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# Soil moisture controls over carbon sequestration and greenhouse gas emissions: a review

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This literature review synthesizes the role of soil moisture in regulating carbon sequestration and greenhouse gas emissions (CS-GHG). Soil moisture directly affects photosynthesis, respiration, microbial activity, and soil organic matter dynamics, with optimal levels enhancing carbon storage while extremes, such as drought and flooding, disrupt these processes. A quantitative analysis is provided on the effects of soil moisture on CS-GHG across various ecosystems and climatic conditions, highlighting a "Peak and Decline" pattern for $CO_2$ emissions at 40% water-filled pore space (WFPS), while $CH_4$ and $N_2O$ emissions peak at higher levels (60–80% and around 80% WFPS, respectively). The review also examines ecosystem models, discussing how soil moisture dynamics are incorporated to simulate photosynthesis, microbial activity, and nutrient cycling. Sustainable soil moisture management practices, including conservation agriculture, agroforestry, and optimized water management, prove effective in enhancing carbon sequestration and mitigating GHG emissions by maintaining ideal soil moisture levels. The review further emphasizes the importance of advancing multiscale observations and feedback modeling through high-resolution remote sensing and ground-based data integration, as well as hybrid modeling frameworks. The interactive model-experiment framework emerges as a promising approach for linking experimental data with model refinement, enabling continuous improvement of CS-GHG predictions. From a policy perspective, shifting focus from short-term agricultural productivity to long-term carbon sequestration is crucial. Achieving this shift will require financial incentives, robust monitoring systems, and collaboration among stakeholders to ensure sustainable practices effectively contribute to climate mitigation goals.

Ecosystem carbon sequestration and greenhouse gas emissions (CS-GHG) are complex and crucial aspects of climate change mitigation. These primarily involve two interconnected processes: carbon sequestration and the dynamic interplay in the emissions of nitrous oxide ($N_2O$) and methane ($CH_4$)[1,2]. Carbon sequestration, known for its cost-efficiency and natural approach, not only addresses global warming[3] but also improves soil fertility[4], enhances water retention[5], and increases agricultural productivity[6,7]. While carbon sequestration effectively reduces atmospheric $CO_2$ levels through storage in land-based ecosystems such as forests, grasslands, wetlands, and agricultural lands[8–10], it can inadvertently lead to increased emissions of $N_2O$ and $CH_4$, gases with higher global warming potentials than $CO_2$[11,12]. For example, the application of nitrogen fertilizers in afforestation projects can enhance soil carbon storage but also stimulate nitrification and denitrification processes that release $N_2O$[13]. Similarly, efforts to enhance carbon sequestration by wetlands can lead to waterlogged conditions, creating anaerobic environments ideal for methanogenesis, thus increasing $CH_4$ emissions[14]. Recognizing carbon sequestration's effectiveness in reducing $CO_2$ levels and its potential impact on GHG dynamics, the Intergovernmental Panel on Climate Change (IPCC) acknowledges the importance of carbon sequestration in soils and the relevance of managing $N_2O$ and $CH_4$ emissions as integral components of climate change mitigation strategies[15].

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Various factors influence CS-GHG, including soil and vegetation types, climate factors, and human management practices such as irrigation and fertilization[16–18]. Among these factors, the amount of water available in soil impacts plant growth, microbial activity, and soil organic matter, all of which play crucial roles in determining the rate and efficiency of CS-GHG[19–21]. Model-based studies have also found that the variability in global modeled land carbon uptake is chiefly driven by the effects of temperature and vapor pressure deficit, both of which are modulated by soil moisture[22]. The impact of soil moisture on CS-GHG is more often analyzed as a part of multiple environmental variables than stand-alone, and most experimental data are derived from site-specific studies, lacking comprehensive analysis. There is also a significant need to understand how extreme weather events like droughts and flooding impact CS-GHG dynamics in different regions and to better understand soil moisture thresholds for CS-GHG. Additionally, it is crucial to evaluate how various models simulate the effects of soil moisture on CS-GHG to improve prediction accuracy and guide future research.

The primary objective of this literature review is to synthesize the current state of knowledge on the interactions between soil moisture and CS-GHG. This review seeks to elucidate the intricate relationships between soil moisture, microbial activity, plant physiology, and soil organic matter dynamics, as well as to identify the critical thresholds and mechanisms that govern these processes across diverse ecosystems. To achieve this goal, the review aims to: 1) provide an overview of key mechanisms involved in CS-GHG and examine the impacts of soil moisture on these processes; 2) explore the patterns of $CO_2$, $CH_4$, and $N_2O$ emissions in response to soil moisture variations, identifying the specific conditions that lead to peak emissions and the implications for climate change mitigation; 3) explore how sustainable soil moisture-related land management practices can enhance carbon sequestration and reduce GHG emissions, emphasizing the implementation of techniques like conservation agriculture, agroforestry, and optimized water management, and 4) highlight the importance of integrating soil moisture considerations into climate mitigation policies and outline future research directions to address knowledge gaps and improve the modeling of soil moisture-carbon dynamics. By reviewing the literature on soil moisture and CS-GHG interactions, this review aims to provide valuable insights for researchers, practitioners, and policymakers working to develop effective strategies for enhancing terrestrial carbon storage and mitigating climate change.

## Mechanisms of soil moisture influence on carbon sequestration and greenhouse gas emissions

Soil moisture influences CS-GHG through three key mechanisms (Fig. 1): plant photosynthesis and respiration, soil microbial activity, and soil organic matter decomposition and stabilization. These mechanisms are not isolated but are interdependent, each influencing and being influenced by the others[23]. Soil moisture, for instance, affects plant health and photosynthesis rates, which in turn impact soil microbial communities through root exudates and litter inputs[24]. Microbial activity influences the decomposition of organic matter, altering soil structure and nutrient availability, which feedback into plant growth and soil moisture dynamics[25].

