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REVIEW ARTICLE



Grassland soil organic carbon stocks along management intensity and warming gradients

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Abstract

Grasslands are a major terrestrial ecosystem type and store large amounts of soil organic carbon (SOC) per unit area. Quantitative and mechanistic knowledge on the effects of management on SOC stocks in grasslands is limited. Also, climate change can be seen as an indirect anthropogenic threat to SOC stocks, with warming effects on grassland SOC being currently understudied. Here, several studies investigating the effects of management and warming on SOC stocks are summarised, with a central to northern European focus. SOC sequestration increased with management intensity, i.e. cutting frequency and mineral fertilisation, even without external C inputs. This was partly explicable by increased productivity in more intensively managed grasslands. In addition, the availability of nutrients was found to foster microbial anabolism, leading to a more efficient build-up of SOC in fertilised as compared to unfertilised soils. Interestingly, the addition of 1 kg nitrogen as NPK fertiliser consistently led to approximately 1 kg of additional SOC. Sequestration of SOC might thus compensate for a major part of the increased greenhouse gas emissions associated with highly intensive grassland management. Including perennial grasses in agricultural crop rotations is multi-beneficial and proved to be a very efficient measure to increase SOC stocks. At the same time, soil warming depleted SOC, both in natural subarctic as well as in managed temperate grasslands. Climate change can thus be expected to counterbalance efforts of SOC build-up to some extent. Future research should focus on the interactive effects of climate change and management, which will be important for future management decisions.

KEYWORDS

cutting frequency, fertilisation, perennial grasses, soil warming

| INTRODUCTION

Soil organic matter is the largest terrestrial carbon pool. Globally, it stores more carbon than vegetation and atmosphere combined (Ciais, 2013). Relatively small changes in soil organic carbon (SOC) stocks can thus have strong impacts on the atmospheric CO2 concentration. For this reason, accumulating SOC is considered as a potential negative emission technology to achieve international climate mitigation goals. Furthermore, soil organic matter content is a key soil quality indicator, due to numerous positive effects of organic

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matter on soil properties. Loss of organic matter and SOC is thus considered as soil degradation (Global Soil Partnership, 2017).

In research and policy, there is a strong focus on cropland soils as potential carbon sinks or sources. This might be related to the fact that croplands are acknowledged to store the lowest amounts of SOC per area and are the most intensively managed systems. Debreczeni and Körschens (2003) listed more than 600 agricultural long-term soil experiments globally, of which only 49 were initiated on pasture or meadow soils. Although this list of experiments was neither complete, nor is it up to date, it indicates that croplands have been the focus of agricultural soil science. However, grasslands cover 68% of the total global agricultural area (Leifeld et al., 2015) and store an estimated amount of 245 Pg SOC (Bolin et al., 2000). In Europe, 21% of the total land area is covered by grassland and 22% by cropland (Eurostat, 2015). Also, in urban areas grassland is a major land cover type (Ignatieva et al., 2017). Especially in Europe, grasslands are managed intensively. Accordingly. management-induced SOC changes need to be well understood to develop climate-smart farming and management solutions, as well as to feed earth system models. Management interventions, such as grazing, cutting, fertilisation, reseeding or irrigation have been found to affect SOC to some extent (Conant et al., 2017; Rumpel et al., 2015). For most of the mentioned interventions existing literature is limited and controversial, and involved mechanisms remain insufficiently understood. In addition, SOC sequestration potential, as derived from scattered field trials, may not be representative for a wide range of soils and climate zones, and not always be applicable to real-world agriculture. Recently, Batjes (2019) underlined the large discrepancy between potential SOC sequestration and technically achievable SOC sequestration. For example, the implementation of best management practices on degraded grasslands has the potential to sequester 0.12-0.34 Pg C/year globally, while the currently achievable range was estimated at 0.01-0.05 Pg C/year. Total annual anthropogenic C emissions amount to approximately 10 Pg C (Ciais, 2013). Soil carbon sequestration can thus only be one out of many means undertaken to effectively mitigate climate change.

