



Missing the input: The underrepresentation of plant physiology in global soil carbon research

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Abstract. Plant processes regulating the quantity and quality of soil organic carbon inputs such as photosynthesis, above- and belowground plant growth, and root exudation are integral to our understanding of soil carbon dynamics. However, based on a bibliometric analysis including almost 50 000 scientific papers, we found that plant physiology has been severely underrepresented in global soil organic carbon research. Less than 10% of peer-reviewed soil organic carbon research published in the last century addressed plant physiological processes relevant to soil carbon inputs. Similarly, plant physiology was overlooked by the overwhelming majority (>90%) of peer-reviewed literature investigating linkages between soil organic carbon, climate change, and land use and management. These findings highlight that our understanding of soil carbon dynamics and hence the carbon sequestration potential of terrestrial ecosystems is largely built on research that neglects the fundamental processes underlying organic carbon inputs. We advocate that the active engagement of plant scientists in soil carbon research is imperative to shed light on this blind spot. Long-term interdisciplinary research will be essential to develop a comprehensive perspective on soil carbon dynamics and to inform effective policies that support soil carbon sequestration.

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1 Introduction

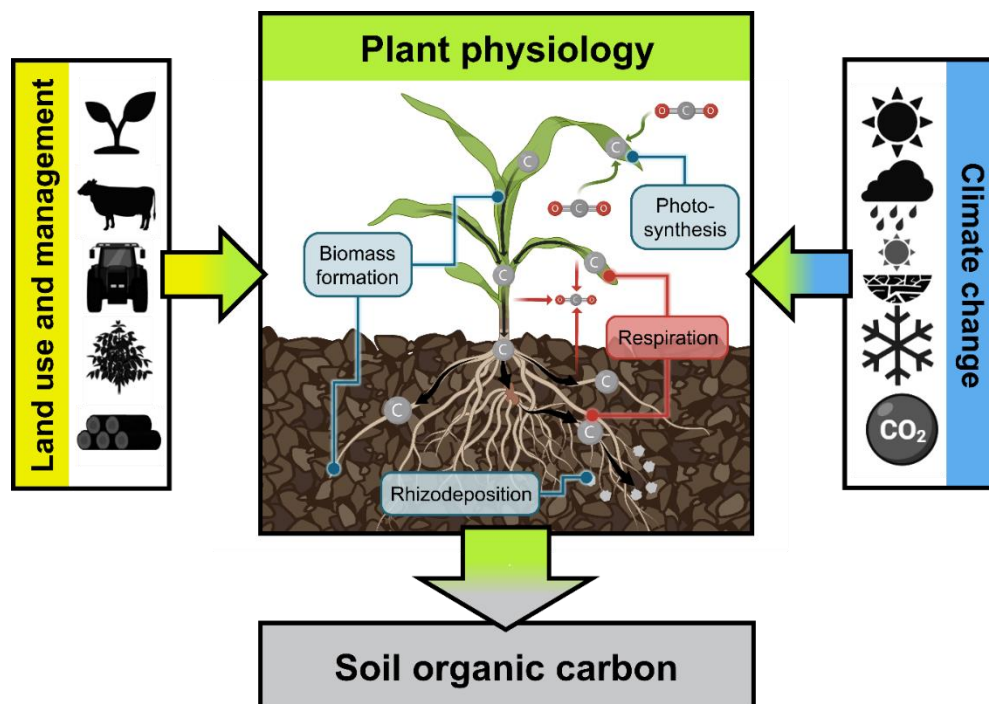
Plants and their ability to fix atmospheric carbon dioxide (CO₂) through photosynthesis are essential to organic matter buildup in soil (Hirt et al., 2023), the second largest carbon pool on earth (Lal, 2018). The overwhelming majority of organic carbon in soil is derived directly or indirectly from above- and belowground plant residues or rhizodeposits, referring to all organic compounds released by roots (Pausch and Kuzyakov, 2018) (Figure 1). Beyond its critical role in terrestrial carbon sequestration, soil organic carbon supports soil fertility and ecosystem productivity through improved water infiltration and retention, enhanced soil structure formation, and greater soil biological activity (Lal, 2018). Since the United Nations Conference on Environment and Development (UNCED) held in Rio de Janeiro, Brazil in 1992, soil organic carbon and its fundamental importance in climate change mitigation and adaptation gradually gained importance in the public discussion on sustainable development (Montanarella and Alva, 2015). Recently launched international policy frameworks and initiatives such as the ‘European Green Deal’ (European Commission, 2019) and the ‘4 per mille initiative’ (Lal et al., 2015) aim to enhance soil organic carbon levels through adaptations in land use and management. Moreover, the Intergovernmental Panel

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30 on Climate Change (IPCC) highlighted the vulnerability of soil organic carbon stocks to environmental disturbances associated with climate change including rising temperatures and extreme weather events (IPCC, 2023).

