditions, and further enhanced in waterlogged conditions. Aerenchyma formation increases porosity above level due to the usual intercellular spaces. The O_2 released to the rhizosphere of roots and the immediate environment (ROL) exerts differential effects on soil microbial activity. ROL inhibits the metabolism of anaerobic microorganisms such as methanogens (Archaea). Consequently, ROL abundance reduces CH_4 production. In contrast, ROL promotes the metabolism of obligate aerobic organisms (methanotrophs or methane-oxidizing bacteria), allowing them to oxidize CH_4 as their sole source of energy. Aerenchyma provides a low-resistance internal pathway for gas transport between shoot and roots extremities, and this pathway supplies O_2 to the roots and rhizosphere. About 90% of CH_4 emitted by crop cultivation is conveyed by plants during gas exchange events and long-distance transport. Whereas, nearly 10% is released through ebullition or diffusion from water or soil surface. This model was created using the biorender design platform (<https://app.biorender.com/>, accessed on 2023.05.25).

Pereira-Mora, *et al.* [173] investigated the response of plants to organic acids, found that organic acids the abundance of methanogenic archaea and the *mcrA* gene in plants was reduced in treatment with organic acid under the SRI-rotational cultivation system.

5.4. Biochar reduces mineral fertilizers use, improves soil properties and mitigate GHG emissions

Biochar is widely used as a soil amendment in different agricultural ecosystems. The application of biochar in agriculture increased over the years for various purposes [174], and their recognition as an effective tool for reducing soil GHG emissions has been reinforced in recent years [175-179]. Joseph, *et al.* [180] define biochar as the carbon-rich product obtained when biomass, such as wood manure or leaves, is heated in a closed container with little or no available air. In other words, biochar is produced by thermal decomposition of organic material under limited O_2 supply, and at relatively low temperatures. Unlike charcoal, biochar is mainly produced to improve soil properties, carbon

storage or filtration of percolating soil water. Reports indicate that biochar is not only more stable than any other amendment to soil [181], but it helps increase the availability of nutrients beyond a fertilizer effect [174]. Biochar also contributes to (the): (i) improvement of water-holding capacity and other physical properties [182,183], (ii) increase in the stable pool of carbon [184], absorption/complexation of soil organic matter and toxic compounds [185], (iii) absorption and reaction with gases within the soil [186], affect carbon and nitrogen transformation and retention processes in soil [174,187], and (iv) promotion of the growth of beneficial soil microorganisms.

A number of studies proposed that incorporating biochar within soil reduces N₂O emissions and impacts on CH₄ uptake from soil [188-190]. However, the mechanisms through which biochar influences CH₄ and N₂O fluxes are not yet well elucidated. Studies suggest that the properties of biochar and its effects within agricultural ecosystems largely depend on feedstock and pyrolysis conditions. As biochar ages, it is incorporated into soil aggregates, and promotes the stabilization of rhizodeposits and microbial products [190]. In addition, Joseph, *et al.* [191] indicated that the properties of biochar can vary with their element compositions, ash content, and composition, density, water absorbance, pore size, toxicity, ion absorption and release, recalcitrance to microbial or abiotic decay, surface chemical properties (i.e. pH), or surface area. Biochar can catalyze abiotic and biotic reactions in the rhizosphere, which may increase nutrient availability and uptake by plants, reduced phytotoxins, stimulate plant development, and increase resilience to disease and environmental stimuli [190]. Recent evidence suggest that biochar generally increase soil CO₂ emission, reduce N₂O emissions and NO₃ leaching [192,193], and have varying effects on CH₄ emissions [194,195]. Kalu, *et al.* [196] reported an increased CO₂ efflux after applying biochar 2–8 years before planting but did not observe any significant effect on the fluxes of N₂O or CH₄ in soil with a high soil organic carbon (SOC). A tendency of biochar to reduce N₂O fluxes was observed in soils with high silt content and lower soil carbon. The authors recorded as well an increased NUE in the long term, while soils with a high SOC underwent continuous freeze-thaw cycles, which may lead to differential effects of biochar. Thus, biochar is emerging as a sustainable source of plant nutrients for crops and soil quality, with interesting environmental benefits.

