Geoderma 442 (2024) 116807

Contents lists available at ScienceDirect

Geoderma

journal homepage: www.elsevier.com/locate/geoderma

Rapid loss of organic carbon and soil structure in mountainous grassland topsoils induced by simulated climate change

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ARTICLE INFO

Handling Editor: C. Rumpel

Keywords:
Plant-soil mesocosms
Soil aggregates
Grassland management
Mountainous soils

ABSTRACT

Mountainous grassland soils are considered one of the most unique biological hotspots, rich in organic carbon (OC). At the same time, they are exposed to great threats, as climate warming is more pronounced in mountainous regions than in lowland areas. In this study, we assessed the effect of simulated warming (+1K, +2K, and + 3 K) on OC stocks and soil structure in grassland soils of the Northern Limestone Alps in Germany by translocating plant-soil mesocosms from high- (1260 m a.s.l., Rendzic Phaeozem) and mid- (860 m a. s. l., Haplic Cambisol) to low-elevation (600 m a.s.l). Plant-soil mesocosms were exposed to both extensive and intensive grassland management practices. Four years after translocation, we observed a rapid decrease of topsoil SOC stocks under intensive (−1.0 t C ha yr^{-1}) and extensive management (-2.2 t C ha yr^{-1}), under the highest temperature increase. Intensive management with about 1 t C ha^{-1} yr^{-1} higher manure C return than extensive management (1.6 vs. 0.8 t C ha^{-1} yr^{-1} intensive and extensive, respectively) may explain the difference in SOC losses between different management treatments. Under both management practices, the loss of SOC was mainly associated with a decrease of large macroaggregates, at both management practices. In addition, different aggregate specific OC loss rates resulted in an altered distribution of OC among the aggregate size classes. Our study provides evidence that simulated climate change induced a rapid and substantial decline of SOC in mountainous, OC-rich grassland soils, which may be attributed to decreased physical OC protection within large macroaggregates. Optimized grassland management in form of increased application of organic fertilizers could only partially offset the SOC loss by improved formation of small macroaggregates.

1. Introduction

Climate warming in Central and Northern European mountainous regions is far stronger than anywhere else (Bojko and Kabala, 2017; Adler et al., 2022). In fact, the European Alps experienced a 2 °C increase in annual temperatures during the 20th century, with a marked rise since the early 1980 s, a trend that is expected to continue or even accelerate in the coming decades (Wagner et al., 2013; Pepin et al., 2015; Kiese et al., 2018). This warming increases the vulnerability of Alpine and pre-Alpine grassland soils, which are considered one of the most unique biological hotspots and represent one of the largest soil organic carbon (SOC) reservoirs in Central Europe. In fact, grassland soils in the European Alps store exceptionally high amounts of SOC with up to 260 Mg ha^{-1} (Leifeld et al., 2009; Seeber et al., 2022). However, these large organic matter (OM) reservoirs contain high proportions of unprotected labile OM (Leifeld et al., 2009; Budge et al., 2011; Kühnel

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https://doi.org/10.1016/j.geoderma.2024.116807
Received 25 July 2023; Received in revised form 15 January 2024; Accepted 30 January 2024
Available online 6 February 2024

et al., 2019), and a loss of this SOC may have dramatic ecological and socio-economic consequences for alpine regions (Schlingmann et al., 2020; Adler et al., 2022). High SOC and total nitrogen (tN) contents facilitate economic soil functions such as high forage production and quality (Rabot et al., 2018; Berauer et al., 2020) while also providing different ecological functions such as water and nutrient retention and a high diversity of plants and soil organisms (Wilson et al., 2012). As a result, the interest of studying impacts of changing climate conditions on SOC and N cycles and budgets in mountainous grassland ecosystems has recently increased (Yang et al., 2008; Hoffmann et al., 2014; Chen et al., 2016). Climate change was shown to alter the SOC dynamics of mountainous soils, from the modification of plant C inputs and respiration losses as well as from changes in various physico-chemical mechanisms of soil organic matter (SOM) protection (Puissant et al., 2017). Furthermore, Crowther et al. (2016) found that the effects of warming are contingent on the size of the initial SOC stock, with considerable losses occurring in high-latitude areas, which can have potentially severe implications also for SOC storage in high elevation alpine regions (Sjögersten et al., 2011).