Besides affecting the stabilisation and turnover of soil organic carbon, environmental conditions have significant impacts on plants and their physiology, thereby affecting the quantity and quality of soil carbon inputs. For example, a global meta-analysis including natural and managed ecosystems across biomes provided evidence that increasing temperatures lead to a shift in carbon allocation from shoots to roots, especially in drier climates (Zhou et al., 2022). Similar shifts in carbon allocation from shoots to roots have been reported for wheat in response to decreasing fertilisation intensity (Hirte et al., 2021). Moreover, it has been shown that decreasing fertilisation intensity and water availability increases rhizodeposition rates in arable crops (wheat and maize; Hirte et al., 2018) and temperate tree species (*Picea abies* and *Fagus sylvatica*; Brunn et al., 2022), respectively. Besides affecting carbon allocation between different plant organs and metabolic pathways, environmental conditions such as temperature (Wang et al., 2012), atmospheric CO₂ concentration, and nutrient availability (Blaschke et al., 2002) alter the biochemical composition of plant tissues and thus the quality of plant litter inputs to soil. Hence, plant physiological responses to climatic conditions or changes in land use and management are absolutely imperative to our understanding of soil carbon dynamics and thus the carbon sequestration potential of terrestrial ecosystems (Figure 1).



45 **Figure 1: Conceptual schematic depicting the central role of plants and their responses to land use and management and climatic conditions for soil carbon dynamics. Carbon fluxes from the atmosphere into the soil underlying the quantity and quality of soil organic carbon inputs are driven by a suite of plant physiological processes such as photosynthesis, biomass formation, rhizodeposition, and shoot and root respiration rates. Responses of these physiological processes to changing environmental conditions due to (e.g.) alterations in land use and management or climatic conditions have therefore direct consequences for soil carbon dynamics, determining the current and future potential for soil carbon sequestration. Some elements were created with**

50 **BioRender.com**

2 Soil carbon research largely overlooks plant physiology

Despite the intrinsic linkages between plants, environmental conditions, and soil carbon inputs and dynamics, plant physiological processes have been severely underrepresented in global peer-reviewed research on soil organic carbon. We quantified this underrepresentation through bibliometric analyses of data extracted from Web of Science™ (https://www.webofscience.com/). To obtain a comprehensive picture on the importance of plant physiology in soil organic carbon research, we included 24 different plant processes that are directly linked to soil organic carbon inputs (Supplemental Table S1). These bibliometric analyses revealed that only 8% of the peer-reviewed research on soil organic carbon published between 1904 and 2023 addressed plant physiology (3 907 out of 49 971 publications; Figure 2A). More than 95% of the publications on soil organic carbon were published after 1990 and the yearly research output increased exponentially between 1990 and 2023. We observed a parallel temporal trend for peer-reviewed publications on soil organic carbon that addressed plant physiological processes. Therefore, the relative proportion of publications addressing plant physiological processes in the total number of soil organic carbon publications remained approximately constant between 1990 and 2023 (5% to 12%; Figure 2A).

