Nitrogen Cycling

Review

Open Access

https://doi.org/10.48130/nc-0025-0012

Impacts of climate change on global terrestrial nitrogen cycles

Miao Zheng[1,2,3], Qin Huang[2], Jinglan Cui[1,2,3] and Baojing Gu[1,2,3*]

Received: 7 November 2025

Revised: 1 December 2025

Accepted: 10 December 2025

Published online: 31 December 2025

Abstract

Terrestrial ecosystems are fundamental to human well-being, providing essential services such as food production, biodiversity maintenance, water regulation, carbon sequestration, and soil conservation. However, the accelerating pace of climate change is profoundly reshaping these ecosystems, heightening the urgency and complexity of their sustainable management. Although considerable advances have been made in understanding how climate change affects terrestrial ecosystems, global assessments of its impacts on nitrogen cycles remain fragmented, lacking systematic feedback analyses at the global scale and robust quantification of regional heterogeneity. This fragmentation constrains the incorporation of nitrogen feedback into Earth system models, thereby reducing the precision and reliability of future climate projections. This review synthesizes current knowledge on how key climate change drivers, including elevated atmospheric CO_2 concentrations, rising temperatures, and altered precipitation regimes, individually influence nitrogen dynamics across terrestrial ecosystems. This review further assesses the potential impacts of climate change on nitrogen budgets in global croplands, forests, and grasslands. The review also identifies critical challenges and emerging research priorities, emphasizing the need for integrated nitrogen cycle management under a changing climate. By advancing a unified understanding of climate–nitrogen interactions, this work provides a scientific basis for designing adaptation strategies that promote both ecological resilience and progress toward the Sustainable Development Goals (SDG).

Keywords: Elevated CO_2 concentration, Warming, Altered precipitation regimes, Cropland, Grassland, Forest, Nitrogen cycle

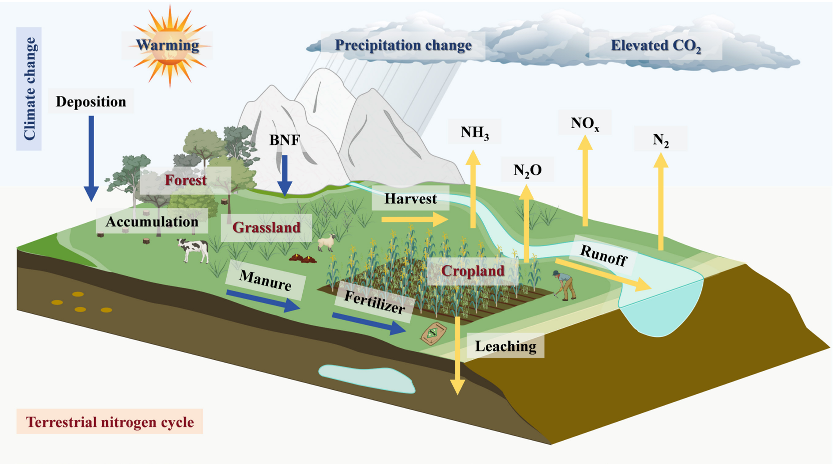
Highlights

- Elevated CO_2 concentrations, warming, and altered precipitation regimes are reshaping global terrestrial nitrogen cycles.
- Insufficient knowledge of climate-nitrogen feedback limits the reliability of future predictions.
- Integrated governance of the nitrogen cycle is essential for effective climate adaptation strategies.

* Correspondence: Baojing Gu (bjgu@zju.edu.cn)

Full list of author information is available at the end of the article.

Graphical abstract



Introduction

Climate change is accelerating at an unprecedented pace, threatening human well-being and planetary health[1]. This includes elevated carbon dioxide concentrations (eCO_2)[2], warming[3], and altered precipitation regimes[4]. In 2024, the atmospheric CO_2 concentration reached a record high of 423.9 ± 0.2 parts per million (ppm), 152% of the pre-industrial level of 278.3 ppm[5], while the year also became the warmest on record in the past 175 years, with the temperature nearly 1.55 ± 0.13 °C above the 1850–1990 average[2]. Additionally, precipitation patterns showed significant regional variability, with changes in both rainfall frequency and intensity[6] (Fig. 1a–c). Terrestrial ecosystems, including croplands, forests, and grasslands, are vital for providing essential resources that sustain human well-being (Fig. 1d). However, climate change can alter nitrogen (N) cycling as well as other biogeochemical processes, thereby negatively impacting these ecosystems and threatening their ability to sustain vital services[1]. Cropland, vital for food security, is under threat from climate change[7,8]. Extreme rainfall can limit N availability during rice tillering, leading to yield losses[9]. Forests and grasslands, which play crucial roles in biodiversity maintenance, water regulation, soil retention, and carbon (C) sequestration, are increasingly exposed to extreme weather events such as droughts and wildfires[10–15]. In particular, increased fire frequency can lead to significant losses of soil N and C in broadleaf forests and savanna grasslands, thereby reducing ecosystem C storage[16].

Terrestrial N cycling plays a key role in sustaining ecosystem productivity and ensuring food security[17–19]. The main terrestrial N transformation processes include ammonification, assimilation, biological N fixation (BNF), nitrification, denitrification, and anaerobic ammonium oxidation (anammox)[20–22] (Table 1). Based on N mass balance principles, this study investigates changes in N inputs (including N deposition, BNF, fertilizer, and manure) and N outputs (including N harvest and N surplus) in terrestrial ecosystems under climate change, as well as variations in N accumulation within forests. Nitrogen surplus encompasses the losses of reactive N (N_r) compounds and dinitrogen gas (N_2) emissions (Fig. 2, Tables 1 and 2). N_r emissions increased from 164 Tg in 1997 to 210 Tg in 2017[23], primarily from industrial sources like fossil fuel combustion, and agricultural sources such as fertilizer application[24,25]. N_r pollution is a significant challenge of the 21st century, causing a cascade of negative impacts across environmental systems[18,26–31]. Its interactions with climate change make effective N management even more difficult[24,32]. Therefore, balancing N levels to maximize benefits while minimizing harmful effects is critical[33].

This review summarizes the impacts of climate change on terrestrial ecosystem N cycling, focusing on the mechanisms by which elevated CO_2 concentrations, global warming, and altered precipitation regimes influence N cycling, and explores the potential impacts of climate change on N budgets in global croplands, forests, and grasslands, highlighting the existing challenges and future research directions. Through these discussions, this review aims to provide a critical foundation for understanding the mechanisms underlying terrestrial ecosystem N cycling in response to climate change, and to offer theoretical support for developing strategies to optimize N use efficiency (NUE) while reducing N_r emissions in this context (Table 1).

Elevated CO_2 levels

Elevated atmospheric CO_2 levels (eCO_2) generally promote crop yield by 21% (95% confidence interval [CI], 18% to 25%) relative to the ambient CO_2 level, with positive effects observed for major crops such as wheat, rice, maize, and soybeans[34]. Elevated CO_2 also increases net primary productivity (NPP) in grasslands (10%; 8% to 12%) and forests (27%; 23% to 31%) (Table 1), although the extent of these effects varies depending on the vegetation type[34,35] (Fig. 3). In C_3 grasslands, NPP increases by 10% (8% to 13%) under eCO_2, primarily due to enhanced photosynthesis[36]. Elevated CO_2 increases intercellular and chloroplastic CO_2 concentrations, thereby raising the ratio of Rubisco carboxylation to oxygenation, which reduces photorespiration and enhances net C assimilation[36,37]. In contrast, C_4 grasslands show no significant response (10%; −9% to 15%) because their CO_2 concentrating mechanism already maintains high local CO_2 around Rubisco, making carboxylation relatively insensitive to additional CO_2[38,39]. However, under drought stress, eCO_2 improves water-use efficiency by reducing stomatal conductance and increasing intercellular CO_2 concentrations, thereby alleviating water limitation and indirectly promoting NPP[40,41]. Notably, the predicted CO_2 increase by 2050 is +109 ppm under the SSP2-4.5 middle-of-the-road scenario and +39 ppm under the SSP1-1.9 sustainability scenario, both of which are lower than the CO_2 increase in the current eCO_2 experiments. This suggests that adaptive responses are unlikely to occur before 2050[35].