### Plant photosynthesis and respiration

Soil moisture is a critical factor in regulating photosynthesis, and insufficient soil moisture has been observed to limit plant photosynthesis globally[26]. Variability in soil moisture accounts for approximately 90% of the interannual variability in global land carbon uptake, mainly through its influence on plant carbon assimilation[22]. In dryland regions like central Asia, soil moisture promotes photosynthesis in up to 94% of vegetation areas, with its effects surpassing those of vapor pressure deficit in 74% of these areas,

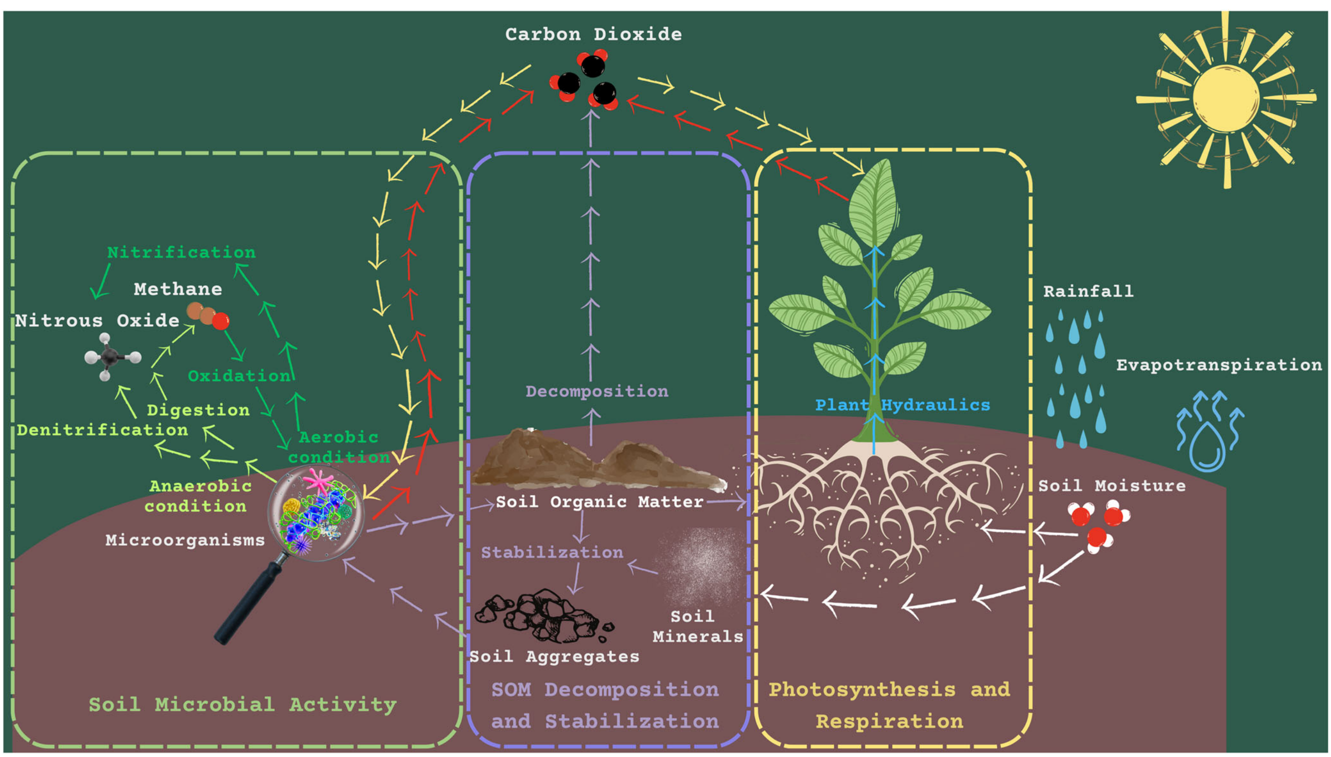


**Fig. 1 | Conceptual diagram: the role of soil moisture in carbon sequestration and greenhouse gas emissions.** In the right yellow box, white arrows represent soil moisture, yellow arrows indicate $CO_2$ absorption during photosynthesis, red arrows denote $CO_2$ release during autotrophic respiration, and blue arrows show water transport from soil to plants through plant hydraulics. The left green box includes light green arrows for $N_2O$ and $CH_4$ release under anaerobic conditions, and dark green arrows for methane oxidation and nitrification to $N_2O$ under aerobic conditions. The middle purple box features purple arrows illustrating $CO_2$ production through decomposition and stabilization. The diagram illustrates how soil moisture participates in various CS-GHG processes, indicating interrelated feedback mechanisms within terrestrial ecosystems.

especially in croplands, grasslands, and forests[27]. Globally, soil moisture constraints are estimated to reduce annual photosynthesis by around 15% and intensify interannual variability by over 100% across 25% of vegetated land[28]. Increased precipitation in desert steppes has been shown to enhance net photosynthetic rates by 159.5% and 178.9% for C3 and C4 plants, respectively, underscoring soil moisture's role in promoting photosynthetic activity[29].

Soil moisture influences respiration in both plants and soil organisms, affecting autotrophic respiration (Ra) and heterotrophic respiration (Rh) differently. Studies show that Ra, which includes respiration from all plant tissues (roots, stems, and leaves) and associated organisms, is generally more sensitive to soil moisture fluctuations than Rh, which is driven by microbial decomposition of organic matter. For example, drought reduced Ra contributions to total soil respiration from 33% to 16% in a subtropical forest[30] and from 66% to 35% in dry grasslands[31], highlighting Ra's sensitivity to water limitations. In contrast, Rh remained relatively stable, decreasing by only 21% under drought compared to a 26.8% reduction in Ra[32]. Moisture thresholds further underscore this sensitivity in Mediterranean forests, Ra decouples from temperature below a 17% soil moisture threshold, while Rh is moisture-controlled below 20%[33]. Moisture pulses also reveal differential responses, with Rh increasing over sixfold within hours of rainfall, while Ra takes days to respond[33].

Adding to the complexity, the inclusion of plant hydraulics into our understanding of carbon sequestration mechanisms provides a critical dimension[34]. Plant hydraulics, the system plants use to transport water from the soil through their roots and stems to the leaves, is integral to photosynthesis and overall plant health[35]. Adequate soil moisture ensures that plants have sufficient water to maintain this transport, which is essential for optimal photosynthetic performance[36]. When plants efficiently photosynthesize, they absorb more $CO_2$ and convert it into organic carbon, thus contributing to carbon sequestration. Conversely, under conditions of water stress, hydraulic failure can occur, reducing photosynthetic efficiency and consequently carbon assimilation.

### Soil microbial activity

Soil moisture critically influences soil microbial activity by affecting the habitat conditions of microorganisms such as bacteria, fungi, and archaea[37]. Microbial processes are enhanced at optimal moisture levels, with studies showing that microbial activity at 100% water holding capacity (WHC) can be up to 41% higher than at 60% WHC[38]. Soil moisture impacts not only the overall activity but also the enzyme activities, distribution, and function of specific microbial groups[39]. It determines the balance between aerobic and anaerobic conditions, thereby influencing which microorganisms dominate[40].

The influence of soil moisture on microbial activity directly affects carbon sequestration. Microorganisms decompose organic matter and convert it into stable soil carbon forms through enzymatic reactions[37]. Under optimal, moist, and aerobic conditions, microbes efficiently break down organic matter, with a portion being stabilized through association with soil minerals, contributing to long-term carbon storage. Fungi, for example, assimilate carbon into their hyphae, and their growth is significantly influenced by soil moisture levels[41]. Additionally, microbial autotrophy including autotrophic bacteria and phototrophic protists fixes atmospheric $CO_2$ into soil carbon[42]. Soils with optimal moisture, such as paddy soils, support a higher proportion of these organisms, resulting in higher $CO_2$ fixation rates compared to drier upland and forest soils[43].