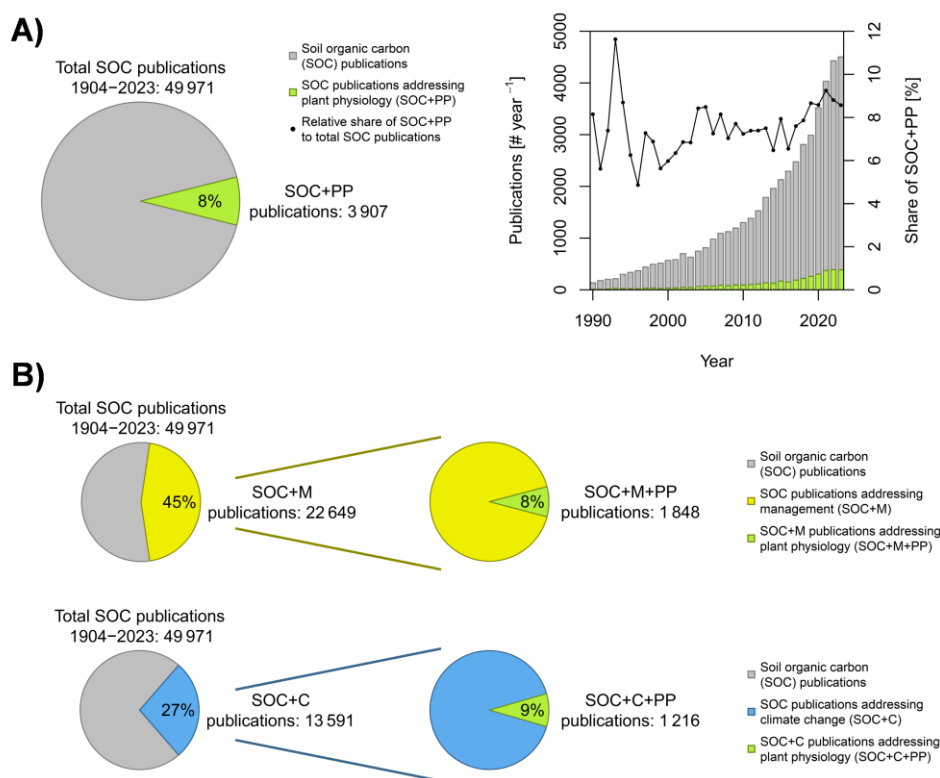


Figure 2: The representation of plant physiology in global soil organic carbon research. A) Share of soil organic carbon publications addressing plant physiological processes displayed (left) cumulatively from 1904 to 2023 and (right) yearly from 1990 to 2023. B) Soil organic carbon publications that addressed (top) land use and management and (bottom) climate change effects and the share of publications within these two categories addressing plant physiological processes from 1904 to 2023.

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70 Further bibliometric analyses were conducted to quantify the importance of land use and management and climate change in
soil organic carbon research. For these analyses, we included more than 45 keywords to capture relevant land use and
management systems and more than 25 keywords to cover climate change and associated environmental conditions
(Supplemental Table S1). Land use and management was addressed by 45% of the peer-reviewed research on soil organic
carbon published between 1904 and 2023 (22 649 out of 49 971 publications), while climate change and concomitant
75 environmental conditions were addressed in 27% of the publications (13 591 out of 49 971 publications; Figure 2B). In contrast
to plant physiology, land use and management as well as climate change have been increasingly represented in global research
on soil organic carbon. The share of publications on soil organic carbon that addressed land use and management increased
from around 35% in the 1990s to almost 50% in the 2020s. Similarly, the share of soil organic carbon publications addressing
climate change and associated environmental conditions increased from around 10 to 15% in the early 1990s to more than
80 30% in the 2020s (Supplemental Figure S1). This increase can likely be attributed to discussions in the public arena on the
role of land use and management for climate change mitigation and sustainable development (European Commission, 2019;
Lal et al., 2015) that followed the United Nations Conference on Environment and Development (UNCED) in 1992
(Montanarella and Alva, 2015).

However, plant physiology was severely underrepresented in global research elucidating associations between soil organic
85 carbon and land use and management or climate change. Less than 10% of the research covering linkages between soil organic
carbon and land use and management (1 848 out of 22 649 publications) and climate change (1 216 out of 13 591 publications),
respectively, addressed plant physiological processes (Figure 2B). In the case of climate change, the share of publications
addressing plant physiological processes even decreased from around 15% in the 1990s to around 7% in recent years. For land
use and management, the percentage of publications addressing plant physiological processes remained around 8% between
90 the 1990s and the 2020s (Supplemental Figure S1). Hence, our bibliometric analyses highlighted that our current understanding
of soil carbon dynamics is overwhelmingly based on research that does not account for plant physiological responses to
changes in land use and management or climatic conditions. We can only speculate why plant physiology was largely
overlooked in soil organic carbon research but the recently reported separation of soil and agricultural sciences in the 1980s
(Sigl et al., 2023) may have been a key driver. Ultimately, the staggering underrepresentation of plant physiology in soil
95 organic carbon research reported here (Figure 2; Supplemental Figure S1) severely limits the predictive power of terrestrial
carbon models and prevents a comprehensive perspective on the potential for soil carbon sequestration (Fatichi et al., 2019).