Cropland soils are assumed to have the largest potential to sequester SOC, since they are most depleted (Angers et al., 2011). This assumption is based on the concept, that each soil has a specific limit of how much SOC can be sequestered, the so called "saturation" level (Hassink, 1997). Grasslands and soils under natural vegetation are considered as being "saturated" in this concept. However, the fact that grassland soils already store large amounts of SOC doesn't seem to play a major role for additional SOC accumulation: after 43 years of organic manure fertilisation, Fornara et al. (2016) still found linear increases in SOC stocks for various input rates, which questions this saturation concept. Consequently, grassland soils deserve similar attention as cropland soils when considering SOC sequestration as negative emission technology (Smith, 2014). At the same time, C imports from other systems in the form of manure or compost to increase SOC at one specific location, might not impose a net negative emission, because the C is lost where it was produced. For this reason, we focused our research on management interventions that could increase SOC without external C inputs. A further

focus was on grasslands without livestock, with intensity gradients ranging from unfertilised mountain grasslands to well-maintained urban lawns. Such a wide range of management intensities cannot be found in forests or croplands but is unique for grasslands. It is therefore of uttermost importance to quantify and understand grassland management effects on ecosystem properties.

Apart from direct management interventions, also humaninduced climate change is likely to be a threat to SOC. Increasing temperatures are acknowledged to catalyse microbial activity and thus SOC mineralisation, inducing a climate-carbon cycle feedback loop (Davidson & Janssens, 2006). However, warming and CO₂ fertilisation will also affect plant production, which could counterbalance SOC mineralisation to some extent. Thus, how the ecosystem carbon balance and SOC will respond to climate change is highly uncertain (Conant et al., 2011). The aim of this synthesis work was to summarise and couple own recent studies backed up by further literature on effects of management and warming on SOC dynamics in European grassland soils. It is thus not a classical review paper but rather a compilation of studies that partly build on each other and give, when presented and discussed together, a comprehensive picture of relevant mechanisms in grassland SOC cycling. The work evolved from a keynote talk at the 28th General Meeting of the European Grassland Federation in Helsinki, Finland.

2 | EFFECT OF CUTTING FREQUENCY ON SOIL ORGANIC CARBON DYNAMICS IN URBAN LAWNS

The cutting frequency of grasslands can vary strongly due to climate and vegetation cover, and affects growth patterns, total net primary production (NPP) and aboveground-belowground carbon allocation of grasslands (Wohlfahrt et al., 2008). Mechanistic and quantitative understanding of cutting frequency effects on SOC stocks is limited, however. This might be related to the fact that experiments including cutting frequency are often combined with varying fertiliser additions. Kramberger et al. (2015) tested cutting frequency effects at equal fertiliser rates and did not find any effect on SOC stocks. The cutting interval varied between 2 and 12 weeks and the biomass was exported.

In the course of the Swedish LAWN project, we conducted a cutting frequency experiment in three Swedish cities (Gothenburg, Malmö and Uppsala) in order to analyse the differences between two lawn types in residential areas that were managed differently, i.e., as utility lawns and meadow-like lawns (Ignatieva et al., 2017; Poeplau et al., 2016). In all three cities, the unfertilised lawns were established along with multi-family housing in the beginning of the 1950s and were managed similarly since then. On average, the short utility lawns were mown every eighteen days (eight times per growing season), while meadow-like lawns were cut only once a year. Accordingly, utility lawns were dominated by small fast-growing, defoliation-tolerant species such as *Poa pratensis* (L.), *Agrostis capillaris* (L.) and *Lolium* spp. (L.), while the most abundant grass species in meadow-like lawns were tall, slow-growing species *Phleum pratense* (L.), *Alopecurus pratense* (L.)

and Arrhenaterum spp. In each of the three cities, three test sites were selected. At each test site, three plots were established on each lawn type. Soil samples for assessing SOC, total nitrogen, soil pH, soil texture and bulk density were taken to a depth of 20 cm using a thin auger. Net primary productivity (NPP) was determined by harvesting regrowth several days after each cutting event (utility lawns) or by determining total aboveground biomass before the cutting event (meadow-like lawns) and fitting a climate-driven vegetation model to the cumulative growth curve.