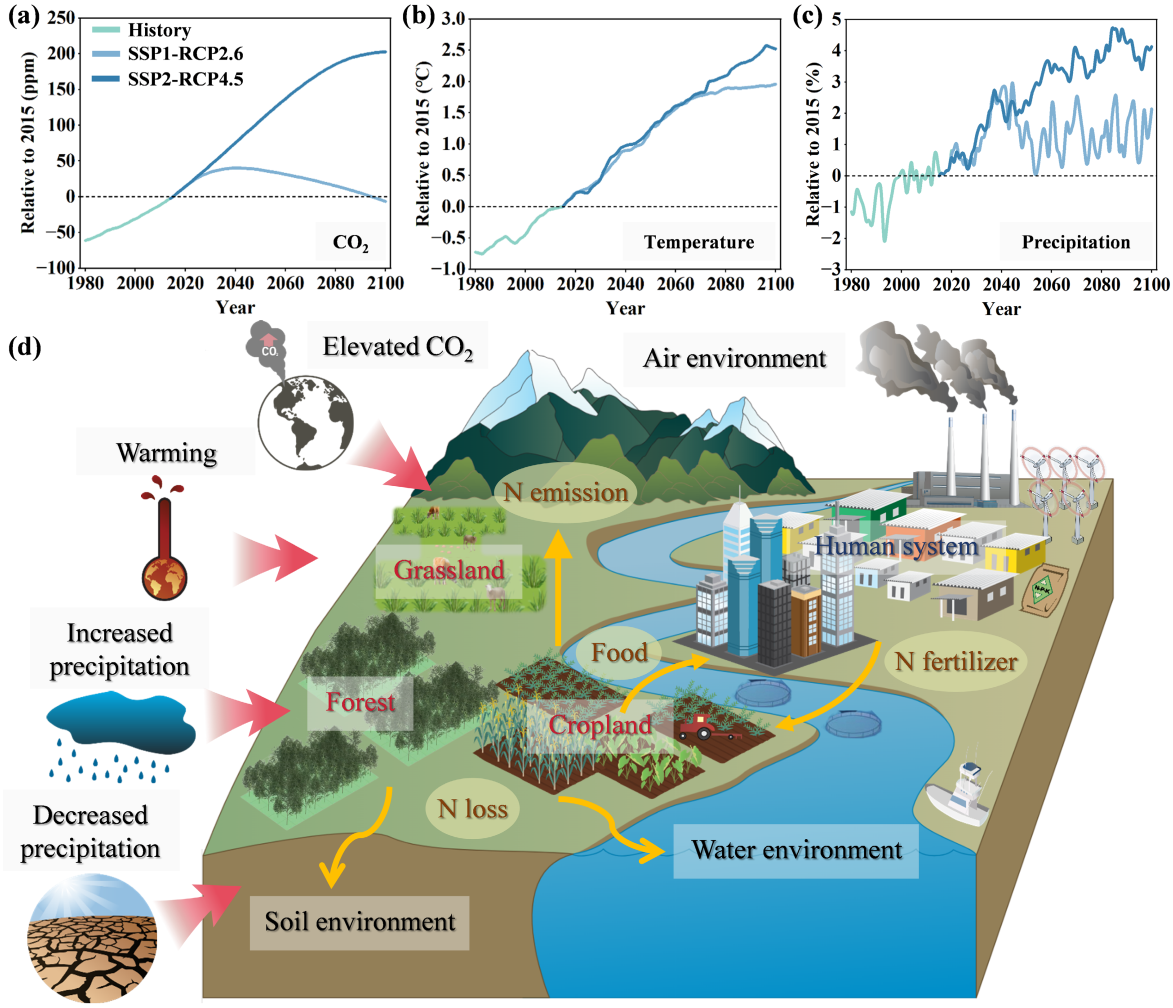


Fig. 1 Global climate change and terrestrial ecosystems. (**a**) Changes in global atmospheric CO_2 from 1980 to 2100 under different Shared Socioeconomic Pathways-Representative Concentration Pathways (SSP-RCP) scenarios. (**b**) Changes in global air temperature from 1980 to 2100 under different SSP-RCP scenarios. (**c**) Changes in global land precipitation from 1980 to 2100 under different SSP-RCP scenarios. (**d**) Effects of different climate change factors on the nitrogen cycle in global terrestrial ecosystems. Yellow arrows denote interactions between systems; Red arrows indicate the impacts of climate change on terrestrial ecosystems. N, nitrogen. The symbols are from Integration and Application Network (https://ian.umces.edu/media-library/).

Table 1 Terminologies included in this paper

Variable	Description
Yield	Crop yield is a metric of the quantity of harvested crop production per land area.
Net primary productivity	NPP includes both aboveground net primary productivity (ANPP) and belowground net primary productivity (BNPP).
Ammonia emission	NH_3 is emitted into the atmosphere from soil or water bodies of terrestrial ecosystems.
Nitrous oxide emission	N_2O emission is released into the atmosphere during nitrification and denitrification.
Nitrogen oxide emission	NO_x emission refers to a collection of N and oxygen compounds including NO, NO_2, and N_2O_3.
Nitrate leaching	NO_3^- leaching is the movement of inorganic N from soil, fertilizer, and residues into groundwater or deep soil through rainfall or drip irrigation.
Nitrate runoff	NO_3^- runoff refers to the loss of inorganic N to surface water.
Nitrogen use efficiency	NUE is defined as the N harvest divided by the N input in the terrestrial ecosystems.
Biological nitrogen fixation	BNF is the conversion of N_2 to NH_4^+ by N-fixing microorganisms, including symbiotic and non-symbiotic ones.
Accumulation	Accumulation is the process by which N is gradually retained and concentrated in soil, litter, and vegetation, mainly in forests, while N accumulation in croplands and grasslands is assumed stable and therefore not considered here.
Denitrification	Denitrification is the process by which denitrifying microorganisms convert NO_3^- to gaseous N (N_2O, NO, and N_2).
Nitrification	Nitrification is the process by which nitrifying microorganisms convert NH_4^+ to NO_3^- under aerobic conditions.
Ammonification	Ammonification refers to the conversion of organic N to NH_4^+ by microorganisms.
Assimilation	Assimilation is the process by which plants and microorganisms incorporate inorganic N (NH_4^+, NO_3^-) into organic compounds for growth and metabolism.
Anammox	Anammox is the process by which ammonium (NH_4^+) is oxidized with nitrite (NO_2^-) under anaerobic conditions to produce N_2.
Leaf nitrogen content	Leaf [N] denotes the N content in the leaf of a plant.
Grain nitrogen content	Grain [N] denotes the N content in the grain of a plant.
Stem nitrogen content	Stem [N] denotes the N content in the stem of a plant.

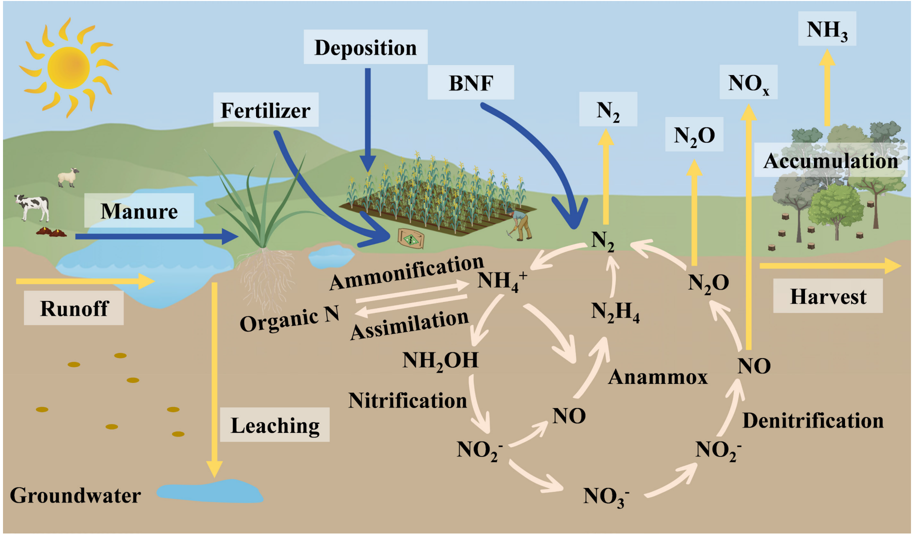


Fig. 2 Nitrogen flows in terrestrial ecosystems. Nitrogen inputs and outputs are differentiated by blue and yellow arrows, respectively. Nitrogen inputs include biological nitrogen fixation (BNF), deposition, fertilizer, and manure. Nitrogen outputs include harvest, reactive nitrogen losses, and non-reactive nitrogen emissions. Simplified soil nitrogen cycle, such as ammonification, ammonium assimilation, BNF, nitrification, denitrification, and anaerobic ammonium oxidation (anammox) are shown in light pink arrows. The symbols are from the Integration and Application Network (https://ian.umces.edu/media-library/).

Table 2 Nitrogen fluxes in croplands, grasslands, and forests derived from models in 2020

Variable	Ecosystem value	Component	Ecosystem value
N input (Tg)	Cropland: 253 Grassland: 138 Forest: 91	BNF (Tg)	Cropland: 40 Grassland: 16 Forest: 66
		Deposition (Tg)	Cropland: 21 Grassland: 15 Forest: 21
		Fertilizer (Tg)	Cropland: 141 Grassland: 27 Forest: 4
		Manure (Tg)	Cropland: 51 Grassland: 80 Forest: /
N harvest (Tg)	Cropland: 118 Grassland: 95 Forest: 22		
N surplus (Tg)	Cropland: 135 Grassland: 43 Forest: 32	NH_3 (Tg)	Cropland: 29 Grassland: 9 Forest: 2
		N_2O (Tg)	Cropland: 5 Grassland: 1 Forest: 3
		NO_x (Tg)	Cropland: 2 Grassland: 0.4 Forest: 3
		NO_3^- (Tg) (Including leaching and runoff)	Cropland: 54 Grassland: 11 Forest: 11
		N_2 (Tg)	Cropland: 45 Grassland: 22 Forest: 13
N accumulation (Tg)	Forest: 37		
NUE (%)	Cropland: 47 Grassland: 69 Forest: 65		

All nitrogen budgets refer to the year 2020. The cropland data are derived from the Integrated Model to Assess the Global Environment (IMAGE), the grassland data from the Model of Agricultural Production and its Impact on the Environment (MAgPIE), and the forest data from the Dynamic Land Ecosystem Model (DLEM).

Additionally, elevated CO_2 reduces plant N content, including grains, leaves, and stems, likely due to N dilution resulting from increased C assimilation and decreased investment in Rubisco for photosynthesis[42,43]. Leaf N content in woody plants decreases under eCO_2[44] (Table 1), with non-leguminous trees showing approximately twice the reduction compared to legumes, and evergreen species exhibiting more substantial declines than deciduous ones. Needle-like leaves experience a two- to four-fold greater decrease in leaf N compared to other leaf types. Meanwhile, woody plants tend to exhibit greater N reductions than herbaceous plants[45]. In crops, eCO_2 typically induces a N dilution effect, although its magnitude varies among species. Potato and major cereal crops such as barley, rice, and wheat generally show notable reductions in N content, whereas soybean exhibits only a minimal decrease[46]. Long-term trends also indicate a decline in N availability in forests and natural grasslands under eCO_2[47]. Decreased N content may progressively diminish the productivity gains typically associated with eCO_2 and constrain ecosystem C sequestration[47,48]. In agricultural systems, although mineral fertilization can compensate for N deficits, plants under eCO_2 tend to allocate more N to roots rather than leaves, leading to lower leaf N content[49]. Overall, despite the reduction in plant N content, the rise in NPP and crop yields under eCO_2 ultimately leads to an increase in total N harvest in terrestrial ecosystems[34,35] (Fig. 3).