3. Long-term interdisciplinary research efforts are key

Interdisciplinary research efforts that explicitly integrate plant physiological processes into studies on soil carbon dynamics
are urgently needed to develop a more holistic understanding of the drivers underpinning soil carbon sequestration (Hirt et al.,
100 2023). Recent technological and methodological advancements have substantial potential to decipher the complex interactive
effects between plant physiological processes and environmental conditions on soil carbon dynamics (Ahkami et al., 2024;



Mueller et al., 2024). For example, the combination of three-dimensional imaging approaches such as X-ray and positron emission tomography with spectroscopic techniques and carbon isotope tracing facilitate quantifying the fate of photosynthates along the shoot-root-soil axis (Jahnke et al., 2009; Lippold et al., 2023). Especially if combined with mathematical models (Ahkami et al., 2024), these approaches enable new mechanistic and predictive insights into the interactions between plant physiological processes and soil carbon dynamics. However, long-term data obtained at the field and landscape scale is indispensable when quantifying temporal trajectories of soil organic carbon stocks (Smith et al., 2020). We therefore advocate that the regular quantification of plant physiological processes that govern the quality and quantity of soil carbon inputs must become standard in long-term field experiments and observation networks dedicated to soil carbon dynamics. This includes, but not limited to, above- and belowground plant growth (Hirte et al., 2021; Zhou et al., 2022), degrees of lignification and suberisation of plant tissues determining the biochemical quality of plant litter (Blaschke et al., 2002; Wang et al., 2012), and the quantity and composition of rhizodeposits (Brunn et al., 2022; Hirte et al., 2018).

Plant scientists including geneticists, physiologists, and ecologists must become an active and integral part of the global soil organic carbon research community. Otherwise, the environmental and genetic drivers underpinning soil carbon inputs will remain a blind spot in our collective understanding of the capacity for soil carbon sequestration (Hirt et al., 2023). Therefore, it is crucial for the global scientific community, including researchers and funding agencies, to recognise the pivotal role of plant physiology in shaping soil carbon dynamics. Without this recognition, our understanding of soil carbon sequestration potential across diverse terrestrial ecosystems will remain incomplete. To accurately model and predict these dynamics—whether through empirical, mechanistic, or geostatistical models—long-term data collection at appropriate spatial and temporal scales is essential (Fatichi et al., 2019; Smith et al., 2020). These models are indispensable for extrapolating interactions across ecosystems and for quantifying effects of climatic conditions and land use and management on plant physiological processes and the resulting impacts on soil carbon dynamics. However, developing such models requires sustained investment in long-term research and improved funding mechanisms that facilitate collaboration among interdisciplinary groups of researchers. Only with these continued efforts can we develop the comprehensive understanding necessary to inform effective policies that support and enhance soil carbon sequestration.

Appendix: Query design, data extraction and processing

Comprehensive bibliometric analyses were conducted using the ‘advanced search’ option in the Web of Science™ data base from Clarivate™ (Web of Science Core Collection; <https://www.webofscience.com/>). Thereby, the topic search function (“TS”) was used to cover publication titles, abstracts, keywords and the field (i.e. keywords plus®), and author keywords. To quantify the share of publications addressing plant physiology, land use and management, climate change and associated environmental conditions, or combinations thereof in global research on soil organic carbon, four separate queries were built: i) Soil organic carbon, ii) Plant physiological processes, iii) Land use and management, and iv) Climate change and associated environmental conditions. For each of the four queries a list of relevant key words and corresponding search terms were defined



(i): 2 key words, 11 search terms; ii): 24 key words, 31 search terms; iii): 47 key words, 66 search terms; iv): 28 key words,
135 41 search terms; Supplemental Table S1).

Within each query, the different search terms were connected with the Boolean operator “OR” to ensure the retrieval of all relevant records. Combining the different queries then allowed us to quantify the share of peer-reviewed publications on soil organic carbon addressing plant physiological processes, land use and management, climate change and associated environmental conditions, or combinations thereof. To do so, the search terms of the soil organic carbon query were connected
140 to the search terms of one or several of the other three queries using the Boolean operator “AND”. Data searches were conducted on 10 September, 2024 including all records available on Web of Science™ and results were exported as .BIB, .CSV, and .RIS files.

Quality checks of the raw data exported from Web of Science™ were performed with a standardised data filtering pipeline implemented in R version 4.0.2 (R Core Team, 2020) using the package ‘bibliometrix’ (Aria & Cuccurullo, 2017). First,
145 duplicates and non-English publications were removed. Then, we removed all publications published in 2024 to ensure that only complete years were included. Finally, the data was limited to what is typically considered primary research or scholarly works, i.e. articles, proceedings papers, review articles, early access papers, and data papers (Supplemental Figure S2). These filtering steps reduced the total number of publications included in our analyses by around 10% from 55 986 to 49 971. Data visualisation was performed in R using the packages ‘stats’ (R Core Team, 2020).