As management (e.g., cutting and organic fertilization regimes) is a further controlling factor on ecosystem carbon exchange, the studies on SOM dynamics in grassland soils should focus on the interactive effects of climate change and management practices (Poeplau, 2021). Climate-smart management of mountainous grassland soils intends to increase both forage production and SOC storage (Garcia-Franco et al., 2019; Berauer et al., 2020). However, the knowledge of the effects of management on SOC stocks in mountainous grasslands is limited and climate change is expected to counterbalance the efforts of SOC build-up to some extent (Poeplau, 2021). Although SOC dynamics in mountainous grasslands are primarily controlled by climatic conditions (Doetterl et al., 2015) and land management practices (Sebastiá 2004), there is still uncertainty about the direction and magnitude of SOC stock changes and the contribution of each of the main drivers to changes in SOC stocks. In fact, there is no consistent trend across Europe regarding the development of SOC stocks of grassland soils in the last decades (Kühnel et al., 2019). Because SOC stock changes are affected by the influence of human activities over centuries, it is difficult to distinguish between the effects of climate warming and human induced changes of grassland management (Cannone et al., 2007; Li et al., 2016; Peters et al., 2019), which can interact in either a synergistic or antagonistic way (Berauer et al., 2020). Moreover, even changes of SOC stocks are not readily detectable due to the spatial heterogeneity and overall high level of SOC in mountainous soils as compared to often two order of magnitude lower annual OC rate changes (Bojko and Kabala, 2017). Given these limitations of detecting bulk SOC changes in soils, water-stable aggregate size fractions have been identified as promising indicators for predicting SOC changes in mountainous soils (Cécillon et al., 2010; Gu et al., 2016; Garcia-Franco et al., 2021). Since macroaggregate stability and formation are representing "functional soil characteristics", soil structural properties in particular may be appropriate indicators for SOC dynamics than bulk SOC changes (Rabot et al., 2018; Wiesmeier et al., 2019).

Climate warming experiments are a valuable approach to gain insights on how SOC and soil structural properties respond to climate change (Sjögersten et al., 2011). Space-for-time approaches, particularly the translocation of plant-soil mesocosm along elevation gradients, are among the most powerful "natural experiments" and have provided helpful information on the responses of SOC and associated aggregation to climate change (Melillo et al., 2002; Djukic et al., 2010; Hou et al., 2021). However, to date only a few studies have been carried out on Alpine grassland soils (Volk et al., 2016; Puissant et al., 2017). Moreover, the combination of plant-soil mesocosm translocation experiments including different land management practices, e.g., frequency and intensity of organic fertilization and cutting/ grazing events, is still scarce (Soussana et al., 2004; Ward et al., 2016; Wang et al., 2021). In general, the knowledge on SOC storage as affected by grassland management intensity is limited (Soussana et al., 2007; Schlingmann et al., 2020). Zeller et al. (1997), and Bitterlich et al. (1999) found no relationship between the intensity of management and SOC stocks in Alpine grasslands.

In order to disentangle the effects of climate change and grassland management intensity on SOC, we conducted a climate manipulation experiment based on the translocation of plant-soil mesocosms, from high to low elevations in the Northern Limestone Alps of Germany. Relocated (control), and translocated (climate change) plant-soil mesocosms were intensively extensively managed for four years. We aimed specifically to determine and assess (i) how different degrees of climate warming are altering SOC stocks, how ii) these changes differ between different management intensities, and iii) if changes in soil aggregation and associated OC can help to more mechanistically explain changes of bulk OC storage and serve as diagnostic indicators.