Soil moisture also impacts GHG emissions by influencing the metabolic pathways of soil microorganisms. In well-aerated soils with optimal moisture, aerobic microbial activity predominates, leading primarily to $CO_2$ production[44]. However, in waterlogged or anaerobic soils, microbial pathways shift toward anaerobic processes. Denitrifying bacteria become more active under these conditions, producing increased levels of $N_2O$, while methanogenic archaea generate $CH_4$[45]. Soil moisture affects the activity of methanotrophic bacteria that oxidize $CH_4$ into $CO_2$, mitigating methane emissions. This activity is especially crucial in environments like wetlands and rice paddies, where methane production is prevalent[46,47].

### Soil organic matter decomposition and stabilization

Building upon the role of soil microbial activity discussed in Section 2.2, soil moisture further influences CS-GHG through its impact on soil organic matter (SOM) decomposition and stabilization. Adequate moisture enhances microbial metabolism and enzyme activity, leading to increased breakdown of organic matter. For instance, $CO_2$ production can be 31–40% higher at 65% WHC compared to 45% WHC, indicating that moisture availability significantly affects SOM mineralization rates[48]. Soil moisture also influences carbon stabilization by promoting the formation of mineral-associated organic matter; in wetter climates, greater root growth and interaction of organic inputs with soil minerals enhance carbon stabilization[49].

The balance between SOM decomposition and stabilization is crucial for carbon sequestration. While decomposition releases $CO_2$, the stabilization of organic matter within soil aggregates or bound to minerals contributes to long-term carbon storage. Soil moisture facilitates the formation of stable soil aggregates through the swelling of clay minerals and cohesion of soil particles, encapsulating organic matter and protecting it from further decomposition[50,51]. Changes in moisture regimes can significantly impact carbon stabilization in soils, with a tipping point observed where precipitation equals evaporation[49].

SOM decomposition and stabilization processes influenced by soil moisture have significant implications for GHG emissions. Increased decomposition rates under optimal moisture conditions lead to higher $CO_2$ emissions due to enhanced microbial respiration. Excessive moisture can create anaerobic conditions, shifting microbial activity towards methanogenesis and resulting in increased $CH_4$ production[52]. Soil aggregates significantly influence GHG dynamics, particularly $CH_4$ and $N_2O$ emissions, by modulating soil gas diffusion and water availability[53,54].

### The interplay of soil moisture and other key factors regulating CS-GHG dynamics

Soil moisture interacts with various other soil properties—such as temperature, texture, type, pH, carbon-to-nitrogen (C/N) ratio, bulk density, and nitrogen input—to regulate the complex dynamics of CS-GHG. Soil temperature, in particular, has a profound influence on microbial activity and organic matter decomposition, both of which drive $CO_2$ and $N_2O$ fluxes[55,56]. In well-moistened soils, higher temperatures can accelerate microbial decomposition, leading to increased carbon mineralization and subsequent carbon losses[57]. However, in dry soils, microbial activity may decrease despite elevated temperatures. For example, soil microbial respiration in global drylands often adapts to the ambient thermal regime, reducing the expected increase in $CO_2$ emissions[58,59]. These findings suggest that temperature-driven increases in soil respiration are modulated by other factors, with soil moisture playing a critical role in shaping how microbial communities respond to warming. Soil texture also governs the interaction between temperature and moisture, as coarse-textured soils (e.g., sandy soils) typically exhibit faster drainage, which limits the water availability for microbial processes[60]. In contrast, fine-textured soils (e.g., clay soils) retain moisture, allowing temperature and moisture to co-regulate carbon cycling processes more effectively[60]. Additionally, the C/N ratio and nitrogen input are critical factors that shape microbial nutrient availability and nitrogen cycling, significantly impacting $N_2O$ emissions[61]. In organic soils from mid-latitude regions, $N_2O$ emissions follow a Gaussian distribution with respect to the C/N ratio, peaking at values around 18–19[62]. Research has shown that the C/N ratio alone can explain up to 36% of the variability in $N_2O$ fluxes. However, when other factors—such as mineral nitrogen input and water table depth—are considered, the explanatory power increases to 75%[63]. To further the complexity, soil pH has been used as an integrated proxy of land use change, parent material and climate to determine the site-specific effects of land management strategies on soil organic accumulation, thus CS-GHG[64]. The combination of these factors—temperature, moisture, soil

**Table 1 | Influence of soil moisture on carbon sequestration for different location, landcover and conditions**

| Location | Climate/Landcover | HSM-ECS | LSM-RCS | HSM-RCS | Conditions | Ref |
|---|---|---|---|---|---|---|
| Global | N/A | | √ | | Drought | 26,67 |
| | Peatlands | √ | | | Wetland | 74 |
| Amazon | Tropical rainforest | | √ | | Drought | 71 |
| India | Forest | | | √ | After rainfall | 79 |
| Germany | Cropland | | | √ | Elevated $CO_2$ | 81 |
| Australia | Dryland vegetation | √ | | | After rainfall | 77 |
| Pan-arctic | Shrub wetlands | | √ | | Drought | 70 |
| Africa | Savanna | | √ | | Drought | 68,69 |
| China | Desert | | | √ | After rainfall | 80 |
| | Areas with poor water conditions | √ | | | After rainfall | 78 |
| | Humid and warm eastern regions | | √ | | Drought | 72 |
| | Subtropical forest | | √ | | Drought | 73 |

**HSM-ECS**: Higher soil moisture enhanced carbon sequestration.
**LSM-RCS**: Lower soil moisture reduced carbon sequestration.
**HSM-RCS**: Higher soil moisture reduced carbon sequestration.

texture, pH, and nutrient availability—collectively influences CS-GHG dynamics. Among them, soil moisture, as one of the most rapidly changing and sensitive factors[65], becomes the pivotal element in determining the overall outcome of CS-GHG emissions[66].

## Quantitative impact of soil moisture variability on carbon sequestration and greenhouse gas emissions

### Influence of soil moisture on carbon sequestration

Table 1 presents the impact of soil moisture on carbon sequestration across various global locations and ecosystems. Generally, there are three distinct scenarios: lower soil moisture reducing carbon sequestration, higher soil moisture enhancing carbon sequestration, and higher soil moisture reducing carbon sequestration.

