Overview: 'Global change effects on terrestrial biogeochemistry at the plant-soil interface'

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Abstract. 'Global change' significantly alters organic matter and element cycling, but many of the underlying processes and consequences remain poorly understood. The interface of plants and soil plays a central role, coupling atmosphere, hydrosphere, biosphere and lithosphere and integrating biological and geochemical processes. The contributions to this special issue address questions on both biotic and abiotic interactions underlying responses of terrestrial biogeochemical cycling to a range of global changes, including increases in atmospheric CO_2 concentrations, warming, drought and altered water regimes. In this overview, we synthesize key findings of the contributing empirical, conceptual, and modelling-based studies covering responses of plants to elevated CO_2, the role of soil organisms in modulating responses to warming, impacts of global change on soil organic carbon, nitrogen, and mineral nutrient availability and the influence of altered water table-depth caused by global change on greenhouse gas emissions. The showcased studies were conducted in regions from the Arctic to the tropics and highlight the manifold impacts of global change on various ecosystem components controlling biogeochemical processes occurring at the plant-soil interface. This multi-ecosystem interdisciplinary understanding is crucial for deciphering feedbacks of terrestrial ecosystems to the climate system.

Introduction

Global change poses manifold threats on different components of ecosystems and can significantly impact biogeochemical cycling. Increased atmospheric carbon dioxide (CO_2) concentrations, primarily driven by human activity, have strongly altered the Earth's energy budget, resulting in unprecedented global warming and shifts in precipitation patterns. The last decade has witnessed the hottest years on record, accompanied by intensified droughts and an increased frequency of extreme weather events (Intergovernmental Panel on Climate Change, 2023). These strong environmental changes

significantly impact terrestrial ecosystems through a complex interplay of direct and indirect effects (Bardgett et al., 2008). Elevated CO_2 and temperatures can directly stimulate plant growth, but also trigger a series of indirect effects (e.g. changed carbon supply for soil microbial communities), so that subsequent short and long-term impacts on soil organic carbon (SOC)

35 sequestration and total ecosystem carbon budgets remain unclear. Likewise, changing moisture and temperature can directly affect soil microorganism activity and SOC decomposition (Kim et al., 2012; Moyano et al., 2013; Schimel, 2018; Verbrigghe et al., 2022), but also indirectly influence soil nutrient availability, SOC stocks and plant feedbacks (Melillo et al., 2011). The magnitude and direction of responses to different global change factors depends largely on the ability of living organisms to tolerate or adapt to changed conditions (Allison, 2023). As greenhouse gas emissions to the atmosphere

40 are driven by autotrophic and heterotrophic organisms, understanding the resistance and resilience of all components in an ecosystem to changing conditions is integral for assessing potential feedbacks on the climate system. Overall, the plant-soil interface stands out as a hotspot for assessing these feedbacks, as it couples atmosphere, biosphere and lithosphere and integrates biological and geochemical processes across multiple trophic levels. Modelling approaches can help to understand this complex system, and to predict future ecosystem feedbacks to environmental and climate change, particularly through

45 altered biogeochemical cycling (e.g. Medlyn et al., 2015). However, the efficacy of models relies on a robust mechanistic understanding of the underlying physiological and biogeochemical processes.

The contributions to this special issue 'Global change effects on terrestrial biogeochemistry at the plant-soil interface' could be categorized in four functional topics. Studies investigated 1) the ability of plants to regulate resource optimization in

50 response to elevated atmospheric CO_2, 2) the role of soil organisms as agents for modulating responses to warming, with a strong focus in particular on artic ecosystems, 3) the effects of climate change on soil organic carbon, nitrogen and mineral nutrient availability, and 4) the impact of changing soil water-tables on greenhouse gas emissions from boreal to tropical ecosystems (Figure 1). The contributing studies integrate knowledge originated from understudied ecosystems, encompass studies conducted in arctic, high-latitude, dry- and wetland ecosystems, which are not only potentially largest soil carbon