Elevated CO_2 also enhances BNF rates, boosting microbial capacity to convert inert N_2 into plant-available N and reducing nitrates to N_2[50–52]. Concurrently, eCO_2 stimulates N uptake by plants, improving NUE by 19%–32% in terrestrial ecosystems[34,35]. This increase in NUE reduces N_r losses, including the emissions of ammonia (NH_3), nitrous oxide (N_2O), and nitrogen oxides (NO_x) to the atmosphere, as well as decreases in nitrate leaching and runoff (NO_3^-) into water bodies[34,35] (Table 1). Nitrogen deposition, influenced by ammonia and nitrogen oxide emissions, generally declines under eCO_2, and anthropogenic N inputs, such as fertilizers and manure, are also expected to decrease[34,35] (Fig. 3). In summary, eCO_2 has a positive impact on N cycling in terrestrial ecosystems. It

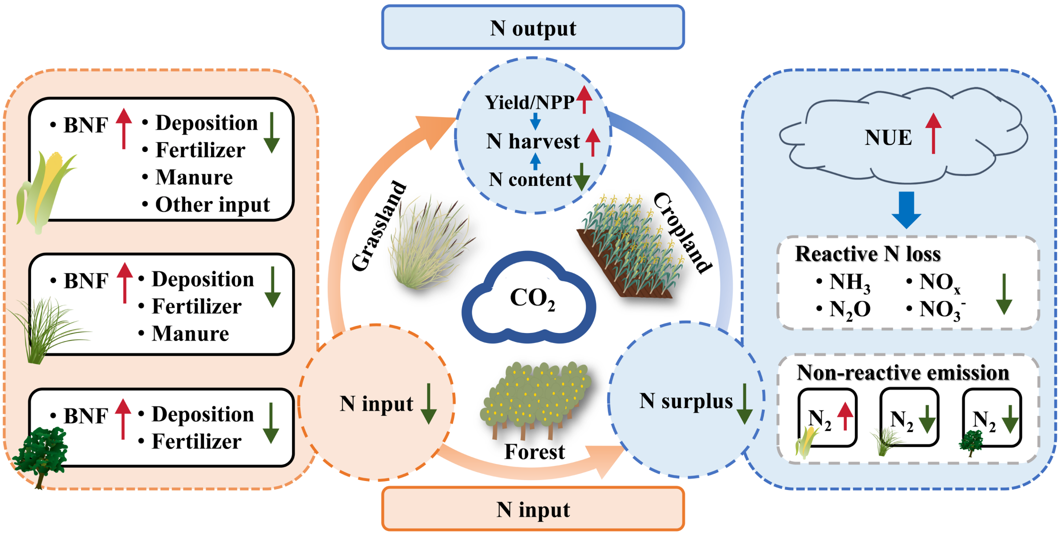


Fig. 3 The impacts of elevated CO_2 levels on terrestrial nitrogen cycles. The orange box represents changes in nitrogen input. The blue box represents changes in nitrogen output. Red arrows indicate positive effects, green arrows represent suppressive effects, and blue arrows indicate their interrelations. BNF, biological nitrogen fixation; NPP, net primary productivity; NUE, nitrogen use efficiency; NH_3, ammonia; N_2O, nitrous oxide; NO_x, nitrogen oxides; NO_3^-, nitrate leaching and runoff; N, nitrogen. Specific ecological processes corresponding to each arrow: Red arrow → increased BNF → increased nitrogen input; Green arrow → decreased deposition/fertilizer/manure/other input → decreased nitrogen input; Red arrow → increased yield/NPP → increased nitrogen harvest; Green arrow → decreased nitrogen content → decreased nitrogen harvest; Red arrow → increased NUE → decreased nitrogen surplus; Green arrow → decreased ammonia/nitrous oxide/nitrogen oxides/nitrate leaching and runoff → decreased nitrogen surplus. The symbols are from the Integration and Application Network (https://ian.umces.edu/media-library/).

reduces the need for external N inputs, mitigates N surplus, and promotes greater NUE.

Overall, elevated CO_2 levels not only have the potential to increase food production but also offer an opportunity to reduce environmental pollution. This highlights a significant opportunity to accelerate progress toward several Sustainable Development Goals[53,54]. Specifically, improving NUE by 19%–32% can reduce nitrate leaching and mitigate water eutrophication[34,35], directly supporting SDG 6 ('clean water and sanitation'). Elevated CO_2 can also increase productivity by 10%–27%[34,35], contributing to SDG 2 ('zero hunger'). In addition, enhancing NUE and reducing excess N_r losses can lower environmental pollution[34,35], supporting SDG 13 ('climate action'), and improving health and well-being. However, the anticipated rise in BNF under eCO_2 needs careful monitoring to avoid excessive N inputs and losses in terrestrial ecosystems. Excessive N input can be reduced by decreasing reliance on mineral fertilizers and promoting the reuse of organic N sources, such as organic fertilizers and straw[55]. Meanwhile, the reduction in N concentrations could impact protein supply in human diets[56], suggesting the need to adjust dietary recommendations to balance human nutritional requirements with protein content[57].

Global warming

Climate warming is expected to have both positive and negative impacts on N cycles. In croplands, warming generally reduces crop yields, with maize experiencing the most significant decline[58], especially in tropical and arid regions due to heat stress and water limitations[59,60]. While wheat yields show no significant response in high-latitude regions[58], warming in general has a negative impact on wheat yields in low-latitude regions[61,62]. In grasslands and forests, warming increases NPP, primarily through prolonged growing seasons and enhanced photosynthetic activity[63–65]. Since most vegetation has not yet reached its optimal temperature for photosynthesis under current climate conditions, moderate warming typically promotes overall vegetation growth[66]. C_3 grasslands, which thrive in temperate and cold climates, benefit from effective photosynthesis under moist, cool conditions[67]. As a result, NPP increases by about 10% (5% to 15%)[63]. In contrast, C_4 grasslands, which dominate subtropical and tropical climates, are more efficient in water use under warm, drought-prone conditions[67]. However, their NPP response to warming remains statistically elusive[63]. Although C_4 grasslands tend to be heat-tolerant[68], the combined effects of erratic precipitation and increased evaporation due to climate warming may still limit plant growth[69]. Additionally, warming increases N concentrations in grains, leaves, and stems, likely due to elevated N uptake and improved soil N availability[70]. Consequently, warming tends to decrease N harvest in croplands, while increasing it in forests and grasslands. However, forest N accumulation is projected to decrease globally, with the most pronounced reductions in regions such as the Amazon, Congo basins, and Southeast Asia. In contrast, slight increases are expected in parts of North America, northern Eurasia, and high-elevation regions such as mountains and plateaus. These patterns indicate that temperature, elevation, latitude, and precipitation jointly shape regional N accumulation, driving spatial heterogeneity[64] (Fig. 4).

Warming also stimulates microbial activity, accelerating C decomposition and microbial respiration, which in turn provides more substrates for microbial processes and enhances BNF[71,72]. BNF, which is likely influenced by changes in root exudates and microbial activity, becomes a key contributor to increased N input in croplands and grasslands[58,63]. The primary focus of this review is on the individual effects of warming on BNF. Although it is recognized that soil moisture and temperature are key drivers[73], the complex interactive effects of CO_2, temperature, and drought are complex and will be explored in future studies. Meanwhile, N deposition, influenced by ammonia and nitrogen oxides emissions, generally increases under warming, and anthropogenic N inputs (e.g., fertilizers and manure) are expected to remain stable. However, warming

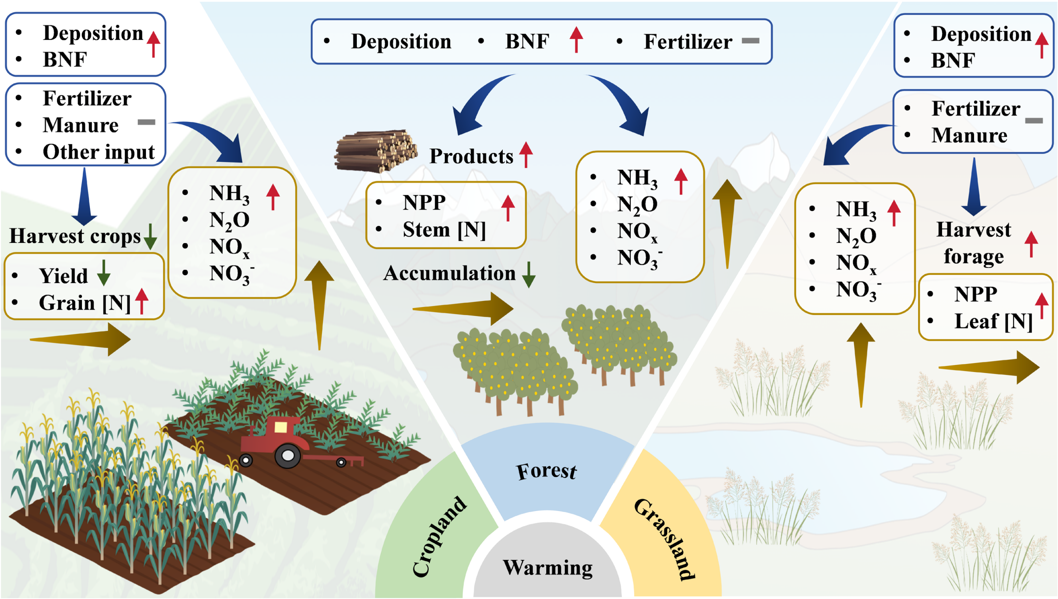


Fig. 4 The impacts of global warming on terrestrial nitrogen cycles. The left box represents the impacts of warming on the cropland nitrogen cycles. The middle box represents the impacts of warming on the forest nitrogen cycles. The right box shows the impacts of warming on the nitrogen cycle in grasslands. The nitrogen fluxes, including nitrogen input and output, are shown by blue and yellow arrows, respectively. Red arrows indicate positive effects, while green arrows represent suppressive effects. The gray solid lines indicate nonsignificant effects. Feedback mechanisms differ across various ecosystems. BNF, biological nitrogen fixation; NPP, net primary productivity; NUE, nitrogen use efficiency; NH_3, ammonia; N_2O, nitrous oxide; NO_x, nitrogen oxides; NO_3^-, nitrate leaching and runoff; [N], nitrogen content. Specific ecological processes corresponding to each arrow: Red arrow → increased BNF/deposition → increased nitrogen input; Gray solid line → unchanged fertilizer/manure/other input → unchanged nitrogen input; Green arrow → decreased yield → decreased nitrogen harvest; Red arrow → increased NPP → increased nitrogen harvest; Red arrow → increased nitrogen content → increased nitrogen harvest; Red arrow → increased ammonia/nitrous oxide/nitrogen oxides/nitrate leaching and runoff → increased nitrogen surplus; Green arrow → decreased nitrogen accumulation. The symbols are from the Integration and Application Network (https://ian.umces.edu/media-library/).

also leads to substantial increases in N_r losses, ranging from 22% to 169%[58,63,64]. Enhanced microbial processes and thermodynamic reactions result in higher emissions of ammonia, nitrous oxide, and nitrogen oxides, as well as increased nitrate leaching and runoff into aquatic systems[58,63,64] (Fig. 4). These increased N losses highlight the potential for significant environmental pollution.