We found significantly higher SOC stocks in utility lawns as compared to meadow-like lawns (Poeplau et al., 2016). After an average of 62 years, the different lawn management caused a SOC stock difference of 7.8 \pm 14.8 Mg/ha (12%). Across nine sites, the mere difference in cutting regime thus led to SOC sequestration at a rate of 0.13 ± 0.24 Mg C ha⁻¹ year⁻¹ during six decades. This increase in SOC stocks correlated well with the increase in aboveground NPP. which amounted to 0.70 ± 0.51 Mg C ha⁻¹ year⁻¹ (24%; Figure 1). In this case, the combination of plant functional groups and cutting had led to an increase in aboveground biomass production and carbon inputs as well as an efficient nutrient recycling, since clippings were not removed. The study results highlighted that NPP, i.e. the amount of carbon that is assimilated by plants, is a primary driver of soil carbon dynamics. Other studies found unchanged or even decreased SOC stocks upon the increased cutting frequency with biomass removal (Balasubramanian et al., 2020; Kramberger et al., 2015), which might point to the fact that the found SOC sequestration was mainly achieved by leaving the clippings on site. Leaving the clippings on-site

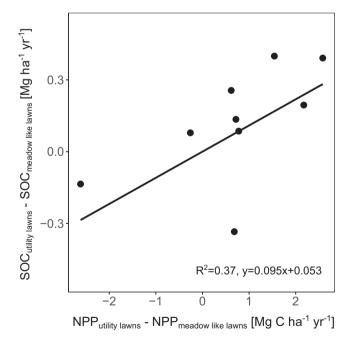


FIGURE 1 Average difference in soil organic carbon (SOC) stocks in 0–20 cm depth between utility and meadow-like urban lawns (divided by the time since treatment establishment, which was on average 62 years) as a function of the average difference in aboveground net primary production (NPP) for nine different sites in three Swedish cities (Adapted from, Poeplau et al., 2016)

might in turn stimulate N₂O emissions, which could potentially lead to a certain greenhouse gas trade-off of SOC sequestration. However, at the same time, we also detected significantly narrower soil C:N ratios in the utility lawns, indicating that N stocks were even more promoted by frequent cutting, although both systems were unfertilised. This can only be explained by a much more efficient N recycling in the utility as compared to the meadow-like lawns, with most likely less N-losses due to better synchronisation of N mineralisation and plant uptake. Generally, urban soils are among the most intensively managed soils (Trammell et al., 2020). The study showed that they can provide ideal study systems to understand management effects on ecosystem functioning. Beyond that, a better quantification of SOC and nutrient stocks and cycling in these soils is required in a rapidly urbanising world (Turner et al., 2004). This is important for reporting national greenhouse gas emissions as well as for the design of sustainable and climate-friendly urban areas.

3 | MINERAL FERTILISATION EFFECTS ON SOIL ORGANIC CARBON STOCKS

Besides cutting frequency, fertilisation with major plant nutrients is the most effective means to increase net primary productivity. Accordingly, mineral fertilisation might positively affect SOC stocks. In long-term cropland fertilisation experiments, Kätterer et al. (2012) found that approximately 1 kg/ha of nitrogen fertiliser sequestered 1 kg/ha SOC within 4-5 decades, which they related to increased C inputs. Also Conant et al. (2001) found slightly positive fertilisation effects on grassland SOC, analysing results of 40 different studies. At the same time, the major carbon input in managed and harvested grasslands is root-derived and mineral fertilisation is acknowledged to shift plant root:shoot ratios towards shoots (Hermans et al., 2006; Olff et al., 1994). Also, symbioses with mycorrhiza are less when plants are supplied with sufficient nutrients (Sochorová et al., 2016). The fertilisation effect on C input, and thus SOC, might therefore also be negligible or negative (Fornara et al., 2016; Sochorová et al., 2016). Also Li et al. (2014) found that subsoil SOC losses upon fertilisation in Alpine meadows were potentially driven by shifts in root:shoot ratios in plant biomass.