5.5. Enhancing Sink Strength

A growing interest in investigating the starch metabolism in plants to explore the possibility to reducing GHG emissions from agriculture, especially CH₄ has been observed [197,198]. A study by Su, *et al.* [199] suggested that increasing sink strength would help enhance the sugar metabolism, while reducing the substrate required for methanogenesis, therefore lowering the activity of methanogens, and consequently affecting CH₄ generation in the soil. However, a pending question on how the methanotrophs population would be affected in their role of contributing to the nitrification and denitrification processes [162,200], while relying on CH₄ as their sole carbon source for their metabolism remains unanswered.

Root exudation is an important process determining plant interactions with the soil environment [201]. On the one hand, the exudates (low molecular weight compounds: amino acids, organic acids, sugars, phenolics, and other secondary metabolites [202]; high molecular weight compounds: mucilage (polysaccharides) and proteins [203,204]) continuously secreted to the rhizosphere by the roots of plants, are involved in several processes [205]. Plants can modify soil properties to adapt and ensure their survival under adverse conditions, by modulating the composition of the root exudates [206]. Plant root exudates are important factors that structure the bacterial community and their interactions in the rhizosphere [204], or promoting the interactions between plants and soil microorganisms [207], and enhancing resources use efficiency in the rhizosphere [208]. In addition, root exudates are involved in the inhibition of harmful microorganisms [209] or stimulating beneficial micro-organisms [201], keeping the soil moist and wet, mobilizing nutrients, stabilizing soil aggregates around the roots, changing the chemical properties of the soil, inhibiting the growth of competitor of plants [203,210], etc. It is well established that root exudates provide nutrients that favor enhanced growth and a higher prevalence of degrading strains of bacteria [211].

On the other hand, Lu, *et al.* [212] suggested that stronger roots could secrete more carbon-containing root exudates into the rhizosphere for methanogenesis. The authors found that soils amended with acetate or glucose, root exudates, and straw caused an increased CH₄ production. Likewise, Moscôso, *et al.* [213] recorded an increased CH₄ emission induced by short-chain organic acids in lowland soil. In the same way, Aulakh, *et al.* [214] assessed the impact of root exudates on CH₄ production revealed that CH₄ production commenced soon after treatment, and the emission increased over time.

For grain crops, yield is the cumulative result of both source and sink strength for photoassimilates and nutrients during seed development. Source strength is determined by the net photosynthetic rate and the rate of photoassimilates remobilization from source tissues [215]. The long distance transport (sugar export from leaves) and the corresponding demand by sinks has been examined as a possible target for improving plant productivity. The transfer of materials from source to sink is governed by a highly regulated signaling network elicited by resource availability. Sink strength is regarded as the function of size and sink activity, which is tightly related to the source availability. It is accepted that carbon allocation to various sinks is controlled by both sink demand (activity and size) and source control of photosynthate production [216].

Furthermore, Studies indicated that carbohydrates signaling gives insights into the understanding of changes in resources such as N. Increased N uptake and inorganic N availability in leaf tissue favors the synthesis amino acids over gluconeogenesis. As a result, carbohydrates are retained in source tissue at the expense of allocation to heterotrophic tissues such as roots [216,217]. Similarly, a decreased leaf inorganic N leads to decreased amino acids synthesis but increases carbohydrate availability for transport to heterotrophic tissues, including roots. With the increase in carbon availability, genes involved in storage and use are induced [218], leading to root growth and increased N acquisition, more exudates secretion and GHG production.

5.6. Use of Nitrification Inhibitors or Low GHG-Emitting Crop Cultivars

It is widely accepted that excessive application of N-rich fertilizers (mineral N source or organic matter) [219] significantly exacerbate CH₄ and N₂O production and emissions, especially during nitrification and denitrification processes (the microbial reduction of NO₃ to intermediate gases nitric oxide (NO) and N₂O and finally to N₂). Although N is an indispensable macronutrient for plant growth and development, productivity, quality of products, as well as plant defense, and knowing that doing agriculture without N is nearly utopic; however reducing N application, while optimizing its use, remains one of the major target and one the best options with multiple benefits for the environment and production costs. Organic matter are commonly applied to satisfy soil fertility and improve water retention capacity. The application of green manure, crop residues, manure and composted products contribute to reducing CH₄ emissions as discussed earlier.