Lower soil moisture often results from drought conditions, which significantly impact carbon sequestration. On a global scale, data from four Earth system models indicate that drying soil moisture trends reduce the current land carbon sink by about 2–3 Gt C per year[67]. This effect is particularly pronounced in arid regions, where drought conditions limit the carbon sequestration potential[68,69]. For instance, in Sudan's sparse savanna, rainy season carbon uptake averages 152 mmol $CO_2$ $m^{-2}$ $day^{-1}$, while dry season uptake drops to just 14.7 mmol $CO_2$ $m^{-2}$ $day^{-1}$, a nearly tenfold difference that significantly reduces the region's annual carbon sink capacity. Similarly, in the cold Pan-Arctic area, decreased soil moisture during summer limits peak plant productivity, with gross primary production (GPP) declining by up to 27% as soil moisture decreases from 60% to 31%[70]. In moisture-rich ecosystems like the Amazon rainforest, drought can severely impact carbon sequestration, causing significant tree mortality, reduced carbon uptake, and leading to a net biomass carbon loss of 1.2 to 1.6 Pg out of the 18 Pg it processes annually[71]. In China's humid and warm eastern regions[72], national and regional net ecosystem productivity anomalies were closely correlated with drought index, highlighting the drought impact on carbon dynamics. In subtropical forests[73], drought led to soil carbon storage declines of up to 12.2%, reflecting significant reductions in carbon sequestration under moisture stress.

In some regions, inherently high soil moisture leads to enhanced carbon sequestration. For instance, in peatlands and wetlands, high soil moisture content creates low-oxygen conditions that slow down decomposition, resulting in effective carbon storage[74]. Although carbon storage is expected to decline under warming and drying in boreal peatlands[75], declining soil moisture alone does not seem to necessarily cause reduced carbon storage[76]. In semi-arid regions like Australia, significant carbon sink activity has been observed following heavy rainfall, with an increase in annual rainfall of about 350 mm leading to an additional carbon absorption of approximately 0.4 ± 0.2 Pg C by Australia's terrestrial ecosystems[77]. Similarly, higher soil moisture in areas like the Qinghai-Tibetan Plateau, Xinjiang, and Northwest China has been shown to promote carbon sink activity, contributing to net ecosystem productivity increases of up to 3.0 g C $m^2$ per year[78].

However, high soil moisture can also reduce carbon sequestration under certain conditions. In ecosystems that have experienced prolonged dry periods, a sudden increase in soil moisture due to rainfall can lead to rapid carbon loss[79]. This occurs because the added moisture reactivates previously dormant microorganisms in the soil, causing them to release $CO_2$ as they metabolize organic material[80]. Additionally, increased moisture enhances the diffusion of organic matter, which, in combination with higher microbial activity, contributes to a spike in $CO_2$ emissions[80]. Additionally, elevated $CO_2$ concentrations can exacerbate this effect[81]. High $CO_2$ levels typically promote plant growth, leading to more extensive root systems[82]. Under high moisture conditions, increased root respiration generates more $CO_2$, thereby reducing net carbon sequestration[83,84].

### Hot spots and hot moments in soil moisture thresholds for GHG emissions

Table 2 provides a detailed analysis of the correlation between soil moisture (measured as water-filled pore space, WFPS) and GHG emissions across diverse locations and landcover types. The correlation patterns for $CO_2$ are consistently described as "Peak and Decline" (PD), indicating that $CO_2$ emissions tend to reach a peak at a specific soil moisture level before declining. In contrast, $CH_4$ and $N_2O$ correlations exhibit more variability, with patterns described as "Positive" (P), "Peak and Decline" (PD), and "Trough and Rise" (TR). Table 2 also identifies the WFPS thresholds at which peak emissions occur, revealing that $CO_2$ emissions typically peak at around 40% WFPS. Meanwhile, $CH_4$ and $N_2O$ emissions generally peak at higher soil moisture levels, with $CH_4$ peaking between 60% and 80% WFPS and $N_2O$ peaking at approximately 80% WFPS. The consistent "Peak and Decline" pattern observed for $CO_2$ emissions across various landcovers suggests that there is an optimal soil moisture level for microbial activity and root respiration, beyond which emissions decline due to either excess moisture limiting oxygen availability or insufficient moisture restricting microbial processes. This optimal level is typically around 40% WFPS, indicating a critical threshold for $CO_2$ emissions regulation. For instance, in European landcover categories[21], $CO_2$ emissions peak at around 40% WFPS before declining. In contrast, $CH_4$ and $N_2O$ emissions show significant variability in response to soil moisture. $CH_4$ emissions tend to peak at higher

**Table 2 | Soil moisture and GHG emission correlations and thresholds**

| Landcover | Location | SM-GHG Emission Correlation | | | GHG Peak Emission WFPS Thresholds (%) | | | Ref. |
|---|---|---|---|---|---|---|---|---|
| | | $CO_2$ | $CH_4$ | $N_2O$ | $CO_2$ | $CH_4$ | $N_2O$ | |
| Cropland | European | PD | PD | P | 40% | 60% | 80% | 21 |
| | European | N/A | N/A | P | N/A | N/A | 75% | 83 |
| | North America | PD | P | P | 40% | 80% | 80% | 84 |
| | USA | N/A | N/A | P | N/A | N/A | >80% | 185 |
| | USA | N/A | PD | PD | N/A | 72–94% | 63–85% | 186 |
| | USA | N/A | N/A | P | N/A | N/A | 60–90% | 187 |
| | North America | PD | N/A | N/A | 60% | N/A | N/A | 188 |
| | East Asia | N/A | P | PD | N/A | 99% | 78–85% | 86 |
| Forest | European | PD | P | P | 40% | 80% | 80% | 21 |
| | North America | N/A | N/A | PD | N/A | N/A | 60% | 189 |
| | East Asia | PD | TR | PD | 70–90% | 50–70% | 70–90% | 190 |
| Grassland | European | PD | PD | P | 40% | 60% | 80% | 21 |
| | East Asia | N/A | N/A | P | N/A | N/A | >73% | 191 |
| | East Asia | PD | N/A | PD | 50 % | N/A | 50 % | 88 |
| Wetland | European | PD | P | P | 40% | 95% | 80% | 21 |

*WFPS* denotes Water-filled pore space, *P* Positive, *PD* Peak and decline, *TR* Trough and Rise. Due to the variation in maximum WFPS settings across different experiments, when the correlation is listed as "Positive," the value for GHG Peak Emission WFPS Thresholds (%) represents the maximum WFPS observed in that particular experiment.

soil moisture levels, ranging from 60% to 80% WFPS, which aligns with the anaerobic conditions favorable for methane production[85]. For example, $CH_4$ emissions in European wetlands peak at 95% WFPS[21], and in Chinese paddy fields, they peak at 99% WFPS[86]. Similarly, $N_2O$ emissions peak at even higher moisture levels, around 80% WFPS, reflecting the conditions that promote denitrification processes. This is evident in the European forest landcover category, where $N_2O$ emissions peak at around 80% WFPS[21]. Other landcover types also exhibit similar trends. For example, in UK croplands, $N_2O$ emissions peak at around 75% WFPS[83]. In Danish forests, $N_2O$ emissions peak at 60% WFPS, while $CH_4$ emissions show a positive correlation at 80% soil water content[87]. For grasslands experiencing freeze-thaw cycles in China, $CO_2$ and $N_2O$ emissions both peak at around 50% WFPS[88].