Another important driver of SOC dynamics is microbial anabolism, because a major proportion of stabilised SOC consists of microbial necromass and other products (Liang et al., 2017; Ludwig et al., 2015). Microbes have a relatively narrow, and globally well constrained stoichiometric range, with C:N:P ratios around 60:7:1 (Cleveland & Liptzin, 2007). Microbial growth is thus strongly dependent on nutrient availability (Manzoni et al., 2017). Alterations in microbial carbon use efficiency (CUE), i.e. the ratio of growth over total carbon uptake, could thus be an important driver of SOC dynamics in fertilised grasslands. Finally, fertiliser application will affect species richness and functional biodiversity, which can affect SOC to some extent (Lange et al., 2015). In consequence, SOC levels can either increase or decrease, as involved mechanisms are diverse and hardly quantifiable at the same time. All

together hampers the identification of key processes driving SOC dynamics in grasslands after changes in nutrient availability. For this reason, we identified and sampled a total of seven different long-term (>10 years) mineral fertilisation experiments to study effects on SOC stocks, potential litter decomposition, above-and belowground biomass and microbial metabolism (Poeplau, Helfrich, et al., 2018; Poeplau, Zopf, et al., 2018). Most of these experiments did not investigate belowground changes at all—neither biomass nor soil properties—but had a strong focus on the quality and quantity of aboveground biomass.

The experiments were located in central Europe, Germany (n=6) and the Netherlands (n=1) and comprised both shallow mountain grasslands as well as fertile floodplain grasslands. They covered a wide range of abiotic site properties and thus differed in natural productivity. Cutting frequency varied between two and four times and the length of the experiments ranged between 16 and 58 years. Soils were sampled to a maximum depth of 100 cm or until the bedrock, using a power-driven soil auger. Soil cores were split along fixed depth increments and vertically, to derive samples for root biomass quantification and for soil analyses.

For the topsoil (0-30 cm), we detected significant effects of PK, NPK and NPK+ (+ stands for enhanced NPK fertilisation) on SOC stocks, with sequestration rates of 0.28 (PK), 0.13 (NPK) and 0.37 (NPK+) Mg C ha⁻¹ year⁻¹ in 34 (PK, NPK) and 20 (NPK+) years. In contrast to Fornara et al. (2013), we did not detect a significant effect of N-only fertilisation on SOC stocks. In the case of NPK fertilisation, we found a significant correlation between the amount of N fertilised and the amount of C sequestered: 1.15 kg N was needed to sequester 1 kg C (Figure 2). Notably, sequestered C corresponded to the amount of C (1.16 kg C or 4.25 kg CO₂) that is emitted by N fertiliser production and not accounting for on-site (field) N₂O emissions (Edwards et al., 2017). In view of that, SOC sequestration may widely counterbalance NPK-fertilisation related emissions, but that cannot be viewed upon as climate mitigation measure. This might be different for PK fertilisation, which was found to have comparably positive effects on SOC stocks. The CO2 emissions related to production of P (0.54 kg CO_2 kg⁻¹) and K (0.42 kg CO_2 kg⁻¹) are much lower and PK fertilisation favours the abundance of legumes, which supply the grassland with extra nitrogen (Bordeleau & Prévost, 1994). In the investigated experiments, the proportion of legumes increased by 12% upon PK fertilisation, which is in line with other grassland fertilisation studies (Kacorzyk & Głąb, 2017; Spohn et al., 2016). Afterall, the positive effects of fertilisation on yields, on the one hand, and SOC sequestration, on the other hand, might lead to a better product-based greenhouse gas balance of fertilised, as compared to unfertilised grasslands. However, in such a calculation, on-site greenhouse gas emissions would have to be accounted for. The positive fertilisation effect on grassland biomass and thus C inputs appeared to be the most obvious explanation for increased SOC stocks. However, due to strong shifts in above- and belowground C allocation, root biomass tended to be lower in fertilised than in unfertilised plots. Furthermore, much of the aboveground biomass was harvested. We concluded that changes in input might