The application of straw often reduces N₂O emissions [88]. Generally, straw with a high carbon/nitrogen (C/N) ratio likely immobilizes available N, thus reducing its availability for both nitrification and denitrification [220,221]. However, the reducing effect of straw on N₂O emissions varies from one crop species to another [221], and long-term application of high C/N straw may result in increased N availability which, in turn, may increase N₂O emission [222]. Additionally, farmers can take advantage of the nitrification inhibitors, which have been widely shown to reduce N₂O emissions in a wide range of crop species [223-225]. Evidence showed that GHG emissions from crops production is also crop variety-dependent.

5.7. Improving Management of Crop Residues

Burning of crop residues is a global issue rooted in many farming systems, although in many countries, several initiatives are being implemented and measures are being taken to curb the use of this linear type of agricultural practice. Burning of crop residues remains harmful to the environment, human being and negatively affect agriculture and food production. To tackle this issue, a global attention is required. To reduce significantly the practice of stubble burning, governing authorities and scientists in several countries are encouraging or introducing effective crop residue management

practices as alternative solutions to crop residue burning. Scientists and governments have suggested a number of techniques of crop residue management to efficiently transition to a more friendly agriculture. These include the use of technological interventions to: (i) incorporate crop residues into soils through adoption of conservation agriculture practices (although straw incorporation and organic matter amendments can increase CH₄ and N₂O production [88,162]) and to prevent soil erosion from wind and water, and augment the soil moisture; (ii) promote the use of crop residue for preparation of bio-enriched compost or vermi-compost and its utilization as farm yard manure; (iii) use of agri-machineries such as Happy seeder (used for sowing of crop in standing stubble), rotavator (used for land preparation and incorporation of crop stubble in the soil), zero till seed drill (used for land preparation directly sowing of seeds in the previous crop stubble), baler (used for collection of straw and making of bales for cereal crops stubble), paddy straw chopper (cutting of crop stubble for easily mixing with the soil), or reaper binder (used for harvesting paddy stubble and making into bundles), zero-seed-cum fertilizer drill, to facilitate in-situ management of crop residue and retaining the straw as surface mulching; (iv) use crop residue for mushroom cultivation.

There is a strong consensus that practicing conservation agriculture (minimize soil disturbance by not tilling, maintaining soil cover, and diversifying crop species) can be an effective, sustainable and productive method of agriculture that can play an important role in containing and curbing the practice of crop residues burning, which is regarded as this environmentally unjustifiable practice. Other alternative solutions considered include the (i) diversification of crop residue as fuel (for power plants, production of cellulosic ethanol, etc.); (ii) use of crop residue in paper, board, panel and packing material industry; (iii) collection of crop residue for feed, brick making, etc. (<https://www.downtoearth.org.in/blog/agriculture/stubble-burning-a-problem-for-the-environment-agriculture-and-humans-64912>, accessed on January 12, 2023). Agricultural residues equally offer a valuable resource worth saving, since crop stubble can be used as an energy source when converted into pellets, and straw is useful in livestock feed or bedding (<https://www.ccacoalition.org/en/activity/open-agricultural-burning>, accessed on January 13, 2023).

5.8. Improving Livestock Production and Feeding Efficiency

The global demand for meat and dairy products is growing, and over the past 50 years, meat production has significantly increased in the recent years and is projected to increase by two to three folds by 2050 [226], reaching about 340 million tons each year. The contribution of livestock to the recorded global CH₄ emissions is high (<https://ourworldindata.org/meat-production>, accessed on April 26, 2023). Meat and dairy products are important sources of proteins and vitamins and essential minerals useful to human health in many countries [227-229] but also present potential risks for health [230-232]. Likewise, the production of meat and dairy products has environmental impacts, as it contributes to GHG emissions such as CH₄, among others. Today, one of the most pressing global challenges is the sustainable production and consumption of meat, dairy, and other protein products.

The major source of GHG emissions from agricultural production is enteric fermentation of ruminant livestock, and the interest to reducing CH₄ production in ruminants continues to grow globally [233]. According to the UNEP Emissions gap report 2022 [234], beyond the necessity to change diets, the reduction of CH₄ emissions from ruminants can be achieved via changes in feed level and feed composition, which can also increase animal productivity. Frank, *et al.* [235] found that the adoption of technical and structural mitigation options could help agriculture achieve at a carbon price of 25\$/tCO₂ non-CO₂ reductions of around 1GtCO₂eq by 2030. In the same way, Arndt, *et al.* [236] indicated that to meet the 1.5 °C target, CH₄ from ruminants must be reduced by 11–30% by 2030 or 24–47% by 2050 as compared to the record in 2010. The authors identified strategies to decrease product-based (PB, CH₄ per unit meat or milk) and absolute (ABS) enteric CH₄ emissions, while maintaining or increasing animal productivity (AP, weight gain or milk yield). Other independent studies [237] claimed that enhancing the activity of the major ruminal sulfate-reduction bacteria (SRB: *Desulfovibrio*, *Desulfohalobium*, *Sulfobus*) through dietary sulfate addition, can be used as an effective approach to mitigate CH₄ emissions in ruminants, which may lead to a decreased ruminal CH₄ production. The major target would be hydrogen (H₂), which is the primary substrate for