150 **Data availability**

The bibliometric data is provided in the supplement (Supplemental Data S1).

Author contribution

SR and TC conceived the study. All authors contributed to query design. SR performed the bibliometric analyses with help of MSK. SR and TC wrote the original draft with inputs from HVC. NTG, MSK, MJB, and SJM, contributed to reviewing and
155 editing.

Competing interests

The authors declare that they have no conflict of interest.

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BioRender (<https://www.biorender.com/>) was used to create Figure 1.



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References

- 165 Ahkami, A. H., Qafoku, O., Roose, T., Mou, Q., Lu, Y., Cardon, Z. G., Wu, Y., Chou, C., Fisher, J. B., Varga, T., Handakumbura, P., Aufrecht, J. A., Bhattacharjee, A., and Moran, J. J.: Emerging sensing, imaging, and computational technologies to scale nano-to macroscale rhizosphere dynamics – Review and research perspectives, *Soil Biol. Biochem.*, 189, 109253, <https://doi.org/10.1016/j.soilbio.2023.109253>, 2024.
- Blaschke, L., Forstreuter, M., Sheppard, L. J., Leith, I. K., Murray, M. B., and Polle, A.: Lignification in beech (*Fagus sylvatica*) grown at elevated CO₂ concentrations: interaction with nutrient availability and leaf maturation, *Tree Physiol.*, 22, 469–477, <https://doi.org/10.1093/treephys/22.7.469>, 2002.
- 170 Brunn, M., Hafner, B. D., Zwetsloot, M. J., Weikl, F., Pritsch, K., Hikino, K., Ruehr, N. K., Sayer, E. J., and Bauerle, T. L.: Carbon allocation to root exudates is maintained in mature temperate tree species under drought, *New Phytol.*, 235, 965–977, <https://doi.org/10.1111/nph.18157>, 2022.
- 175 European Commission: The European Green Deal, 1–23 pp., 2019.
- Fatichi, S., Pappas, C., Zscheischler, J., and Leuzinger, S.: Modelling carbon sources and sinks in terrestrial vegetation, *New Phytol.*, 221, 652–668, <https://doi.org/10.1111/nph.15451>, 2019.
- Hirt, H., Al-babili, S., Almeida-trapp, M., Martin, A., Aranda, M., Bartels, D., Bennett, M., Blilou, I., Boer, D., Boulouis, A., Bowler, C., Brunel-muguet, S., Chardon, F., Colcombet, J., Colot, V., Daszkowska-golec, A., Dinneny, J. R., Field, B., 180 Froehlich, K., Gardener, C. H., Gojon, A., Gomès, E., Gomez-alvarez, E. M., Gutierrez, C., Havaux, M., Hayes, S., Heard, E., Hodges, M., Alghamdi, A. K., Laplaze, L., Lauersen, K. J., Leonhardt, N., Johnson, X., Jones, J., Kollist, H., Kopriva, S., Krapp, A., Masson, M. L., McCabe, M. F., Merendino, L., Molina, A., Ramirez, J. L. M., Mueller-roeber, B., Nicolas, M., Nir, I., Orduna, I. O., Pardo, J. M., Reichheld, J., Rodriguez, P. L., Rouached, H., Saad, M. M., Schlögelhofer, P., Singh, K. A., Smet, I. De, Stanschewski, C., Stra, A., Tester, M., Walsh, C., Weber, A. P. M., Weigel, D., Wigge, P., Wrzaczek, M., Wulff, 185 B. B. H., and Young, I. M.: PlantACT! – how to tackle the climate crisis, *Trends Plant Sci.*, 28, 537–543, <https://doi.org/10.1016/j.tplants.2023.01.005>, 2023.
- Hirte, J., Leifeld, J., Abiven, S., Oberholzer, H. R., and Mayer, J.: Below ground carbon inputs to soil via root biomass and rhizodeposition of field-grown maize and wheat at harvest are independent of net primary productivity, *Agric. Ecosyst. Environ.*, 265, 556–566, <https://doi.org/10.1016/j.agee.2018.07.010>, 2018.
- 190 Hirte, J., Walder, F., Hess, J., Büchi, L., Colombi, T., van der Heijden, M. G., and Mayer, J.: Enhanced root carbon allocation through organic farming is restricted to topsoils, *Sci. Total Environ.*, 755, 143551,