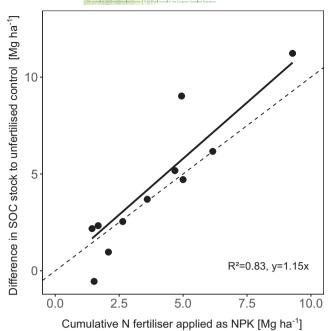


FIGURE 2 Soil organic carbon (SOC) stock changes (0–30 cm depth) in response to cumulative nitrogen fertilisation in seven Central European grassland fertilisation experiments over a period of up to 58 years. Regression (black line) is forced through origin; dashed line represents the 1:1 line (Adapted from Poeplau et al., 2018)

not be the only driver of SOC sequestration upon fertilisation, and hypothesised that fertilisation increased microbial CUE, i.e. growth over C uptake, being a major pathway of SOC stabilisation.

To test this hypothesis, we conducted an incubation experiment with two out of seven experiments (Poeplau, Helfrich, et al., 2018). Soils from the unfertilised and NPK-fertilised treatments were labelled with ¹⁸O water and incubated for 24 hr, after which respiration and microbial biomass were determined and the microbial DNA was quantified and analysed for the ¹⁸O content. In this way, it was possible to determine microbial growth under steady-state conditions (Spohn et al., 2016). Specific respiration was significantly decreased by fertilisation, while microbial growth doubled. In consequence, microbial CUE was 53 \pm 21% higher in fertilised soils as compared to unfertilised soils. Furthermore, CUE correlated negatively with substrate C:N ratio ($R^2 = 0.48$), which provided evidence that N availability was strongly driving microbial metabolism. The more N is available, the more C can be taken up by microbes (Manzoni et al., 2017). Typical microbial C:N ratio range is around 8 (Cleveland & Liptzin, 2007). It can thus be assumed, that the closer the C:N ratio of a substrate comes to that value, the more efficiently it can be used for microbial biosynthesis. Once C is taken up, and not respired, it can be further stabilised in the soil (Cotrufo et al., 2013; Perveen et al., 2014). A modelling exercise with all the seven fertilisation experiments using the introductory carbon balance model (ICBM) revealed that C input alone cannot explain SOC stock changes. We concluded that the microbial anabolic pathway is likely to have directly contributed to increased SOC stocks, which has been hypothesised but not directly proven in field experiments before.

4 | LEYS AND PERENNIAL COVER CROPS IN AGRICULTURAL CROP ROTATIONS

In the previous sections, it has been shown that increasing NPP, by either cutting frequency or fertilisation, has positive effects on SOC stocks. In croplands, another option to increase NPP is to maximise the duration of active vegetation cover (i.e. time of photosynthesis) and to minimise bare fallow period. This can be obtained by introducing perennial grasses into the crop rotation, either as the main crop or as a cover crop between two cash crops. In this way, the additional root-derived C input is specifically beneficial for SOC buildup (Bolinder et al., 2010; Rasse et al., 2005; Sokol & Bradford, 2019). In Swedish agriculture, the proportion of perennial grasses (leys) and green fallows in crop rotations increased from 32% in 1988 to 48% in 2014 (Poeplau, Bolinder, et al., 2015). In the same time period, three agricultural soil inventories have been conducted with SOC as a key target variable. In the first inventory, between 1988 and 1997, 3,146 locations were sampled to a depth of 20 cm, whereas this number was reduced to 2034 in the second and third inventory (2001–2007 and 2010-2018). Over this whole period, the average SOC content of Swedish agricultural soils increased from 24.8 to 26.7 g/kg, which equals a relative increase of 7.7%. From the first to the third inventory, SOC increased in 18 out of the 21 counties of Sweden. The increase in ley per county was the most important explanatory variable, confirming the importance of perennial grasses for SOC storage. This is in line with Panettieri et al. (2017), who also detected increased SOC in ley rotations and also highlighted the more efficient lignin preservation in aggregates of these soils as compared to continuously cropped soils. The doubling of the Swedish horse population since 1981, which mainly happened in the course of Swedish lifestyle changes, was identified as the most likely driver of increasing leys ($R^2 = 0.72$). Owning a horse for recreational purposes increased the demand for hay and established a new market for farmers, who could sell hay to the often wealthy horse owners at a good price. Approximately 1 ha of ley is needed to feed one horse per year, which means that 13% of the current Swedish agricultural land (cropland) is used for horses alone.