Overall, climate warming is projected to lead to crop yield losses in croplands and increased N_r losses in global terrestrial ecosystems, posing potential risks and challenges for both human society and the environment[27]. Reduced food production may have particularly severe consequences for developing economies in Africa, Latin America, and Asia, where crop losses could exacerbate hunger and malnutrition[8]. On the other hand, increased feed production in grasslands may bolster global livestock production[74], prompting policymakers to prioritize livestock production to meet the growing demand for food and protein from an expanding global population[75]. While current projections suggest an increase in NPP in grasslands and forests, sustained global warming could push more ecosystems beyond their optimal temperatures for photosynthesis, potentially reducing productivity and exacerbating negative impacts[76,77]. Additionally, the accelerating rates of N losses, already a concerning trend, could significantly affect soil and water quality, thereby hindering food production[78,79]. Extreme heat further reduces soil C pools and ecosystem productivity while increasing N_r losses[80–82]. The uneven effects of climate warming could exacerbate spatial inequalities[64], underscoring the need for timely and robust adaptive strategies to mitigate the diverse impacts of global warming[83,84].

Altered precipitation regimes

Decreased precipitation reduces crop yields and NPP by imposing water stress, whereas moderate increases alleviate drought and enhance photosynthesis and microbial activity that support N cycling[85,86] (Fig. 5). However, responses to precipitation variability are region-specific. In arid regions, reductions in precipitation cause relatively smaller declines in plant growth, reflecting adaptations to chronic water limitation, such as deep rooting and enhanced stomatal regulation[87,88]. In contrast, plants in more humid regions, which are adapted to more stable water availability, exhibit greater growth reductions under drought conditions[89,90]. Under decreased precipitation, NPP declines by 15% (−24% to −3%) in arid grasslands, compared to a greater decrease of 29% (−39% to −19%) in humid grasslands[91]. Increased precipitation boosts NPP by 30% (22% to 44%) in arid grasslands, but only 8% (2% to 15%) in humid grasslands[91]. In arid grasslands, increased precipitation provides additional moisture, alleviating the primary constraint on plant growth and significantly enhancing NPP[86]. In humid grasslands, where water is less limiting, growth is more influenced by temperature, leading to a smaller increase in NPP[89]. Overall, increased precipitation tends to enhance terrestrial N harvest, while reduced precipitation exerts the opposite effect.

Water scarcity also restricts microbial activity, including that of N-fixing bacteria[92], leading to a 23%–57% reduction in BNF[91]. Conversely, increased precipitation promotes microbial activity and C availability, thereby stimulating BNF by 36%–129%[91]. These effects may be further mediated by changes in the quantity and composition of root exudates, such as rhizoctonia, which influence

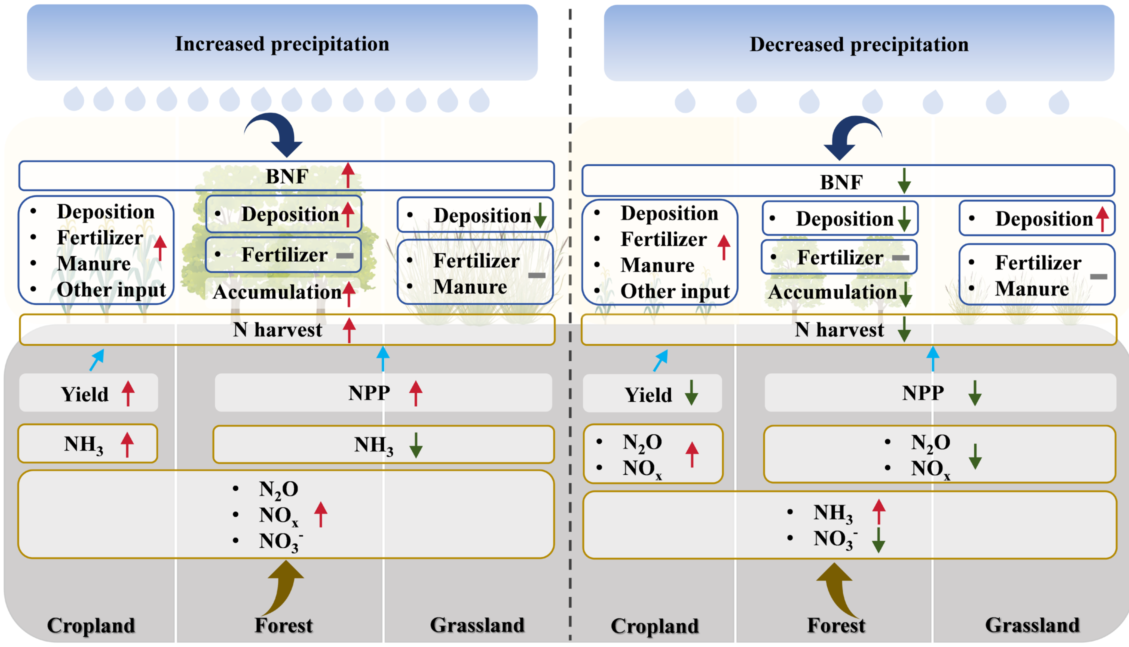


Fig. 5 The impacts of altered precipitation regimes on terrestrial nitrogen cycles. The left box represents the impacts of increased precipitation on the terrestrial nitrogen cycles. The right box represents the impacts of decreased precipitation on the terrestrial nitrogen cycles. The nitrogen fluxes, including nitrogen input and output, are shown by dark blue and yellow arrows and boxes, respectively. Red arrows indicate positive effects, green arrows represent suppressive effects, and light blue arrows indicate their interrelations. The gray solid lines indicate nonsignificant effects. Nitrogen deposition, based on combined ammonia and nitrogen oxides, varies across ecosystems due to differing feedback mechanisms. BNF, biological nitrogen fixation; NPP, net primary productivity; NH_3, ammonia; N_2O, nitrous oxide; NO_x, nitrogen oxides; NO_3^-, nitrate leaching and runoff; N, nitrogen. Specific ecological processes corresponding to each arrow: Red or green arrow → increased or decreased BNF/deposition/fertilizer/manure/other input → increased or decreased nitrogen input; Gray solid line → unchanged fertilizer/manure → unchanged nitrogen input; Red or green arrow → increased or decreased yield/NPP → increased or decreased nitrogen harvest; Red or green arrow → increased or decreased ammonia/nitrous oxide/nitrogen oxides/nitrate leaching and runoff → increased or decreased nitrogen surplus; Red or green arrow → increased or decreased nitrogen accumulation. The symbols are from the Integration and Application Network (https://ian.umces.edu/media-library/).

the colonization and activity of N-fixing microorganisms[93–95]. Meanwhile, N deposition, inferred from the combined inputs of ammonia and nitrogen oxides, exhibits different responses across ecosystems. Anthropogenic N inputs also vary by ecosystem. In forests and grasslands, these inputs remain relatively stable under changing precipitation[91], whereas in croplands, human-driven N inputs generally increase (Fig. 5).

Precipitation changes strongly regulate N_r dynamics by controlling soil moisture and microbial activity[96–98]. Increased precipitation enhances soil water content and hydraulic conductivity, thereby accelerating N cycling and stimulating microbial processes, including the activation of nitrifying and denitrifying bacteria[99–101]. This leads to higher nitrate losses via leaching and increased gaseous N emissions, including nitrous oxide and nitrogen oxides[91]. Excessive precipitation may also impair root functions under waterlogged conditions, promoting ammonia volatilization from croplands[102,103], whereas generally reducing ammonia emissions from forests and grasslands, as more ammonia remains dissolved in the soil solution[104] (Fig. 5). In contrast, decreased precipitation imposes water stress, limiting plant growth, microbial N transformations, and NUE[105,106]. This suppresses the activity of nitrifying and denitrifying microorganisms[107], which reduces N_r losses, including nitrate losses and emissions of nitrous oxide and nitrogen oxides[91]. Meanwhile, ammonia emissions may rise due to inhibited nitrification, leading to ammonium accumulation and volatilization[99,100].