55 sinks, but also sensitively respond to global change. The insights presented in this special issue represent an important step forward in comprehensively understanding the susceptibility of Earth's ecosystems to global change.
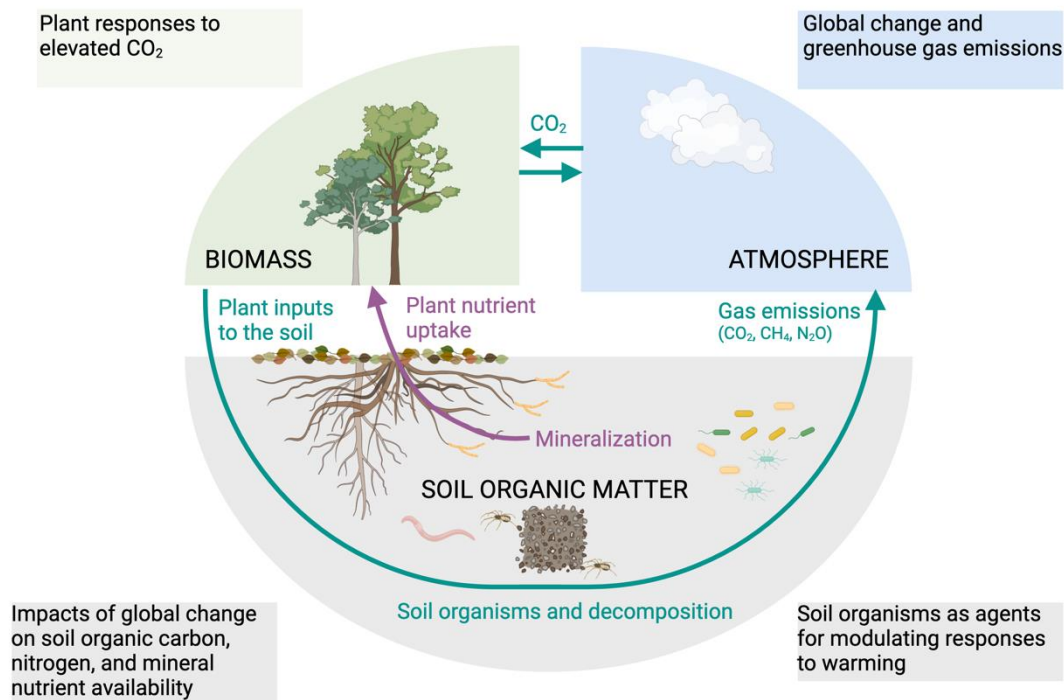
Figure 1: Global change affects all ecosystems, with interconnected feedbacks and links across its different components. For instance, altered environmental conditions have the potential to influence plant growth and plant carbon allocation to maintain resource and nutrient acquisition, consequently changing both quality and quantity of carbon inputs to the soil. Similarly, global change can modify community structure and activity of soil organisms, and subsequently soil organic matter decomposition and mineral weathering, overall affecting soil nutrient availability. Finally, greenhouse gas emissions to the atmosphere respond sensitively to global change, thereby feeding back on the climate system and affecting all other ecosystem components. The figure was created with BioRender.com.

1 Plant responses to elevated CO_2

Plants are a major component in terrestrial carbon cycling, taking up CO_2 from the atmosphere and converting it into biomass. However, the extent and mechanisms of plant resistance and recovery to global change depends on many biotic and abiotic factors. For instance, responses can strongly differ between vegetation types (e.g. crop plants vs. forest stands), physiological traits (e.g., wet vs. drought adapted species) and plant ecological strategies and flexibility (e.g. specialists vs. generalists), as well as depend on the magnitude of the environmental change. In general, the exposure to changing environmental conditions, such as increased CO_2 concentrations, warming or drought episodes, can induce both short (e.g.,