Another option to integrate grasses into agricultural crop rotations is the use of cover crops, also known as catch crops, which reduce nitrogen losses, soil erosion in regions where high autumn precipitation and intensive agriculture coincide. In recent years, the subsequent reduction in the fallow period has gained importance, and has shown to increase SOC stocks in arable systems (Poeplau & Don, 2018). In Nordic countries, grass species like ryegrass (Lolium perenne L.) or timothy (Phleum pratense L.) are often used as catch crops, undersown in the main crop. In three Swedish long-term experiments (16-24 years), we investigated the effect of undersown ryegrass on SOC stocks in 0-20 cm soil depth (Poeplau, Aronsson, et al., 2015). We found an average annual SOC sequestration rate of 0.32 ± 0.28 Mg C/ha across experiments, which matches the value of a global meta-analysis on cover crop effects on SOC (Poeplau & Don, 2018). The produced aboveground ryegrass biomass in the Swedish experiments ranged from 0.5 to 1 Mg drymass (DM) ha⁻¹ year⁻¹. A literature review within the same study revealed, that the growth of grass cover crops strongly depended on temperature, having an upper limit of about 7 Mg DM ha⁻¹ year⁻¹ at a mean annual temperature (MAT) of 16°C and a lower limit of around 1 Mg DM ha⁻¹ year⁻¹ in regions with MAT <7°C. Nonetheless, even at low MAT of 4°C test site in Southern Finland, undersown ryegrass and timothy had considerable yields and reduced N leaching (Känkänen & Eriksson, 2007). In consequence, in intensive cropping systems, perennial grasses have a great potential to improve soil fertility and enhance SOC stocks, while the opposite is true for forage-based cropping systems, which are changed into more cereal-based rotations (Bolinder et al., 2010).

5 | EXPERIMENTAL EVIDENCE FOR NEGATIVE WARMING EFFECTS ON GRASSLAND SOIL ORGANIC CARBON STOCKS AND SOIL STRUCTURE

Studying and quantifying potential warming effects on an ecosystem scale is challenging and costly. Temperature manipulation studies are thus often short-term and restricted to one or two warming treatments, threshold values or new steady-state situations unknown. This in turn hampers accurate model predictions on long-term warming effects (Conant et al., 2011).

Northern biomes, which store huge amounts of carbon and are strongly warmed, are likely to show the most pronounced response to climate change (Carey et al., 2016). In 2008, an earthquake shifted a geothermal channel to a mountain slope covered with unmanaged grassland and a small spruce plantation in the east of Reykjavik, Iceland (Sigurdsson et al., 2016). To analyse the effect of soil warming, on various ecosystem features, research plots of different warming intensities were setup at these grasslands. In 2014, approximately 6 years after the earthquake, the grassland soil was sampled to study changes in bulk soil SOC and SOC fractions. These fractions were isolated following the notion that certain stabilisation mechanisms in the soil, such as organo-mineral interactions, might lead to C pools that show a distinct response to warming. Five transects of six different warming intensities were sampled: ambient temperature, +0.6°C, +1.8°C, +3.9°C, +9.9°C, +16.3°C, +~40°C. The unwarmed grassland was dominated by common bent (Agrostis capillaris L.), common meadow grass (Poa pratensis L.), meadow horsetail (Equisetum pratense L.) and meadow buttercup (Ranunculis acris L.). Interestingly, species composition changed only gradually in warming intensities >10°C, with increasing abundance of mosses. The +40°C plots were entirely vegetated by mosses, so that C input can be considered negligible at this warming intensity. Soil samples in 0-10 cm (topsoil) and 20-30 cm depth (subsoil) were analysed (Poeplau et al., 2017).