These findings highlight the contrasting effects of precipitation variability on N cycling: drought tends to enhance N retention by limiting losses, whereas wetter conditions promote hydrologically mediated microbial processes[101,104,108]. These findings suggest that both the magnitude and spatial heterogeneity of future precipitation changes are likely to increase, amplifying hydrological and climatic pressures on global food production and N cycling, and intensifying disparities in the global N budget[91]. Such imbalances call for the urgent development and implementation of timely, region-specific adaptation strategies to safeguard food security and environmental sustainability[109,110]. In regions experiencing decreased precipitation and reduced yields, these measures alone may not fully mitigate the associated N pollution. To maintain food production, N inputs are likely to increase; however, with limited potential for further improvements in NUE, reactive N losses are expected to persist. As a result, N pollution will remain a long-term and significant challenge, especially under increasingly variable precipitation patterns. Extreme heavy rainfall events further negatively affect soil C pools and N fluxes, enhancing nitrate losses and exacerbating water eutrophication[80,111,112]. These findings highlight the need for integrated policy frameworks that address climate, ecology, and pollution management simultaneously to enhance system resilience and support a sustainable future[113,114].

Challenges and future directions

This paper focuses on the impacts of individual climate change factors on terrestrial N cycling. Climate change encompasses various factors, such as rising atmospheric CO_2 concentrations, global warming, altered precipitation regimes, and extreme weather events[115]. These factors interact through multiple mechanisms to affect terrestrial ecosystems, and the complexity of these interactions makes it challenging to comprehensively address them within a single study. In particular, the frequency and intensity of extreme climate events should be incorporated into Earth system models to more accurately assess N cycling responses of terrestrial ecosystems under climate change[80,116]. Consequently, a comprehensive assessment of the combined effects of multiple climate drivers on N cycling remains an ambitious but necessary research goal. Future studies should employ machine learning and other approaches to explore the interactions among multiple factors[117,118] (Fig. 6). Specific applications include using random forest models for N_r loss prediction and deep learning to integrate remote sensing, field experiments, and model outputs to predict long-term N dynamics.

The data include experimental manipulations of both managed and natural ecosystems. While the distribution of study sites is uneven due to data availability, the current dataset spans all continents and climate zones globally[34,35,58,63,64,91]. However, integrated global datasets with uniform distributions that simultaneously capture CO_2, temperature, and precipitation are lacking, which limits the feasibility of combining these variables in a single unified analysis. In addition, high experimental costs and limited resources in low-latitude developing countries hinder the widespread implementation of climate manipulation experiments, thereby reducing the global applicability of research findings[119]. As more comprehensive datasets and advanced methodologies become available, large-scale synthesis of multi-factor climate impacts will be increasingly feasible. Alternative solutions, such as incorporating satellite inversion data, establishing international cooperation networks, and promoting low-cost observation technologies, should be explored to make climate experiments more feasible and accessible in these regions. Overcoming these challenges will require policy interventions, including financial support and capacity-building projects[120]. Given the accelerating pace of climate change, only through sustained, coordinated global action can we effectively address the interconnected challenges of food security and environmental sustainability (Fig. 6).

The long-term responses of terrestrial ecosystems to climate change are further influenced by factors such as physiological thresholds, species interactions, domestication, and adaptation, all of which may introduce non-linear dynamics[121−123]. These effects are context-dependent and vary over time and across environmental conditions, making it challenging to extrapolate short-term results to long-term predictions, especially those extending to 2100[124,125]. Therefore, the application of century-scale models is essential for capturing the long-term dynamics of terrestrial N cycling and informing adaptation and mitigation strategies under ongoing climate change. Additionally, climate-induced shifts in species composition may indirectly affect productivity, potentially amplifying or mitigating the direct effects of climate change[126]. Future research should integrate species turnover models with climate projections to better understand the feedback mechanisms of N cycling under different climate scenarios (Fig. 6).

Although this study emphasizes the impacts of climate change on N cycling, it is acknowledged that other nutrients, such as phosphorus, potassium, and antibiotics, also play crucial roles in ecosystem responses to climate change[76]. For instance, warming has been shown to exacerbate the release of phosphorus from soils and water bodies[127,128]. Further research is needed to assess the interactive effects of N and other nutrients, expanding from a 'single N cycle' to a 'multi-nutrient synergistic cycle', and to develop strategies for maintaining nutrient stoichiometric balance, which is essential for ecosystem health and service provision[129]. Nitrous acid is also a significant N loss pathway[130], and the effects of climate change on nitrous acid can be a key focus in future research[131]. Given the transboundary nature of N_r loss, it necessitates solid international

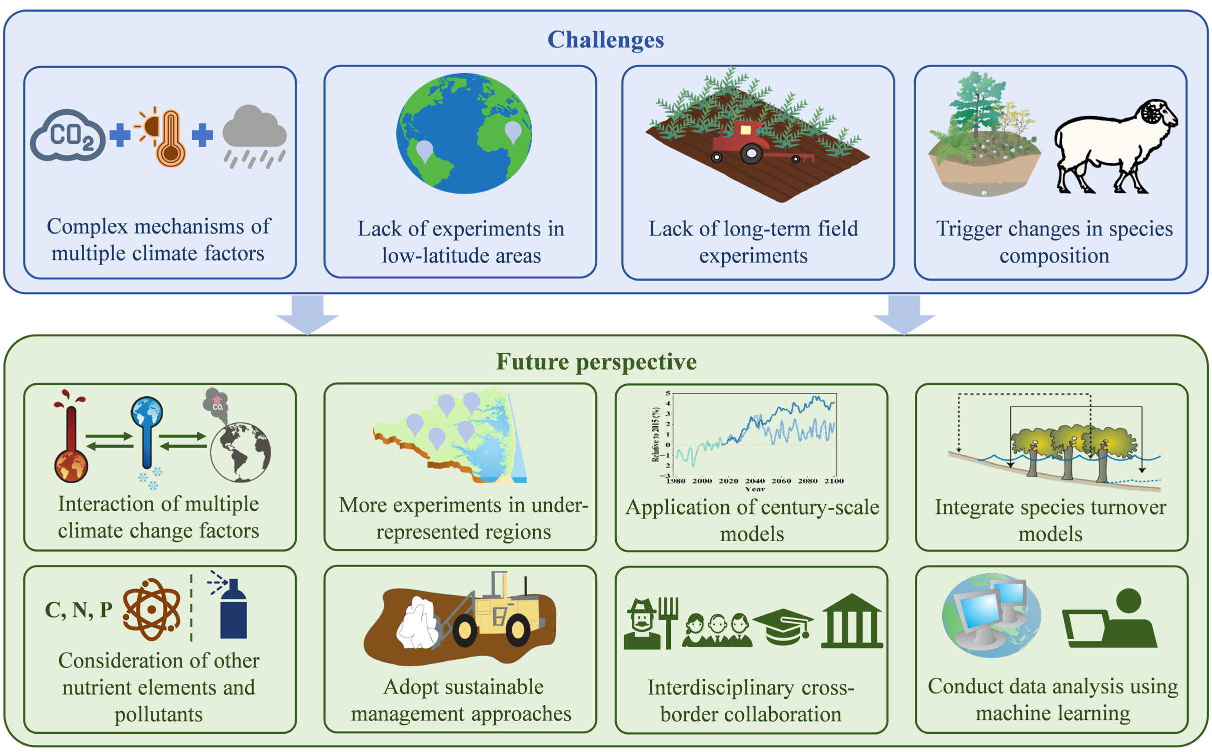


Fig. 6 Challenges and future perspective on terrestrial nitrogen cycles under global climate change. The symbols are from the Integration and Application Network (https://ian.umces.edu/media-library/).

cooperation to manage the global N cycle[24]. Integrating N-related policies into frameworks such as the Paris Agreement can enhance synergies and guide national actions through nationally determined contributions, promoting efficient NUE and reducing environmental threats to support sustainable development goals[132,133].

Policymakers, scientists, and the public must continue to collaborate. Decision-makers should implement strategies to improve productivity and reduce N_r losses in parallel with measures to manage climate impacts[8] (Fig. 6). For example, in rainfed and mixed farming systems of sub-Saharan Africa, combining rainwater harvesting with organic amendments can effectively enhance soil fertility and improve both water- and N-use efficiency[134]. In Panama forests, introducing N_2-fixing tree species helps sustain natural N inputs and reduces dependence on external fertilizers[135]. A comprehensive understanding of the mechanisms controlling terrestrial N cycling is essential for developing effective management strategies[136−138].

Conclusions

This review quantifies the impacts of elevated CO_2, global warming, and altered precipitation regimes on N cycling across croplands, forests, and grasslands, and further identifies the key drivers of regional heterogeneity, highlighting how climate change may exacerbate spatial disparities in N dynamics. Based on these insights, this study outlines several priority future research directions: (1) investigating multi-factor interactions among climate change drivers; (2) integrating comprehensive datasets and refining model structures; (3) exploring cross-nutrient interactions beyond the N cycle; (4) assessing long-term and non-linear ecosystem responses; and (5) developing region-specific adaptation strategies. A comprehensive understanding of these processes is essential for promoting sustainable development under a changing climate.

Author contributions

The authors confirm their contributions to the paper as follows: Miao Zheng: study design, manuscript preparation, and revision; Qin Huang: figure enhancement; Jinglan Cui: language editing; Baojing Gu: study design, funding acquisition, supervision, writing review, and editing. All authors reviewed and approved the final manuscript.

Data availability

The datasets generated or analyzed during the current study were compiled from site-based manipulation experiments. The data cover global locations and span 30 years of field-controlled experiments. Metadata are currently under restricted access due to ongoing analyses, but access can be obtained from the authors upon reasonable request.

Funding

The research presented in this paper was funded by the National Natural Science Foundation of China (Grant Nos 42261144001 and 42325707), and Postdoctoral Fellowship Program of China Postdoctoral Science Foundation (Grant No. GZC20232311).

Declarations

Competing Interests

The authors declare that they have no conflict of interest.