physiological) and longer-term (e.g., vegetation composition change) responses, with implications for biogeochemical cycling at the ecosystem level. Especially, trade-offs between plant resource acquisition (water-use and nutrient uptake) and biomass growth can yield a substantial variation in climate change feedback. Using different modelling approaches, Manzoni et al. (2022) explored whether elevated atmospheric CO_2 concentrations could lead to reduced-transpiration rates from vegetation, potentially reducing water loss and facilitating ecosystem 'greening' in dry regions. They found, however, small variation in canopy-level transpiration with rising atmospheric CO_2 due to the close coordination of physiological (reduced stomatal conductance) and morphological (increased leaf area) characteristics of plants to maximize water use efficiency. Yet, the responses to elevated atmospheric CO_2 are also tightly modulated by nutrient resource availability (Walker et al., 2021). In a field Free-Air-CO_2-enrichment experiment in a mature Eucalyptus forest, Pihlblad et al. (2023) observed a faster nutrient recycling, particularly of available phosphorus forms, but not an additional availability of nutrients through soil organic matter (SOM) decomposition. In the long term, this could lead to plant nutrient limitations and reduce the potential of mature forest ecosystems to fix carbon as biomass in response to elevated CO_2. Both studies (Manzoni et al., 2022; Pihlblad et al., 2023) highlight the importance of accounting for resource limitations of plants in response to elevated CO_2, however also emphasize that adaptions can profoundly differ between ecosystems or plant communities. It is thus essential to improve our understanding of the variability in short- and long-term plant responses to accurately predict ecosystem behavior under climate change.

2 Soil organisms as agents for modulating responses to warming

Global warming is one of the most pronounced climate change factors driving large ecosystem transformations. This is particularly evident in cold ecosystems, with the Arctic containing 50-70% of the total carbon stock (Hugelius et al., 2014) being crucial for terrestrial carbon cycling. Predictions suggest that Arctic regions will experience greater temperature increases compared to other ecosystems, underscoring the importance to understand the unique challenges faced by these regions (Intergovernmental Panel on Climate Change, 2023). Soil (micro-)organisms are key regulators of matter and energy cycling between the soil and the atmosphere via their catabolic and anabolic processes (Ågren and Wetterstedt, 2007). Given the temperature sensitivity of enzymatic reactions, warming has mostly a stimulating effect on microbial activity in cold ecosystems, which can potentially destabilize carbon stored in Arctic soils and contribute to further climate change. Thus, investigating warming effects on soil microbes in cold ecosystems is particularly relevant. Rijkers et al., (2023) identified strong differences in the temperature adaptation of microbial communities in soils from the subarctic to the High Arctic region. They predicted that summer warming can increase the community-level optimal growth temperature, but found no evidence supporting temperature adaptation of the soil bacterial community structure. SOM decomposition is not only strongly affected by microbial communities, but also by the presence of soil fauna. Blume-Werry et al. (2023) proposed that, in Arctic ecosystems, climate warming can create new niches for soil organisms migrating both laterally and vertically belowground. This may introduce new soil-fauna-associated functions that can strongly affect decomposition processes, and

challenges the way we simulate carbon losses under climate change scenarios. Indeed, Monteux et al. (2022) showed that

105 introducing a model microarthropod (Collembola *Folsomia candida*) species can influence bacterial diversity, and prime respiration of the native soil community. These studies highlight the importance of investigating and understanding biotic interactions in soil as well as the need to further explore potential additive or interactive effects of warming and other climate change factors on the soil food web.

3 Impacts of global change on soil organic carbon, nitrogen, and mineral nutrient availability

110 Warming is expected to boost net primary production and potentially enhance ecosystem carbon sequestration (Melillo et al., 2017). However, warming also has a stimulating effect on microbial activity and SOM turnover (e.g., Classen et al., 2015; Davidson and Janssens, 2006), which can lead to significant decreases in soil organic carbon stocks (Verbrigghe et al., 2022). Soil microbes release enzymes transforming SOM into available carbon and nutrients, ultimately releasing CO_2 via intracellular metabolism (Allison et al., 2007). Many studies have examined the temperature sensitivity of SOM

115 decomposition via CO_2 emission or mass loss of carbon substrate (e.g., Kirwan et al., 2014; Wang et al., 2013). However, differentiating contributions by extracellular and intracellular processes is key for a mechanistic understanding of warming. Adekanmbi et al. (2023) investigated these sensitivities and found that depolymerization of high molecular weight carbon was more sensitive to temperature changes at higher temperatures, whereas the respiration of the generated monomers was more sensitive to temperature changes at moderate temperatures. Hence, this study suggested that global warming may shift

120 the importance from extracellular depolymerization to intracellular metabolic processes as the rate-limiting step of SOM mineralization.