The observed variability in $CH_4$ and $N_2O$ emission patterns underscores the complex interactions between soil moisture and microbial processes responsible for GHG production. While $CO_2$ emissions demonstrate a more predictable response to soil moisture changes, $CH_4$ and $N_2O$ emissions are influenced by a broader range of soil moisture conditions, highlighting the need for targeted soil moisture management strategies to mitigate these emissions. Overall, managing soil moisture to maintain optimal conditions for microbial activity can significantly impact the regulation of GHG emissions and contribute to climate change mitigation efforts.

### The impact of free-thaw and drought-rewetting events on GHG emissions

Freeze-thaw cycles (FTCs) and drought-rewetting events cause abrupt shifts in soil physical, chemical, and biological processes, significantly altering GHG emissions. FTCs can increase GHG emissions by disrupting soil aggregates, releasing dissolved organic carbon, and causing microbial cell rupture, which releases carbon and nitrogen[89]. This process can cause $CO_2$ emissions to account for about 45% of annual totals and $N_2O$ emissions to originate 50–70% from these cycles, with emissions increasing by up to 1.7 times for $CO_2$ and up to 5.8 times for $N_2O$[90], especially in agricultural soils where perennial bioenergy crops such as miscanthus and willow are grown, due to accelerated nitrogen losses[91]. Ecosystems respond variably to FTCs, for example, in wetland ecosystems, flooding during FTCs may reduce $CO_2$ emissions by 65% and $CH_4$ emissions by 37%[92]. Alpine forests tend to show increased $CO_2$ emissions during thawing[93], primarily because soil respiration during FTCs averages a fourfold increase compared to non-FTCs. In temperate grasslands, FTCs have varying impacts on GHG emissions depending on soil properties and land cover: meadow steppe, marshland, and typical steppe soils exhibit increased $N_2O$ emissions, whereas arid steppe soils show minimal response[94]. While FTCs primarily disrupt soil structure and enhance microbial activity, rewetting events trigger rapid shifts in soil moisture, which similarly affect the carbon and nitrogen cycling. During droughts, microbial activity slows, leading to temporary carbon accumulation[95]. However, rewetting triggers a sharp increase in microbial respiration, resulting in large $CO_2$ emission bursts as accumulated organic matter is rapidly decomposed[96,97]. A meta-analysis of global drying and rewetting cycles across all ecosystems showed that these cycles increase $CO_2$ emissions by 35.7% compared to constant soil moisture conditions, while having no significant effect on $N_2O$ emissions[98]. In contrast, when wetlands are rewetted and the water table rises near the surface (within −30 cm to −5 cm of the surface), GHG emissions are often reduced to near zero due to waterlogged conditions slowing down microbial activity[99].

In summary, freeze-thaw cycles and drought-rewetting events typically increase $CO_2$ and $N_2O$ emissions by disrupting soil structure and enhancing microbial activity, especially in agricultural soils. Rewetting triggers a surge in $CO_2$ emissions as accumulated organic matter is rapidly decomposed. However, in wetlands, rising water tables tend to reduce GHG emissions by slowing down microbial activity.

## Carbon sequestration and greenhouse gas emission models in the context of soil moisture dynamics

Ecosystem models offer detailed simulations of ecosystem processes, making them valuable for understanding the intricate dynamics of carbon, nutrient, energy, and water cycles[100–109]. Table 3 provides a detailed comparison of how various state-of-science ecosystem models incorporate soil moisture's influence on the CS-GHG.

In carbon sequestration, different ecosystem models incorporate soil moisture's role in CS with varying emphasis on specific mechanisms. For example, the Common Land Model (CoLM) focuses on stomatal conductance, a vital process for photosynthesis, where water availability regulates the opening and closing of plant stomata, directly impacting carbon uptake by vegetation[109]. Similarly, Biome-BGC emphasizes drought stress levels, which impact net primary productivity by influencing plant growth

**Table 3 | Comparative roles of soil moisture in carbon sequestration and greenhouse gas emissions across selected ecosystem models**

| Model | Role of soil moisture in | | Refs |
|---|---|---|---|
| | Carbon sequestration | Greenhouse gas emissions | |
| Biome-BGC | • Impacts drought stress levels, which in turn affect net primary productivity and carbon uptake. | • Indirectly represented through its impact on plant-mediated $CO_2$ fluxes. | 100 |
| BEPS-TerrainLab V2.0 | • Affects plant photosynthesis and microbial decomposition | | 110 |
| CoLM | • Affects stomatal conductance, which in turn influences photosynthesis and carbon uptake. | • Impacts $CO_2$ release through both autotrophic (plant-related) and heterotrophic (microbial-related) respiration rates.<br>• Regulates $CO_2$ emissions from nutrient mineralization and decomposition processes, as controlled by soil moisture levels.<br>• The vegetation dynamics component includes fire parameterizations that respond to soil moisture and litter availability. Reduced soil moisture elevates fire occurrence probabilities, resulting in $CO_2$ release. | 109 |
| ORCHIDEE | • Incorporates water stress factors into photosynthesis parameterizations<br>• Influences the allocation of carbon to different plant tissues | | 103 |
| LPJ-GUESS | • Influences photosynthesis, carbon allocation and vegetation dynamics | | 104 |
| DLEM | • Influences plant photosynthesis and respiration, affecting carbon uptake and storage in biomass.<br>• Acts as a connecting variable among model components, impacting overall carbon cycling processes in the ecosystem. | • Modulates $CO_2$ release through plant photosynthesis, soil respiration, and microbial decomposition.<br>• Affects $CH_4$ dynamics by promoting methanogenesis in saturated, anaerobic conditions and enhancing $CH_4$ oxidation in drier, aerobic soils.<br>• Influences $N_2O$ emissions by facilitating nitrification under optimal aerobic conditions and enhancing denitrification in high-moisture, anaerobic environments. | 107,108 |
| DNDC | • Tracks physiological processes, such as water stress and nutrient uptake. | • Track daily soil moisture content, which directly affects respiration rates and, consequently, $CO_2$ fluxes.<br>• Simulates $CH_4$ fluxes under varying hydrological conditions.<br>• Simulates $N_2O$ and $N_2$ emissions based on soil moisture and redox potential, influenced by the 'anaerobic balloon' concept that models simultaneous aerobic and anaerobic microsites. | 101 |
| CLM5 | • By maintaining healthy vegetation through improved plant hydraulics, soil moisture directly and indirectly supports carbon sequestration and storage in terrestrial ecosystems. | • Influences plant photosynthesis, soil respiration, microbial decomposition and fire susceptibility, thereby affecting $CO_2$ emissions through both vegetation stress and combustion processes.<br>• High soil moisture levels in wetlands create anaerobic conditions essential for $CH_4$ production<br>• Affects nitrification and denitrification processes, facilitating $N_2O$ production and emissions | 105 |
| ELM | | | 106 |