Author details

[1]State Key Laboratory of Soil Pollution Control and Safety, Zhejiang University, Hangzhou 310058, China; [2]College of Environmental and Resource Sciences, Zhejiang University, Hangzhou 310058, China; [3]Policy Simulation Laboratory, Zhejiang University, Hangzhou 310058, China

References

[1] Intergovernmental Panel on Climate Change (IPCC). 2023. Summary for policymakers. In *Climate Change 2023: Synthesis Report*, eds. Core Writing Team, Lee H, Romero J. Geneva: IPCC. pp. 1–34 doi: 10.59327/IPCC/AR6-9789291691647.001

[2] World Meteorological Organization (WMO). 2025. State of the global climate 2024. Geneva: WMO. 42 pp https://library.wmo.int/idurl/4/69455

[3] Hoegh-Guldberg O, Jacob D, Taylor M, Guillén Bolaños T, Bindi M, et al. 2019. The human imperative of stabilizing global climate change at 1.5 °C. *Science* 365(6459):eaaw6974

[4] Li C, Liu J, Du F, Zwiers FW, Feng G. 2025. Increasing certainty in projected local extreme precipitation change. *Nature Communications* 16(1):850

[5] World Meteorological Organization (WMO). 2025. *Greenhouse gas bulletin No. 21*. WMO, Geneva. 10 pp https://library.wmo.int/idurl/4/69654

[6] Thackeray CW, Hall A, Norris J, Chen D. 2022. Constraining the increased frequency of global precipitation extremes under warming. *Nature Climate Change* 12(5):441−448

[7] Anderson WB, Seager R, Baethgen W, Cane M, You L. 2019. Synchronous crop failures and climate-forced production variability. *Science Advances* 5(7):eaaw1976

[8] Lobell DB, Schlenker W, Costa-Roberts J. 2011. Climate trends and global crop production since 1980. *Science* 333(6042):616−620

[9] Fu J, Jian Y, Wang X, Li L, Ciais P, et al. 2023. Extreme rainfall reduces one-twelfth of China's rice yield over the last two decades. *Nature Food* 4(5):416−426

[10] Food and Agriculture Organization (FAO). 2025. *Global forest resources assessment 2025*. FAO, Rome. 210 pp doi: 10.4060/cd6709en

[11] Anderegg WRL, Wu C, Acil N, Carvalhais N, Pugh TAM, et al. 2022. A climate risk analysis of Earth's forests in the 21st century. *Science* 377(6610):1099−1103

[12] Rodrigo-Comino J. 2019. Grasslands of the world: diversity, management and conservation. *Systematics and Biodiversity* 17(1):86−87

[13] Bai Y, Cotrufo MF. 2022. Grassland soil carbon sequestration: current understanding, challenges, and solutions. *Science* 377(6606):603−608

[14] Borer ET, Grace JB, Harpole WS, MacDougall AS, Seabloom EW. 2017. A decade of insights into grassland ecosystem responses to global environmental change. *Nature Ecology & Evolution* 1(5):118

[15] Radeloff VC, Mockrin MH, Helmers D, Carlson A, Hawbaker TJ, et al. 2023. Rising wildfire risk to houses in the United States, especially in grasslands and shrublands. *Science* 382(6671):702−707

[16] Pellegrini AFA, Ahlström A, Hobbie SE, Reich PB, Nieradzik LP, et al. 2018. Fire frequency drives decadal changes in soil carbon and nitrogen and ecosystem productivity. *Nature* 553(7687):194−198

[17] Kou-Giesbrecht S. 2025. Nitrogen cycling in earth system models: from constraining carbon budgets to projecting pollution for planetary stewardship. *Journal of Geophysical Research: Biogeosciences* 130(10):e2025JG009209

[18] Stevens CJ. 2019. Nitrogen in the environment. *Science* 363(6427):578−580

[19] Sutton MA, Bleeker A, Howard CM, Bekunda M, Grizzetti B, et al. 2013. Our nutrient world: the challenge to produce more food and energy with less pollution. *Report*. Edinburgh: Centre for Ecology and Hydrology. 128 pp www.unep.org/resources/report/our-nutrient-world-challenge-produce-more-food-and-energy-less-pollution

[20] Mosley OE, Gios E, Close M, Weaver L, Daughney C, et al. 2022. Nitrogen cycling and microbial cooperation in the terrestrial subsurface. *The ISME Journal* 16(11):2561−2573

[21] Kuypers MMM, Marchant HK, Kartal B. 2018. The microbial nitrogen-cycling network. *Nature Reviews Microbiology* 16(5):263−276
[22] Klimasmith IM, Kent AD. 2022. Micromanaging the nitrogen cycle in agroecosystems. *Trends in Microbiology* 30(11):1045−1055
[23] Malik A, Oita A, Shaw E, Li M, Ninpanit P, et al. 2022. Drivers of global nitrogen emissions. *Environmental Research Letters* 17(1):015006
[24] Gruber N, Galloway JN. 2008. An Earth-system perspective of the global nitrogen cycle. *Nature* 451(7176):293−296
[25] Gong C, Tian H, Liao H, Pan N, Pan S, et al. 2024. Global net climate effects of anthropogenic reactive nitrogen. *Nature* 632(8025):557−563
[26] Galloway JN, Aber JD, Erisman JW, Seitzinger SP, Howarth RW, et al. 2003. The nitrogen cascade. *BioScience* 53(4):341
[27] Kanter DR. 2018. Nitrogen pollution: a key building block for addressing climate change. *Climatic Change* 147(1−2):11−21
[28] Fowler D, Coyle M, Skiba U, Sutton MA, Cape JN, et al. 2013. The global nitrogen cycle in the twenty-first century. *Philosophical Transactions of the Royal Society B: Biological Sciences* 368(1621):20130164
[29] Vitousek PM, Aber JD, Howarth RW, Likens GE, Matson PA, et al. 1997. Human alteration of the global nitrogen cycle: sources and consequences. *Ecological Applications* 7(3):737−750
[30] Erisman JW, Galloway JN, Seitzinger S, Bleeker A, Dise NB, et al. 2013. Consequences of human modification of the global nitrogen cycle. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences* 368(1621):20130116
[31] Bodirsky BL, Popp A, Lotze-Campen H, Dietrich JP, Rolinski S, et al. 2014. Reactive nitrogen requirements to feed the world in 2050 and potential to mitigate nitrogen pollution. *Nature Communications* 5(1):3858
[32] Greaver TL, Clark CM, Compton JE, Vallano D, Talhelm AF, et al. 2016. Key ecological responses to nitrogen are altered by climate change. *Nature Climate Change* 6(9):836−843
[33] Galloway JN, Townsend AR, Erisman JW, Bekunda M, Cai Z, et al. 2008. Transformation of the nitrogen cycle: recent trends, questions, and potential solutions. *Science* 320(5878):889−892
[34] Cui J, Zhang X, Reis S, Wang C, Wang S, et al. 2023. Nitrogen cycles in global croplands altered by elevated CO_2. *Nature Sustainability* 6(10):1166−1176
[35] Cui J, Zheng M, Bian Z, Pan N, Tian H, et al. 2024. Elevated CO_2 levels promote both carbon and nitrogen cycling in global forests. *Nature Climate Change* 14(5):511−517
[36] Ainsworth EA, Long SP. 2005. What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO_2. *New Phytologist* 165(2):351−372
[37] Leakey ADB, Ainsworth EA, Bernacchi CJ, Rogers A, Long SP, et al. 2009. Elevated CO_2 effects on plant carbon, nitrogen, and water relations: six important lessons from FACE. *Journal of Experimental Botany* 60(10):2859−2876
[38] Adler L, Díaz-Ramos A, Mao Y, Pukacz KR, Fei C, et al. 2022. New horizons for building pyrenoid-based CO_2-concentrating mechanisms in plants to improve yields. *Plant Physiology* 190(3):1609−1627
[39] Long BM, Förster B, Pulsford SB, Price GD, Badger MR. 2021. Rubisco proton production can drive the elevation of CO_2 within condensates and carboxysomes. *Proceedings of the National Academy of Sciences of the United States of America* 118(18):e2014406118
[40] Fatichi S, Leuzinger S, Paschalis A, Langley JA, Donnellan Barraclough A, et al. 2016. Partitioning direct and indirect effects reveals the response of water-limited ecosystems to elevated CO_2. *Proceedings of the National Academy of Sciences of the United States of America* 113(45):12757−12762
[41] da Silva JR, Patterson AE, Rodrigues WP, Campostrini E, Griffin KL. 2017. Photosynthetic acclimation to elevated CO_2 combined with partial rootzone drying results in improved water use efficiency, drought tolerance and leaf carbon balance of grapevines (*Vitis labrusca*). *Environmental and Experimental Botany* 134:82−95
[42] Taub DR, Wang X. 2008. Why are nitrogen concentrations in plant tissues lower under elevated CO_2? A critical examination of the hypotheses. *Journal of Integrative Plant Biology* 50(11):1365−1374
[43] Wang W, Cai C, He J, Gu J, Zhu G, et al. 2020. Yield, dry matter distribution and photosynthetic characteristics of rice under elevated CO_2 and increased temperature conditions. *Field Crops Research* 248:107605
[44] Mndela M, Tjelele JT, Madakadze IC, Mangwane M, Samuels IM, et al. 2022. A global meta-analysis of woody plant responses to elevated CO_2: implications on biomass, growth, leaf N content, photosynthesis and water relations. *Ecological Processes* 11(1):52
[45] Jayawardena DM, Heckathorn SA, Boldt JK. 2021. A meta-analysis of the combined effects of elevated carbon dioxide and chronic warming on plant %N, protein content and N-uptake rate. *AoB Plants* 13(4):plab031
[46] Taub DR, Miller B, Allen H. 2008. Effects of elevated CO_2 on the protein concentration of food crops: a meta-analysis. *Global Change Biology* 14(3):565−575
[47] Mason RE, Craine JM, Lany NK, Jonard M, Ollinger SV, et al. 2022. Evidence, causes, and consequences of declining nitrogen availability in terrestrial ecosystems. *Science* 376(6590):eabh3767
[48] Reich PB, Hobbie SE. 2013. Decade-long soil nitrogen constraint on the CO_2 fertilization of plant biomass. *Nature Climate Change* 3(3):278−282
[49] Sardans J, Grau O, Chen HYH, Janssens IA, Ciais P, et al. 2017. Changes in nutrient concentrations of leaves and roots in response to global change factors. *Global Change Biology* 23(9):3849−3856
[50] Lam SK, Hao X, Lin E, Han X, Norton R, et al. 2012. Effect of elevated carbon dioxide on growth and nitrogen fixation of two soybean cultivars in northern China. *Biology and Fertility of Soils* 48(5):603−606
[51] Wang B, Guo C, Wan Y, Li J, Ju X, et al. 2020. Air warming and CO_2 enrichment increase N use efficiency and decrease N surplus in a Chinese double rice cropping system. *Science of The Total Environment* 706:136063
[52] Terrer C, Vicca S, Hungate BA, Phillips RP, Prentice IC. 2016. Mycorrhizal association as a primary control of the CO_2 fertilization effect. *Science* 353(6294):72−74
[53] Zhang X, Davidson EA, Mauzerall DL, Searchinger TD, Dumas P, et al. 2015. Managing nitrogen for sustainable development. *Nature* 528(7580):51−59
[54] Sutton MA, Howard CM, Kanter DR, Lassaletta L, Móring A, et al. 2021. The nitrogen decade: mobilizing global action on nitrogen to 2030 and beyond. *One Earth* 4(1):10−14
[55] Shyamsundar P, Springer NP, Tallis H, Polasky S, Jat ML, et al. 2019. Fields on fire: alternatives to crop residue burning in India. *Science* 365(6453):536−538
[56] Beach RH, Sulser TB, Crimmins A, Cenacchi N, Cole J, et al. 2019. Combining the effects of increased atmospheric carbon dioxide on protein, iron, and zinc availability and projected climate change on global diets: a modelling study. *The Lancet Planetary Health* 3(7):e307−e317
[57] Springmann M, Mason-D'Croz D, Robinson S, Garnett T, Godfray HCJ, et al. 2016. Global and regional health effects of future food production under climate change: a modelling study. *The Lancet* 387(10031):1937−1946
[58] Cui J, Gao Y, Van Grinsven H, Zheng M, Zhang X, et al. 2025. Adaptive mitigation of warming-induced food crisis and nitrogen pollution. *Environmental Science & Technology* 59(7):3527−3536
[59] Cairns JE, Crossa J, Zaidi PH, Grudloyma P, Sanchez C, et al. 2013. Identification of drought, heat, and combined drought and heat tolerant donors in maize. *Crop Science* 53(4):1335−1346
[60] Abebe A, Pathak H, Singh SD, Bhatia A, Harit RC, et al. 2016. Growth, yield and quality of maize with elevated atmospheric carbon dioxide and temperature in north-west India. *Agriculture, Ecosystems & Environment* 218:66−72
[61] Dang P, Ciais P, Peñuelas J, Lu C, Gao J, et al. 2025. Mitigating the detrimental effects of climate warming on major staple crop production through adaptive nitrogen management: a meta-analysis. *Agricultural and Forest Meteorology* 367:110524
[62] Giménez VD, Serrago RA, Kettler B, García GA, Impa SM, et al. 2025. Nighttime warming affects yields of major grain crops: a global meta-analysis. *Field Crops Research* 334:110142