The stimulating effect of warming on plant productivity can be constrained by low nutrient availability, for instance by nitrogen (Melillo et al., 2011) and cations (Jonard et al., 2015). In cold ecosystems, the addition of nutrients has been found

125 to stimulate plant aboveground growth (Bergh et al., 2008), but to reduce the allocation of carbon to roots and associated microorganisms (Wallander et al., 2011). Almeida et al. (2022) investigated the impact of forest fertilization on the soil ectomycorrhizal fungal community in an experimental spruce forest in Norway. The authors observed changes in the fungal community composition after three years of N additions, potentially affecting hydrophobic SOM formation and reducing soil carbon sequestration. Myers-Pigg et al. (2023) explored the net response of SOC composition to climate change, assessing

130 its diagenetic state based on lignin-phenol biomarkers. Their biomarker-based approach revealed a coupled increase in carbon and N cycling rates, which may support forest productivity and help maintain SOC stocks. Finally, in a modelling study using the ForSAFE model on different forest systems distributed across Sweden, Kronnäs et al. (2023) found that warming and longer growing seasons for plants could enhance soil weathering rates, inducing substantial changes in soil texture and mineral nutrient stocks. This emphasizes the importance of including soil texture and seasonal climate variations

135 for predicting forest responses to climate change in future studies, and highlights that understanding the interactions between

primary production, carbon sequestration and limiting factors is crucial for predicting and managing the impacts of climate change on terrestrial ecosystems.

4 Influence of altered water-table depth caused by global change on greenhouse gas emissions

One of the most effective and accessible approaches for evaluating effects of global changes on soil biogeochemical cycling
140   is the measurement of gaseous emissions, such as of carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O). From soils, CO_2 is released by plant roots and SOM decomposition by soil organisms under aerobic conditions (autotrophic and heterotrophic respiration), CH_4 under anaerobic conditions by methanogenic microorganisms, and N_2O through nitrification and denitrification processes in soils. All gas fluxes are highly responsive to changes in soil water conditions controlling whether ecosystems are sources or sinks for greenhouse gases (Jungkunst and Fiedler, 2007). Zhao and Zhuang (2023)
145   modelled greenhouse gas flux responses of Northern peatlands in response to warming, revealing increases in both CO_2 and CH_4 emissions due to deeper water-table levels and enhanced permafrost thawing. They demonstrated that warming had limited impact on net primary production due to shifts in plant functional types and nitrogen limitations, which could turn ecosystems into carbon sources. Their estimates proposed that this shift might occur as early as 2050, notably earlier than previously anticipated (e.g., Gallego-Sala et al., 2018; McGuire et al., 2018). Zhang et al. (2022) further explored the effect
150   of water-table levels and nitrogen availability on greenhouse gas emissions in alpine peatlands by conducting a mesocosm experiment. They found that a moderate increase in nitrogen deposition and rising water-table levels stimulated CH_4 emissions, whereas only nitrogen deposition consistently increased N_2O emissions. Finally, in a field study, Castellón et al. (2022) quantified the emissions of CO_2 and CH_4 in a natural mangrove forest experiencing daily and seasonal variations in water-table depths. Higher topography areas generally exhibited increased CO_2 emissions and decreased CH_4 emissions,
155   likely induced by reduced flooding frequency. The study highlighted the role of microtopography, seasonality and soil physicochemical properties in influencing greenhouse gas emissions. Changes in water-table depth thus exert a major influence on greenhouse gas emissions, creating feedback loops that further impact the climate system

Concluding remarks

The studies contributing to this special issue 'Global change effects on terrestrial biogeochemistry at the plant-soil interface',
160   reveal pronounced impacts of global change on biogeochemical processes driven by different trophic levels, extending from autotrophic plants to heterotrophic soil fauna and microbial populations. Both empirical and modeling studies show that global change can affect small soil-scale, as well as large ecosystem-scale fluxes of C and nutrients, inducing substantial feedback loops on the climate system. The diverse methodologies employed in the contributing studies highlights that a combination of techniques is essential for a mechanistic and holistic understanding of the complex interactions at the plant-
165   soil interface. Future research should then prioritize the combination of approaches and focus on regions hosting the largest

organic matter pools and exhibiting the highest sensitivity to climate. This enhanced understanding of multi-scale across-temporal responses is crucial for improving predictions of the resistance and resilience of terrestrial ecosystems to global change, informing effective strategies for mitigating and adapting to future environmental challenges.

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