*CoLM* The Common Land Model, *ORCHIDEE* Organizing Carbon and Hydrology in Dynamic Ecosystems, *LPJ-GUESS* Lund-Potsdam-Jena General Ecosystem Simulator, *DLEM* Dynamic Land Ecosystem Model, *DNDC* Denitrification-Decomposition, *CLM5* Community Land Model Version 5, *ELM* Land Model of U.S. Department of Energy Energy Exascale Earth System Model.

and carbon storage potential, especially under changing water conditions[100]. Other models, such as Organizing Carbon and Hydrology in Dynamic Ecosystems (ORCHIDEE)[103] and Lund-Potsdam-Jena General Ecosystem Simulator (LPJ-GUESS)[104], go further by embedding water stress into carbon allocation processes, thereby affecting carbon dynamics within the ecosystem. Denitrification-Decomposition (DNDC)[101] and Dynamic Land Ecosystem Model (DLEM)[107,108] add layers of complexity by linking soil moisture to microbial activity and nutrient cycling, which are critical for long-term carbon storage in soils.

When addressing GHG emissions, models differ in the extent and processes simulated. Models such as Biome-BGC[100] and BEPS-TerrainLab V2.0[110] only simulate $CO_2$ emissions. In contrast, models like DLEM, DNDC, Community Land Model Version 5 (CLM5), and Land Model of U.S. Department of Energy Energy Exascale Earth System Model (ELM) can also simulate $CH_4$ and $N_2O$ emissions. Additionally, some models have expanded $CH_4$ simulation capabilities by integrating peatland schemes, such as ORCHIDEE-PEAT[111] and LPJ-GUESS version 4.1[112].

For $CO_2$, models such as Biome-BGC and BEPS-TerrainLab V2.0 represent the role of soil moisture in GHG emissions indirectly, focusing primarily on plant-mediated $CO_2$ fluxes. In contrast, models like CoLM, DLEM, CLM5 and ELM take a more comprehensive approach by simulating $CO_2$ release not only from plant photosynthesis, soil respiration, and microbial decomposition but also by incorporating fire susceptibility influenced by soil moisture, where low moisture levels increase fire risk and subsequently $CO_2$ emissions[108,111,112,117,118]. For $CH_4$ and $N_2O$, DLEM links soil moisture to $CH_4$ emissions by modeling anaerobic methanogenesis under wet conditions and $CH_4$ oxidation in drier soils[107,108]. DNDC builds on this approach by tracking daily soil moisture levels, which directly affect microbial respiration and redox conditions essential for $N_2O$ and $N_2$ emissions, using the "anaerobic balloon" concept[101]. CLM5 and ELM capture additional complexities by modeling the anaerobic processes necessary for $CH_4$ and $N_2O$ production, especially in wetlands where high soil moisture creates conducive environments for methanogenesis[106].

In sum, soil moisture serves as a key regulator in balancing CS and $CO_2$ emissions, indirectly influencing ecosystem carbon dynamics through its effects on plant growth, stomatal conductance, and microbial decomposition. However, when it comes to $CH_4$ and $N_2O$, soil moisture plays a direct role, actively controlling emissions by influencing the soil's redox environment and microbial activity. In anaerobic conditions, especially in wetlands or saturated soils, soil moisture promotes methanogenesis, leading to $CH_4$ emissions, while also driving $N_2O$ production through nitrification and denitrification processes.

## Sustainable soil moisture-related land management practices

### Enhancing carbon sequestration

Conservation Agriculture (CA) is a recommended sustainable land management practice for enhancing carbon sequestration[113]. CA involves leaving crop stubble/leaf litters on the soil surface to preserve soil moisture, reduce erosion, and improve soil structure[113]. By incorporating legumes into the cropping system, CA helps sequester carbon by protecting soil organic carbon in aggregates and adding organic carbon to deeper soil layers[114].

Additionally, CA practices not only increase soil productivity and crop yields but also contribute to reverting soil degradation and improving input use efficiency. Therefore, promoting location-specific CA practices is crucial for sustainable soil management and enhancing carbon sequestration. Cover cropping and mulching, as part of CA practices, are essential sustainable soil moisture-related land management practices that play a crucial role in enhancing carbon sequestration[115]. Cover cropping helps to improve soil health by increasing organic matter content, which in turn enhances soil carbon sequestration potential[116]. Mulching, on the other hand, aids in reducing soil erosion, maintaining soil moisture levels, and promoting the decomposition of organic matter, all of which contribute to increased carbon sequestration in the soil[117]. These practices, along with other techniques like conservation tillage, nutrient management, and crop residue management, are vital for maximizing carbon sequestration in terrestrial ecosystems, mitigating greenhouse gas emissions, and promoting sustainable agriculture[118].

Agroforestry practices play a crucial role in sustainable soil moisture-related land management for enhancing carbon sequestration[119]. These practices involve the integration of trees and shrubs into agricultural landscapes, promoting soil health and carbon storage[120]. Agroforestry systems contribute to carbon sequestration by increasing organic matter inputs to the soil, enhancing soil structure, and reducing erosion[119,120]. By combining agriculture with forestry, agroforestry helps maintain soil moisture levels, which are essential for promoting plant growth and carbon sequestration[121]. Additionally, agroforestry practices offer multiple benefits such as improved biodiversity, increased resilience to climate change, and sustainable land use. Therefore, implementing agroforestry techniques can be a valuable strategy for enhancing carbon sequestration while promoting sustainable soil moisture-related land management.

The application of organic amendments, such as compost and manure, can improve soil moisture retention and increase carbon sequestration by enhancing soil structure, organic matter content, and WHC[122]. Aerosols, such as mineral dust and black carbon, can influence soil moisture and carbon sequestration by affecting the Earth's radiation balance and altering precipitation patterns[123]. For instance, mineral dust aerosols can have a cooling effect on the Earth's surface, potentially reducing evapotranspiration and altering soil moisture dynamics[124]. Black carbon aerosols, on the other hand, can have a warming effect, potentially increasing evapotranspiration and reducing soil moisture[125].

### Reducing GHG emission

Sustainable soil moisture-related land management practices are essential for reducing GHG emissions, particularly in agricultural systems like rice paddies, which are significant sources of $CH_4$. One effective practice is improved water management in rice systems, such as alternate wetting and drying (AWD)[126]. AWD involves periodically draining the rice fields rather than keeping them continuously flooded. This practice reduces $CH_4$ emissions by limiting the anaerobic conditions that favor methanogenic bacteria responsible for methane production. Studies have shown that AWD can cut $CH_4$ emissions by up to 50% compared to traditional continuous flooding methods[127]. In addition to AWD, other sustainable practices include optimizing irrigation scheduling to match crop water needs more precisely, thereby avoiding excessive water application that leads to anaerobic soil conditions[128]. Implementing water-saving technologies such as drip irrigation or controlled flooding can further enhance water use efficiency and reduce GHG emissions[129]. Moreover, incorporating organic amendments like biochar into the soil can improve soil structure, increase water retention, and reduce $N_2O$ emissions by promoting more efficient nutrient cycling and reducing the need for synthetic fertilizers[130]. Collectively, these practices not only mitigate GHG emissions but also improve water use efficiency, enhance soil health, and boost crop productivity. Sustainable water management in rice systems exemplifies how targeted land management practices can address both environmental and agricultural challenges, contributing to more resilient and climate-smart agricultural systems.