Soil warming of 0.6°C tended to increase topsoil and subsoil SOC contents by 22 \pm 43% and 27 \pm 54%, respectively (not significant), while further warming led to significant exponential depletion of SOC. As much as 79 \pm 14% (topsoil) and 74 \pm 8% (subsoil) of SOC

was lost in six years only (Figure 3). Drastic changes in SOC were also observed in less unrealistic warming intensities: +3.9°C reduced SOC by 27 \pm 46 and 29 \pm 40%, without strong changes in species composition. Those results demonstrated that potential changes in NPP could not buffer increased microbial activity and associated SOC decay. Indeed, soil warming did neither increase plant productivity nor change ecosystem stoichiometry (plants and soil C:N ratios). This suggested that nitrogen was lost at a similar rate as carbon. However, under climate change, this might have been slightly different, since (a) in this experiment warming came from below and thus plants were most likely less favoured than soil microbes, (b) global warming is associated with CO₂ fertilisation of plants, which was not given and (c) warming happened at once, not gradually. Nonetheless, the very strong and comparatively long soil warming revealed interesting features of SOC response to warming; e.g. SOC associated to stable aggregates as well as the aggregates themselves were almost entirely depleted (Figure 3). We thus hypothesised, that warming might have devitalised biotic aggregate binding mechanisms such as fine roots, mucilage or arbuscular mycorrhiza fungi, which lead to decreased SOC stabilisation. However, also the opposite may be the case; loss of SOC might have caused aggregate break-down, since organic matter as such is acknowledged to stabilise aggregates (Tisdall & Oades, 1982). In any case, the extreme warming treatments proved that loss of SOC is associated with strong soil structural changes, which in turn might feedback to plant productivity. On top, Rock-Eval thermal analysis was used to determine shifts in organic matter quality with warming (Poeplau et al., 2019). The analysis revealed that warming-resistant organic matter was strongly depleted in hydrogen but enriched in oxygen. This matched the results of long-term bare fallow experiments (Barré et al., 2016), who additionally found that those compounds depleted in hydrogen also

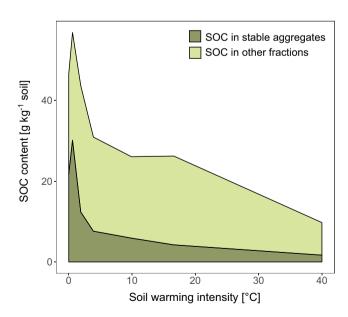


FIGURE 3 Response of soil organic carbon content (0–10 cm depth) to six years of geothermal soil warming on a subarctic grassland (Adapted from Poeplau et al., 2017) [Colour figure can be viewed at wileyonlinelibrary.com]

had the lowest energy densities. SOC persistence in the soil might thus be governed by energetic barriers for microbes to some extent. Despite the fact that the geothermal experiment is located in Iceland on a very specific soil (Andosol), it is of high value for monitoring ecosystem responses to warming (www.ForHot.is). In a neighbouring valley of the experimental site, a comparable but much longer warmed grassland soil (>50 years) has been discovered. This opens unique possibilities to study warming effects as a function of time in a chronosequential approach. (Walker et al., 2019) compared the responses of a wide range of soil and ecosystem variables of both grasslands and found that the majority of variables "overreacted" at the beginning of warming, since the more recently warmed grassland often showed stronger or at least equal responses as compared to the longer warmed site. This indicated that short-term warming experiments, which due to practicality issues are still the most abundant ones, should be interpreted with care and not extrapolated to longer timescales (Crowther et al., 2016).

6 | CLIMATE CHANGE EFFECTS ON SOIL ORGANIC CARBON STOCKS OF GRASSLANDS IN SOUTHERN GERMANY

Although less pronounced than in arctic and subarctic regions, climate change is also affecting ecosystems and agriculture in temperate regions. To estimate SOC stock development in Southern German grassland soils, we applied the RothC model to a total of 30 permanent grassland sites in Bavaria (Wiesmeier et al., 2016). Current SOC stocks and fraction (pool) distribution were known from earlier studies and carbon inputs were estimated by combining regional allocation coefficients and management information from each individual site. For each point, we run a climate model ensemble to predict temperature increase until the end of the century (A1B scenario, +3.3°C).