CH₄ production during ruminal methanogenesis. In the rumen, SRB have the ability to compete with methanogens for H₂, thus resulting in the inhibition of methanogenesis.

From another perspective, research indicates that CH₄ emission is also associated with dietary energy loss that reduces feed efficiency [238]. Another way of mitigating ruminal CH₄ identified in the literature is the use of saponins. According to Newbold, *et al.* [239], low concentrations of saponins act as antiprotozoal. In contrast, at higher concentrations, saponins are able to suppress methanogens [240] and inhibit ruminal bacterial and fungal species [241], limiting the H₂ availability for methanogenesis in the rumen, thereby lowering CH₄ production by up to 50% [240,242]. Other methods for ruminal CH₄ mitigation include forage quality [243-245], type of silage [246-249], proportion of concentrates [250-252] and composition [253-256], the use of organic acids [257-259], essential oils (secondary metabolites) [260-262], or probiotics [263-266]. Additionally, exogenous enzymes, such as cellulase and hemicellulose, are used in ruminant diets. These enzymes can improve the digestibility of fiber as well as animal productivity. They are also capable of lowering the acetate: propionate ratio in the rumen, ultimately resulting in the reduction of CH₄ production [267,268].

An indirect approach to reduce CH₄ production could be the use of antibiotics such as the antimicrobial monensin. The latter enhances the acetate: propionate ratio in the rumen [246] when added to the diet as a premix and has methanogenic effect. According to Hook, *et al.* [269], ionophores do not alter the diversity of methanogens but change the bacterial population from Gram-positive to Gram-negative, therefore resulting in the change in the fermentation from acetate to propionate, and reducing CH₄ [270-272]. Researchers are thinking of employing breeding to explore the possibility for developing low CH₄/GHG-emitting cows/ruminants. Numerous studies have shown a substantial variation in CH₄ production from cows and sheep [238,273,274], which is associated with phenotypic traits and heritability. Thus, this variation suggests a possibility of breeding animals with low CH₄ emission. However, a different view from Eckard, *et al.* [275] suggested that breeding for reduced CH₄ production is unlikely to be compatible with other breeding objectives.

5. Conclusions and Future Prospects

Developing high-yielding and quality crop varieties have been for decades the target of many agricultural-related research programs globally. Although significant progress has been recorded in this regard, the current global warming pattern exposed the linearity and imbalances of current food production systems that are responsible for exacerbating the impact of climate change by contributing to enhancing GHGs emissions. There is a global hunt for effective strategies that allow to lower GHG emissions while maintaining a balanced food production level to meet the increasing food demands. This review presents key approaches previously employed to improve plant nutrient use, fitness, and soil fertility, and here proposed as strategic because they carry a great potential to mitigate GHG emissions from agriculture. Among them, improving nitrogen use efficiency using forward or reverse genetics, and genetic engineering approaches offer the best perspectives for sustainability due to multidimensional impact on fertilizers application, and may confer abiotic stress tolerance, among others. In addition, enhancing radial oxygen loss in plants influences the activity of soil microorganisms, especially methane producing bacteria. Likewise, despite being a major component of agriculture, livestock production produces nearly 30% of GHG emitted from agriculture globally. This challenge offers a great opportunity to improve the livestock production chain and feed use efficiency (dairy farming, beef cattle, etc.), while attempting to lower GHG production and emissions, building on advances in breeding and genetic engineering and feed use efficiency and best nutrients use practices.

These areas of great interest carry the potential to serve as leading approaches with greater impact on the current global efforts to mitigate the effects of climate change and climate crisis.

Supplementary Materials: The following supporting information can be downloaded at the website of this paper posted on Preprints.org, Figure S1: title; Table S1: title; Video S1: title.

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