## Challenges and future directions

### Enhancing CS-GHG monitoring with high-resolution remote sensing and ground-based observations

High-resolution data on water and carbon are crucial for CS-GHG. Synthetic Aperture Radar (SAR) has demonstrated sensitivity to surface soil moisture[131], and when combined with LiDAR, it has become a promising alternative to traditional field data campaigns[132]. For soil moisture, SAR platforms like Sentinel-1 and -2, utilizing multi-orbit time series analysis and incidence angle normalization, and combining various downscaling algorithms, achieve spatial resolutions enabling precise monitoring of soil moisture at scales of 1 km[133], 500 m[134], and even 100 m[135]. LiDAR-derived digital elevation models, combined with machine learning, enable the production of high-resolution soil moisture products down to 2 m[136]. In specific terrains, such as coastal area, combining LiDAR intensity data with machine learning can achieve spatial resolutions at the centimeter to decimeter scale[137]. For carbon, LiDAR missions such as GEDI and ICESat-2 deliver detailed forest canopy height data[138], allowing ecosystem models to dramatically improve the spatial resolution of carbon flux estimates—from 0.25° to 0.01°[139]. This enhanced resolution captures fine-scale forest structures and disturbances, which are crucial for precise CS-GHG analysis and modeling. However, these high-resolution datasets often rely on machine learning, which is constrained by the availability and quality of training data[133,135,136]. In soil moisture mapping, while SAR provides frequent temporal updates, its accuracy declines in areas with dense vegetation[140]. Similarly, LiDAR's detailed spatial resolution is offset by limited temporal coverage, making it challenging to capture fast-changing soil moisture dynamics effectively[141]. In carbon flux modeling, although LiDAR excels at capturing canopy height and overall forest structure, representing critical below-canopy processes for carbon flux remains difficult, further adding to the complexity of accurate modeling[139].

To address these limitations and fill the gaps in remote sensing, site-level to watershed-scale observations provide high-quality, continuous measurements of soil moisture, carbon fluxes, and GHG emissions, which are essential for validating and complementing remote sensing data. FLUXNET is a global network of eddy covariance towers that measure exchanges of carbon dioxide, water vapor, and energy between terrestrial ecosystems and the atmosphere[142]. This network offers detailed insights into ecosystem responses to environmental changes across diverse biomes[143]. The DOE Next-Generation Ecosystem Experiments Arctic (NGEE-Arctic; https://ess.science.energy.gov/ngee-arctic/) and NGEE-Tropics (https://ess.science.energy.gov/ngee-tropics/) programs focus on improving the representation of Arctic and tropical ecosystems in Earth system models by collecting extensive field observations on plant physiology, soil properties, and biogeochemical processes under changing environmental conditions[144,145]. Additionally, the Spruce and Peatland Responses Under Changing Environments (SPRUCE; https://mnspruce.ornl.gov/) experiment investigates the effects of elevated temperature and carbon dioxide levels on peatland ecosystems. These researches provide critical insights into the complex interactions and feedback loops between soil water availability, carbon sequestration, and GHG emissions under shifting environmental conditions[146]. Emphasizing these smaller-scale observations underscores their essential role in validating and complementing remote-sensing data, enhancing our understanding and modeling of soil moisture and CS-GHG dynamics across diverse ecosystems. However, significant challenges remain. Spatial and temporal mismatches between site-level measurements and remote sensing complicate data integration due to differences in scale, protocols, and data quality[147]. Additionally, inconsistencies in instrumentation and methodologies across studies introduce variability, further complicating data synthesis and model validation processes[148].

Future research should prioritize enhancing multiscale observational capabilities by integrating high-resolution remote sensing data with ground-based networks. Specifically, this involves expanding the geographical coverage of observational sites to improve data representation in under-represented and remote regions[149,150]. Developing below-ground sensors to strengthen ground-based observations of below-canopy processes will enhance our understanding of ecosystem dynamics[150,151]. By combining these enriched ground observations with remote sensing results and employing data fusion techniques, we can create high-quality datasets with high spatial and temporal resolution. This comprehensive approach will address limitations in densely vegetated areas and regions with limited temporal coverage, ultimately leading to more accurate modeling and analysis of soil moisture and carbon-greenhouse gas dynamics across various ecosystems.

## Bridging the gaps in modeling soil moisture and CS-GHG dynamics interaction: challenges and opportunities

Aside from the challenges associated with data, accurately modeling interactions between soil moisture and CS-GHG remains a significant challenge. First, carbon dynamics are highly sensitive to water availability[152], and the processes involved are complex[153]. As discussed in Section 3.2, $CH_4$ and $N_2O$ emissions are influenced by a broader range of soil moisture conditions. Modeling these nonlinear and threshold-based responses is challenging. Second, soil moisture exhibits significant spatial and temporal variability. Spatially, it varies across different landscapes due to factors like soil type, topography, climate, and vegetation cover[154]. Temporally, soil moisture can change rapidly due to weather events like rainfall or droughts[155]. This rapid and complex spatiotemporal variability makes it challenging for models, which must balance computational efficiency with the need for detailed process representation. Third, complex plant-soil interactions pose significant modeling challenges. Different plant species and microbial communities respond uniquely to soil moisture changes[156]. These interactions are complex; while small-scale model experiments can capture some aspects, large-scale models require detailed classification of plant functional types and microbial community compositions to accurately represent these dynamics and their impact on ecosystems.

As reviewed in Section 4, current ecosystem models can capture the complex feedback between soil moisture and CS-GHG to varying degrees. However, expanding the representation of these feedback from offline ecosystem models to an Earth system modeling framework presents additional challenges. These challenges include achieving accurate representation of temporal and spatial variability, realistically representing the interactions between soil moisture dynamics and atmospheric processes within a fully coupled, real-time framework, and efficiently managing computational demands[157]. Additional complexities arise in representing the legacy effects of droughts, which can alter soil properties by changing its chemical and physical structure, reducing carbon sequestration (Table 1) and increasing greenhouse gas emissions[158–160]. Accurately modeling plant hydraulic responses and capturing the often-underestimated strength of land–atmosphere interactions are also essential, as they directly influence the simulation of energy, moisture, and carbon exchanges[161]. Moreover, the influence of human activities, such as irrigation, water extraction, and those human land management practices discussed in Section 5, which significantly affect CS-GHG processes and their climate feedback, is often underrepresented in ecosystem models and their parent Earth system models (ESMs)[162–164].