Assuming unchanged management and carbon inputs, the model projected an average decrease in SOC stocks of 7.5 Mg C/ha (11%) until the end of the 21st century. This was in line with other modelling studies (Senapati et al., 2013; Xu et al., 2011). To compensate for C losses caused by increased SOC mineralisation, the required additional C input would be +26% compared to current C inputs. This highlight, that SOC sequestration under climate change will be a challenge.

7 | INTERACTIVE EFFECTS OF CLIMATE CHANGE AND MANAGEMENT—WAYS FORWARD IN GRASSLAND RESEARCH

Agricultural management as well as climate change are the two major, more or less direct anthropogenic threats to grassland ecosystems as a whole and their SOC stocks. The body of scientific literature on both these topics is still limited, but constantly growing. At the same time, not much attention is paid to the fact that both

will also have interactive effects on SOC dynamics. For example, up to date warming experiments are mostly conducted in natural ecosystems. Management, e.g. in the form of fertilisation, liming, cutting and grazing has been shown to affect many ecosystem features, including plant and microbial communities (Grayston et al., 2004) as well as organic matter quantity and quality. It is likely, that also the response to warming of intensively managed systems will differ from that of unmanaged, or less intensively managed grasslands, which could ultimately result in different SOC loss rates. Likewise, climate change will also come along with increased droughts and also the resilience to such weather extremes is management-dependent (Ingrisch et al., 2018). Also, climate change will lead to adapted land use and management in the near future. One example might be an increasing establishment of trees on pasture soils for shaded grazing, which might affect grassland NPP and SOC dynamics. In subarctic regions, agricultural activity can be expected to grow into pristine ecosystems that have partly been permanently frozen for millennia (Grünzweig et al., 2015; Keuper et al., 2020). All of these topics are aspects of climate change and agricultural management interactions and are certainly understudied. For realistic estimates of future SOC sequestration potentials in grassland soils, a better understanding of such interactive effects is crucial.

8 | CONCLUSIONS

Globally, soil organic carbon sequestration as a negative CO2 emission technology is high up on the political agenda. Also, countless private initiatives form up to promote additional SOC storage by selling certificates. It is debatable, if importing C from other systems, e.g. in the form of organic manure or compost, can count as a measure of net C storage, since that C is lost elsewhere. Therefore, we focused our research on measures to increase SOC stocks without external C inputs. The studies suggested, that the growth of perennial grasses in crop rotations has multiple benefits and favours SOC storage due to high belowground C inputs. In temperate, undegraded grasslands, SOC stocks are usually quite high. Nevertheless, we were able to show that intensification in the form of cutting frequency and increased mineral fertilisation can have positive effects on SOC stocks. The importance of N for C storage was ubiquitous. However, this implies, that SOC storage is often accompanied by climate-relevant trade-offs such as high CO2 emissions for fertiliser production or in-situ greenhouse gas emissions. Still, the quantity and quality of the harvested biomass are of uttermost importance in managed grasslands, so potential trade-offs and benefits have to be encountered in the most sustainable way. In this respect, increasing the share of legumes to fix atmospheric nitrogen and increase microbial anabolism might be a way forward. Other multi-beneficial options, such as planting trees on grasslands remain understudied regarding their effects on SOC. Finally, any effort to increase SOC stocks to mitigate climate change will be hampered by climate change as such, which was found and predicted to deplete SOC and soil structure. Grasslands have a wide range of management intensity. It is likely, that management intensity will play a role in the ecosystems' response to climate change, which should be studied in depth. Urban grasslands are among the most intensively managed. Apart from the fact that they can provide ideal experimental systems, urban grasslands can be expected to grow globally, so that greenhouse gas fluxes and SOC dynamics need to be better quantified in these designed ecosystems.

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AUTHOR CONTRIBUTION

Christopher Poeplau: Conceptualization (lead); Writing-original draft (lead).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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