- <https://doi.org/10.1016/j.scitotenv.2020.143551>, 2021.
- IPCC: Sections, Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change, Geneva, Switzerland, 35–115 pp.,
195 <https://doi.org/10.59327/IPCC/AR6-9789291691647>, 2023.
- Jahnke, S., Menzel, M. I., Dusschoten, D. Van, Roeb, G. W., Bu, J., Temperton, V. M., Hombach, T., Streun, M., Beer, S., Khodaverdi, M., Ziemons, K., Coenen, H. H., and Schurr, U.: Combined MRI – PET dissects dynamic changes in plant structures and functions, *Plant J.*, 59, 634–644, <https://doi.org/10.1111/j.1365-313X.2009.03888.x>, 2009.
- Lal, R.: Digging deeper: A holistic perspective of factors affecting soil organic carbon sequestration in agroecosystems, *Glob. Chang. Biol.*, 24, 3285–3301, <https://doi.org/10.1111/gcb.14054>, 2018.
200
- Lal, R., Negassa, W., and Lorenz, K.: Carbon sequestration in soil, *Curr. Opin. Environ. Sustain.*, 15, 79–86, <https://doi.org/10.1016/j.cosust.2015.09.002>, 2015.
- Lippold, E., Schlüter, S., Mueller, C. W., Höschen, C., Harrington, G., Kilian, R., Gocke, M. I., Lehndorff, E., Mikutta, R., and Vetterlein, D.: Correlative Imaging of the Rhizosphere—A Multimethod Workflow for Targeted Mapping of Chemical
205 Gradients, *Environ. Sci. Technol.*, 57, 1538–1549, <https://doi.org/10.1021/acs.est.2c07340>, 2023.
- Montanarella, L. and Alva, I. L.: Putting soils on the agenda: the three Rio Conventions and the post-2015 development agenda, *Curr. Opin. Environ. Sustain.*, 15, 41–48, <https://doi.org/10.1016/j.cosust.2015.07.008>, 2015.
- Mueller, C. W., Baumert, V., Carminati, A., Germon, A., Holz, M., Kögel-Knabner, I., Peth, S., Schlüter, S., Uteau, D., Vetterlein, D., Teixeira, P., and Vidal, A.: From rhizosphere to detritosphere – Soil structure formation driven by plant roots
210 and the interactions with soil biota, *Soil Biol. Biochem.*, 193, 109396, <https://doi.org/10.1016/j.soilbio.2024.109396>, 2024.
- Pausch, J. and Kuzyakov, Y.: Carbon input by roots into the soil: Quantification of rhizodeposition from root to ecosystem scale, *Glob. Chang. Biol.*, 24, 1–12, <https://doi.org/10.1111/gcb.13850>, 2018.
- Sigl, L., Falkenberg, R., and Fochler, M.: Changing articulations of relevance in soil science: Diversity and (potential) synergy of epistemic commitments in a scientific discipline, *Stud. Hist. Philos. Sci.*, 97, 79–90,
215 <https://doi.org/10.1016/j.shpsa.2022.12.004>, 2023.
- Smith, P., Soussana, J. F., Angers, D., Schipper, L., Chenu, C., Rasse, D. P., Batjes, N. H., van Egmond, F., McNeill, S., Kuhnert, M., Arias-Navarro, C., Olesen, J. E., Chirinda, N., Fornara, D., Wollenberg, E., Álvaro-Fuentes, J., Sanz-Cobena, A., and Klumpp, K.: How to measure, report and verify soil carbon change to realize the potential of soil carbon sequestration for atmospheric greenhouse gas removal, <https://doi.org/10.1111/gcb.14815>, 6 January 2020.
- 220 Wang, J., Duan, B., and Zhang, Y.: Effects of experimental warming on growth, biomass allocation, and needle chemistry of *Abies faxoniana* in even-aged monospecific stands, *Plant Ecol.*, 213, 47–55, <https://doi.org/10.1007/s11258-011-0005-1>, 2012.
- Zhou, L., Zhou, X., He, Y., Fu, Y., Du, Z., Lu, M., Sun, X., Li, C., Lu, C., Liu, R., Zhou, G., Bai, S. H., and Thakur, M. P.: Global systematic review with meta-analysis shows that warming effects on terrestrial plant biomass allocation are influenced by precipitation and mycorrhizal association, *Nat. Commun.*, 13, 4914, <https://doi.org/10.1038/s41467-022-32671-9>, 2022.