To address these modeling challenges, recent studies have increasingly advocated for incorporating key ecological processes into ecosystem models and associated ESMs to enhance process-based representations and the accuracy and relevance of these models[165,166]. Integrating advanced machine learning algorithms is another promising approach. At the forefront of this integration are hybrid modeling frameworks, which combine and integrate machine learning methods into classical process-based models[167]. For example, the Knowledge-Guided Machine Learning (KGML) framework combines process-based models with machine learning techniques to improve carbon cycle quantification, revealing 86% more spatial detail than conventional methods[168]. Similarly, the KGML-DA framework improves carbon cycle predictions, reducing RMSE by up to 30.5% for corn and 24.6% for soybean, across three agricultural sites and 627 counties in the U.S. Midwest, using data from 2000 to 2020[169]. Hybrid models that integrate machine learning into ESMs combine the predictive power of machine learning with the interpretability of process-based models for improved accuracy[170]. Recent advancements, such as Bayesian networks and data assimilation techniques, enable these models to dynamically update predictions with new data and manage uncertainty effectively[171].

Beyond challenges inherent in the models themselves, obstacles arise in integrating models with observational data due to differences in spatiotemporal coverage, such as models providing high-frequency carbon flux outputs while MODIS GPP is available only every 16 days. Additional challenges include variations in data scale, resolution, and inconsistencies in data formats and quality[148]. Moreover, uncertainties in observational data can impact the validation and calibration processes, leading to less reliable predictions[172]. The Department of Energy's iterative Model-Experiment (ModEx; https://ess.science.energy.gov/modex/) approach offers a valuable framework for bridging the gaps between observation and modeling. This iterative process emphasizes a synergistic cycle where observational and experimental data inform and refine models, while models guide and prioritize future data collection efforts. By applying the ModEx concept to integrate high-resolution remote sensing data with expanded ground-based observations (as discussed in Section 6.1), researchers can enhance the predictive capabilities of models related to soil moisture and CS-GHG dynamics. This continuous feedback loop enables the identification of critical variables, processes, and locations that warrant further investigation, thereby enhancing the efficiency of data acquisition and informing targeted model development[159–163].

## Policies and incentives for soil moisture management to enhance CS and reduce GHG emissions

Current policies and incentives aimed at optimizing soil moisture for CS and reducing GHG emissions face several key challenges. One major issue is the misalignment between land use policies and climate goals, particularly in the agricultural and forestry sectors[173]. Many existing programs prioritize short-term outcomes like crop yield improvements, often at the expense of long-term soil health and carbon sequestration benefits[174,175]. This narrow focus on immediate agricultural outputs undermines efforts to manage soil moisture effectively for climate mitigation[176,177]. Furthermore, certain management practices that improve carbon sequestration, like afforestation or conservation tillage, may inadvertently increase GHG emissions, highlighting the need for policies that address these trade-offs effectively[44,178]. Financial incentives, such as subsidies and payments for ecosystem services (PES), can encourage the adoption of sustainable land management practices that improve soil health and increase carbon storage[179]. Programs like the USDA's Environmental Quality Incentives Program (EQIP) provide financial and technical assistance to help implement long-term conservation practices that enhance soil, water, and air quality[180]. Economic mechanisms, such as carbon credits and emissions trading, can encourage land use activities that sequester carbon[181,182]. However, challenges in accurately documenting sequestered carbon and integrating land-use activities into emissions trading highlight the need for robust Measurement, Reporting, and Verification (MRV) systems[182].

To overcome these challenges, future policies must adopt an integrated, long-term approach that aligns soil moisture management with broader climate goals. First, policies should shift focus from short-term agricultural outputs to practices that promote soil health and long-term carbon sequestration. Moreover, integrating nutrient management practices, like composting and organic amendments, can further contribute to climate-smart soil management[183,184]. Incentive frameworks should also be refined to encourage the adoption of climate-smart agricultural practices. Financial incentives such as carbon taxes, subsidies, and carbon credit offsets can be powerful tools, but they must be carefully designed to avoid unintended consequences, like increased emissions from certain management practices[176]. Additionally, the development of localized soil information systems can provide tailored data on soil conditions and carbon sequestration potential, enhancing the precision and effectiveness of soil moisture management strategies. Engaging key stakeholders, including farmers, policymakers, and scientists, in the design and implementation of these policies will be essential for fostering widespread adoption and ensuring their success.

## Conclusion

This review has demonstrated the pivotal role of soil moisture in regulating CS-GHG. Soil moisture directly influences plant photosynthesis and respiration, soil microbial activity, and soil organic matter decomposition, with optimal levels enhancing these processes and increasing carbon sequestration. However, extremes in soil moisture disrupt these mechanisms, reducing sequestration efficiency. $CO_2$ emissions exhibit a "Peak and Decline" pattern, peaking at around 40% WFPS, while $CH_4$ and $N_2O$ emissions peak at higher levels, between 60% and 80% WFPS for $CH_4$ and around 80% WFPS for $N_2O$, highlighting the need for targeted soil moisture management. Droughts reduce soil moisture, limiting carbon sequestration and altering GHG emissions, while floods create anaerobic conditions favorable for $CH_4$ production. Sustainable land management practices such as conservation agriculture, agroforestry, and optimized water management are crucial for enhancing carbon sequestration and reducing GHG emissions by improving soil structure and maintaining optimal moisture levels. Moreover, improving the accuracy of soil moisture and CS-GHG simulations hinges on enhancing high-resolution multiscale observations and refining feedback modeling. Integrating remote sensing technologies with expanded ground-based observations, along with employing hybrid modeling frameworks can significantly boost predictive capabilities while addressing data and feedback modeling challenges. Additionally, iterative model-experiment approaches, such as the ModEx framework, play a crucial role in linking observational data with models, enabling continuous refinement and strengthening the predictive power of CS-GHG models. Furthermore, current policies and incentives need to be better aligned with long-term climate goals to enhance soil moisture management for both carbon storage and the reduction of GHG emissions. Addressing these challenges through interdisciplinary approaches and innovative technologies will be essential in mitigating climate change and promoting sustainable land management practices.

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## Author contributions

Y.F.H. and J.F.M. conceived the idea and wrote the manuscript. G.K., J.G.L., L.C.L., M.A., M.J.S., S.K., X.Y.S., Y.P.W., and Y.L.F. contributed to the framework of the manuscript and participated in the writing process. H.Q.T. contributed to the model review section. C.M.B., J.T., J.Y.T., L.B.L., M.Z.J., Q.Z., F.M.H., H.S.C., X.Z., and Y.J.D. contributed to the manuscript and were instrumental in its revision and refinement.

## Competing interests

All authors declare no competing interests.

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