[63] Zheng M, Cui J, Cheng L, Wang X, Zhang X, et al. 2025. Warming promotes nitrogen and carbon cycles in global grassland. *Environmental Science & Technology* 59(5):2505−2518

[64] Cui J, Deng O, Zheng M, Zhang X, Bian Z, et al. 2024. Warming exacerbates global inequality in forest carbon and nitrogen cycles. *Nature Communications* 15(1):9185

[65] Zhang Y, Piao S, Sun Y, Rogers BM, Li X, et al. 2022. Future reversal of warming-enhanced vegetation productivity in the Northern Hemisphere. *Nature Climate Change* 12(6):581−586

[66] Huang M, Piao S, Ciais P, Peñuelas J, Wang X, et al. 2019. Air temperature optima of vegetation productivity across global biomes. *Nature Ecology & Evolution* 3(5):772−779

[67] Edwards EJ, Osborne CP, Strömberg CAE, Smith SA, Bond WJ, et al. 2010. The origins of C_4 grasslands: integrating evolutionary and ecosystem science. *Science* 328(5978):587−591

[68] Gowik U, Westhoff P. 2011. The path from C_3 to C_4 photosynthesis. *Plant Physiology* 155(1):56−63

[69] Chandiposha M. 2013. Potential impact of climate change in sugarcane and mitigation strategies in Zimbabwe. *African Journal of Agricultural Research* 8(23):2814−2818

[70] Robinson SI, O'Gorman EJ, Frey B, Hagner M, Mikola J. 2022. Soil organic matter, rather than temperature, determines the structure and functioning of subarctic decomposer communities. *Global Change Biology* 28(12):3929−3943

[71] García-Palacios P, Crowther TW, Dacal M, Hartley IP, Reinsch S, et al. 2021. Evidence for large microbial-mediated losses of soil carbon under anthropogenic warming. *Nature Reviews Earth & Environment* 2(7):507−517

[72] Davidson EA, Janssens IA. 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 440(7081):165−173

[73] Davies-Barnard T, Zaehle S, Friedlingstein P. 2022. Assessment of the impacts of biological nitrogen fixation structural uncertainty in CMIP6 earth system models. *Biogeosciences* 19(14):3491−3503

[74] Chang J, Viovy N, Vuichard N, Ciais P, Campioli M, et al. 2015. Modeled changes in potential grassland productivity and in grass-fed ruminant livestock density in Europe over 1961–2010. *PLoS One* 10(5):e0127554

[75] Turk J. 2016. Meeting projected food demands by 2050: understanding and enhancing the role of grazing ruminants. *Journal of Animal Science* 94:53−62

[76] Yang Y, Tilman D, Jin Z, Smith P, Barrett CB, et al. 2024. Climate change exacerbates the environmental impacts of agriculture. *Science* 385(6713):eadn3747

[77] Yuan X, Li S, Chen J, Yu H, Yang T, et al. 2024. Impacts of global climate change on agricultural production: a comprehensive review. *Agronomy* 14(7):1360

[78] Chaturvedi A, Pandey B, Yadav AK, Saroj S. 2021. An overview of the potential impacts of global climate change on water resources. In *Water Conservation in the Era of Global Climate Change*, eds Thokchom B, Qiu P, Singh P, Iyer PK. Amsterdam: Elsevier. pp. 99−120 doi: 10.1016/B978-0-12-820200-5.00012-9

[79] Lal R. 2015. Restoring soil quality to mitigate soil degradation. *Sustainability* 7(5):5875−5895

[80] Qu Q, Xu H, Ai Z, Wang M, Wang G, et al. 2023. Impacts of extreme weather events on terrestrial carbon and nitrogen cycling: a global meta-analysis. *Environmental Pollution* 319:120996

[81] García-García A, Cuesta-Valero FJ, Miralles DG, Mahecha MD, Quaas J, et al. 2023. Soil heat extremes can outpace air temperature extremes. *Nature Climate Change* 13(11):1237−1241

[82] Xia Y, Fu C, Liao A, Wu H, Wu H, et al. 2024. Effects of extreme weather events on nitrous oxide emissions from rice-wheat rotation croplands. *Plants* 13(1):25

[83] Grossiord C. 2020. Having the right neighbors: how tree species diversity modulates drought impacts on forests. *New Phytologist* 228(1):42−49

[84] D'Orangeville L, Houle D, Duchesne L, Phillips RP, Bergeron Y, et al. 2018. Beneficial effects of climate warming on boreal tree growth may be transitory. *Nature Communications* 9(1):3213

[85] Gray SB, Dermody O, Klein SP, Locke AM, McGrath JM, et al. 2016. Intensifying drought eliminates the expected benefits of elevated carbon dioxide for soybean. *Nature Plants* 2(9):16132

[86] Hufkens K, Keenan TF, Flanagan LB, Scott RL, Bernacchi CJ, et al. 2016. Productivity of North American grasslands is increased under future climate scenarios despite rising aridity. *Nature Climate Change* 6(7):710−714

[87] Maurel C, Nacry P. 2020. Root architecture and hydraulics converge for acclimation to changing water availability. *Nature Plants* 6(7):744−749

[88] Franks PJ, W Doheny-Adams, T, Britton-Harper ZJ, Gray JE. 2015. Increasing water-use efficiency directly through genetic manipulation of stomatal density. *New Phytologist* 207(1):188−195

[89] Zha X, Niu B, Li M, Duan C. 2022. Increasing impact of precipitation on alpine-grassland productivity over last two decades on the Tibetan Plateau. *Remote Sensing* 14(14):3430

[90] Wang B, Chen Y, Li Y, Zhang H, Yue K, et al. 2021. Differential effects of altered precipitation regimes on soil carbon cycles in arid versus humid terrestrial ecosystems. *Global Change Biology* 27(24):6348−6362

[91] Zheng M, Cui J, Wang X, Zhang X, Xie Z, et al. 2025. Shifts in precipitation regimes exacerbate global inequality in grassland nitrogen cycles. *Nature Communications* 16(1):7888

[92] Bellaloui N, Mengistu A. 2015. Effects of boron nutrition and water stress on nitrogen fixation, seed δ^{15}N and δ^{13}C dynamics, and seed composition in soybean cultivars differing in maturities. *The Scientific World Journal* 2015(1):407872

[93] Backer R, Rokem JS, Ilangumaran G, Lamont J, Praslickova D, et al. 2018. Plant growth-promoting rhizobacteria: context, mechanisms of action, and roadmap to commercialization of biostimulants for sustainable agriculture. *Frontiers in Plant Science* 9:1473

[94] Pritchard SG. 2011. Soil organisms and global climate change. *Plant Pathology* 60(1):82−99

[95] Nihorimbere V, Ongena M, Smargiassi M, Thonart P. 2011. Beneficial effect of the rhizosphere microbial community for plant growth and health. *Biotechnology, Agronomy and Society and Environment* 15(2):327−337

[96] Suolang Y, Luo W, Ma J, Zan Y, Yu Y, et al. 2024. Extreme precipitation alters soil nitrogen cycling related microbial community in karst abandoned farmland. *Applied Soil Ecology* 197:105345

[97] Liu X, Bai Q, Liang K, Pei M, Chen J, et al. 2025. Altered precipitation affects soil enzyme activity related to nitrogen and phosphorous but not carbon cycling: a meta-analysis. *Journal of Environmental Management* 377:124709

[98] Zhang J, Ru J, Song J, Li H, Li X, et al. 2022. Increased precipitation and nitrogen addition accelerate the temporal increase in soil respiration during 8-year old-field grassland succession. *Global Change Biology* 28(12):3944−3959

[99] Ji Y, Ma N, Heděnec P, Peng Y, Yue K, et al. 2025. Impact of seasonal precipitation regimes on soil nitrogen transformation in a subtropical forest: insights from a manipulation experiment. *Plant and Soil* 513(2):2225−2239

[100] Liu L, Zhang X, Xu W, Liu X, Li Y, et al. 2020. Ammonia volatilization as the major nitrogen loss pathway in dryland agro-ecosystems. *Environmental Pollution* 265:114862

[101] Wu Q, Yue K, Ma Y, Heděnec P, Cai Y, et al. 2022. Contrasting effects of altered precipitation regimes on soil nitrogen cycling at the global scale. *Global Change Biology* 28(22):6679−6695

[102] Fan Z, Lin S, Zhang X, Jiang Z, Yang K, et al. 2014. Conventional flooding irrigation causes an overuse of nitrogen fertilizer and low nitrogen use efficiency in intensively used solar greenhouse vegetable production. *Agricultural Water Management* 144:11−19

[103] Karrou M, Nachit M. 2015. Durum wheat genotypic variation of yield and nitrogen use efficiency and its components under different water and nitrogen regimes in the Mediterranean region. *Journal of Plant Nutrition* 38(14):2259−2278

[104] Deng L, Peng C, Kim DG, Li J, Liu Y, et al. 2021. Drought effects on soil carbon and nitrogen dynamics in global natural ecosystems. *Earth-Science Reviews* 214:103501

[105] Sánchez-Rodríguez E, Rubio-Wilhelmi MM, Blasco B, Constán-Aguilar C, Romero L, et al. 2011. Variation in the use efficiency of N under moderate water deficit in tomato plants (*Solanum lycopersicum*) differing in their tolerance to drought. *Acta Physiologiae Plantarum* 33(5):1861−1865
[106] Hoang DT, Hiroo T, Yoshinobu K. 2019. Nitrogen use efficiency and drought tolerant ability of various sugarcane varieties under drought stress at early growth stage. *Plant Production Science* 22(2):250−261
[107] Hammerl V, Kastl EM, Schloter M, Kublik S, Schmidt H, et al. 2019. Influence of rewetting on microbial communities involved in nitrification and denitrification in a grassland soil after a prolonged drought period. *Scientific Reports* 9(1):2280
[108] Homyak PM, Allison SD, Huxman TE, Goulden ML, Treseder KK. 2017. Effects of drought manipulation on soil nitrogen cycling: a meta-analysis. *Journal of Geophysical Research: Biogeosciences* 122(12):3260−3272
[109] Saleem A, Anwar S, Nawaz T, Fahad S, Saud S, et al. 2025. Securing a sustainable future: the climate change threat to agriculture, food security, and sustainable development goals. *Journal of Umm Al-Qura University for Applied Sciences* 11(3):595−611
[110] Lipper L, Thornton P, Campbell BM, Baedeker T, Braimoh A, et al. 2014. Climate-smart agriculture for food security. *Nature Climate Change* 4(12):1068−1072
[111] Raij-Hoffman I, Dahan O, Dahlke HE, Harter T, Kisekka I. 2024. Assessing nitrate leaching during drought and extreme precipitation: Exploring deep vadose-zone monitoring, groundwater observations, and field mass balance. *Water Resources Research* 60(11):e2024WR037973
[112] Wang W, Qiang M, Zuo J, Wang K, Han J, et al. 2025. Effects of extreme moisture events on greenhouse gas emissions and soil ecological functional stability in calcaric cambisols. *Agronomy* 15(11):2461
[113] Suprayitno D, Iskandar S, Dahurandi K, Hendarto T, Rumambi J. 2024. Public policy in the era of climate change: adapting strategies for sustainable futures. *Migration Letters* 21(S6):945−958
[114] Liu J, Mooney H, Hull V, Davis SJ, Gaskell J, et al. 2015. Systems integration for global sustainability. *Science* 347(6225):1258832
[115] Zavaleta ES, Shaw MR, Chiariello NR, Mooney HA, Field CB. 2003. Additive effects of simulated climate changes, elevated CO_2, and nitrogen deposition on grassland diversity. *Proceedings of the National Academy of Sciences of the United States of America* 100(13):7650−7654
[116] Wu H, Su X, Singh VP. 2023. Increasing risks of future compound climate extremes with warming over global land masses. *Earth's Future* 11(9):e2022EF003466
[117] Ren C, Zhang X, Reis S, Wang S, Jin J, et al. 2023. Climate change unequally affects nitrogen use and losses in global croplands. *Nature Food* 4(4):294−304
[118] Xu P, Li G, Zheng Y, Fung JCH, Chen A, et al. 2024. Fertilizer management for global ammonia emission reduction. *Nature* 626(8000):792−798
[119] Cuni-Sanchez A, Aneseyee AB, Baderha GKR, Batumike R, Bitariho R, et al. 2025. Perceived climate change impacts and adaptation responses in ten African mountain regions. *Nature Climate Change* 15(2):153−161
[120] Tessema I, Simane B. 2019. Vulnerability analysis of smallholder farmers to climate variability and change: an agro-ecological system-based approach in the Fincha'a sub-basin of the upper Blue Nile Basin of Ethiopia. *Ecological Processes* 8(1):5
[121] Sullivan MJP, Thomsen MA, Suttle KB. 2016. Grassland responses to increased rainfall depend on the timescale of forcing. *Global Change Biology* 22(4):1655−1665
[122] Sasaki T, Collins SL, Rudgers JA, Batdelger G, Baasandai E, et al. 2023. Dryland sensitivity to climate change and variability using nonlinear dynamics. *Proceedings of the National Academy of Sciences of the United States of America* 120(35):e2305050120
[123] Williamson J, Lu M, Camus MF, Gregory RD, MacLean IMD, et al. 2025. Clustered warming tolerances and the nonlinear risks of biodiversity loss on a warming planet. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences* 380(1917):20230321
[124] Stanimirova R, Arévalo P, Kaufmann RK, Maus V, Lesiv M, et al. 2019. Sensitivity of global pasturelands to climate variation. *Earth's Future* 7(12):1353−1366
[125] Wang C, Vera-Vélez R, Lamb EG, Wu J, Ren F. 2022. Global pattern and associated drivers of grassland productivity sensitivity to precipitation change. *Science of The Total Environment* 806:151224
[126] Taylor SH, Ripley BS, Martin T, De-Wet LA, Woodward FI, et al. 2014. Physiological advantages of C_4 grasses in the field: a comparative experiment demonstrating the importance of drought. *Global Change Biology* 20(6):1992−2003
[127] Guo L, Xiong S, Mills BJW, Isson T, Yang S, et al. 2024. Acceleration of phosphorus weathering under warm climates. *Science Advances* 10(28):eadm7773
[128] Kong X, Determann M, Andersen TK, Barbosa CC, Dadi T, et al. 2023. Synergistic effects of warming and internal nutrient loading interfere with the long-term stability of lake restoration and induce sudden re-eutrophication. *Environmental Science & Technology* 57(9):4003−4013
[129] Ben Keane J, Hartley IP, Taylor CR, Leake JR, Hoosbeek MR, et al. 2023. Grassland responses to elevated CO_2 determined by plant–microbe competition for phosphorus. *Nature Geoscience* 16(8):704−709
[130] Oswald R, Behrendt T, Ermel M, Wu D, Su H, et al. 2013. HONO emissions from soil bacteria as a major source of atmospheric reactive nitrogen. *Science* 341(6151):1233−1235
[131] Wang Y, Li Q, Wang Y, Ren C, Saiz-Lopez A, et al. 2025. Increasing soil nitrous acid emissions driven by climate and fertilization change aggravate global ozone pollution. *Nature Communications* 16(1):2463
[132] Sutton MA, Mason KE, Bleeker A, Hicks WK, Masso C, et al. 2020. *Just enough nitrogen: perspectives on how to get there for regions with too much and too little nitrogen*. Switzerland: Springer Cham. 608 pp doi: 10.1007/978-3-030-58065-0
[133] Vogt-Schilb A, Hallegatte S. 2017. Climate policies and nationally determined contributions: reconciling the needed ambition with the political economy. *WIREs Energy and Environment* 6(6):e256
[134] Debebe Y, Otterpohl R, Birhane E. 2025. Integrating rainwater harvesting and organic soil amendment to enhance crop yield and soil nutrients in agroforestry. *Environment Development Sustainability* 2025:1−19
[135] Batterman SA, Hedin LO, Van Breugel M, Ransijn J, Craven DJ, et al. 2013. Key role of symbiotic dinitrogen fixation in tropical forest secondary succession. *Nature* 502(7470):224−227
[136] Chen H, Ju P, Zhu Q, Xu X, Wu N, et al. 2022. Carbon and nitrogen cycling on the Qinghai-Tibetan Plateau. *Nature Reviews Earth & Environment* 3(10):701−716
[137] Zhu G, Shi H, Zhong L, He G, Wang B, et al. 2025. Nitrous oxide sources, mechanisms and mitigation. *Nature Reviews Earth & Environment* 6(9):574−592
[138] Ding B, Xu D, Wang S, Liu W, Zhang Q. 2025. Additive effects of multiple global change drivers on terrestrial nitrogen cycling worldwide. *Global Change Biology* 31(4):e70176