2. Material and methods

2.1. Site description

The study sites were located in the Northern Limestone Alps of Bavaria (Germany). We selected three experimental sites with grassland soils at different elevations: i) Esterberg at 1,260 m a. s. l. (11.16° N, 47.52° N); ii) Graswang at 860 m a. s. l. (11.03° E, 47.57° N) and iii) Fendt at 600 m a. s. l. (11.07° E, 47.83° N). All sites were located in flat terrain and represented typical soils in the area, developed from calcareous and dolomitic parent material (Garcia-Franco et al., 2021). The soils at the highest elevation (Esterberg, Rendzic Phaeozem, IUSS Working Group WRB, 2015) were characterized by exceptionally high SOC and total nitrogen (tN) contents of 188.9 mg g^{-1} and 18.8 mg g^{-1}, respectively (Garcia-Franco et al., 2021). Soils at the mid-elevation (Graswang, Haplic Cambisol) were less rich in SOC (133.9 mg g^{-1}) and tN (12 mg g^{-1}). The mean annual temperature is 6.0 °C in Esterberg, 7.0 °C in Graswang, and 9.0 °C in Fendt. The average annual precipitation is 1,400 mm, 1,347 mm, and 956 mm in Esterberg, Graswang, and Fendt, respectively (Schlingmann et al., 2020). The plant community composition was typical for montane pastures of the Northern Limestone Alps with Festuca pratensis, Huds; Agrostis capillaris, L.; Carum carvi, L; and Ranunculus acris, L. as the most dominant species. Notably only about 8 % of the species were legumes, particularly Trifolium pratense, L; and Trifolium repens, L. More detailed information on plant communities can be found in Berauer et al. (2019). Prior to the experiment management at the Esterberg site was extensive with 1–2 cuts, occasional organic fertilization, and moderate grazing (Table 1). The experimental sites Esterberg and Graswang were initially sampled in spring 2016 at three blocks per site with an area of around 50 m^2. Soil initial characteristics were described in our previous study (Garcia-Franco et al., 2021). Soil samples were taken at 0–5 and 5–15 cm soil depth for analysis of physical and chemical soil properties as well as for vegetation composition (Table 1). At the same plots soil–plant mesocosms (N = 4) i.e. intact cores of 30 cm diameter and 40 cm height were excavated (Schlingmann et al., 2020, Fig. 1), resulting in a total number of 12 (3x4) and 18 (3x6) mesocosm at Graswang and Esterberg sites. There were no barriers to the surrounding soil at the bottom in order to facilitate water movement, development of roots etc. The plant-soil mesocosms were re-introduced and translocated (N = 6) within the cylinders (there was a side barrier) downslope the elevation gradient in order to simulate warming + 1 K from high (Esterberg, 1,260 a. s. l.) to mid-elevation (Graswang, 860 m a. s. l.), +2 K from mid (Graswang, 860 m a. s. l.) to low elevation (Fendt, 600 m a. s. l.) and + 3 K from high (Esterberg, 1,260 m a. s. l.) to low-elevation (Fendt, 600 m a. s. l.), Fig. 1). In addition, mesocosm (N = 6) were re-located at the sites of excavation as control treatment (Control-1,260, corresponding to the relocation Esterberg to Esterberg; Control-860, corresponding to the relocation Graswang to Graswang). Consecutively, half (N = 3) each of the re-located and translocated mesocosms were exposed to extensive or

Table 1
Description of site and management conditions at the two different grassland sites of relocated and translocated soil–plant mesocosms.

	Esterberg	Graswang	Fendt
Elevation (m a. s. l.)	1260	860	600
MAP (mm)	1400	1347	956
MAT (°C)	6.0	7.0	8.9
Soil type (IUSS Working Group WRB, 2015)	Rendzic Phaeozem	Haplic Cambisol	Fluvisol
Parent material	Calcareous and dolomitic	Calcareous and dolomitic	Calcareous and dolomitic
Proportion of grass/ legume/herbs species (%)	59/10/31	57/5/38	90/8/2
Management history*			
Cutting frequency (times per year)	1	2	4–5
Grazing	*moderate in summer*	moderate autumn	none
Manure application frequency (times per year)	1 x farmyard manure	occasional slurry	4–5
Management practices during the experiment**			
Extensive management			
Fertilizer application rate (C/N/ P_2O_5 t ha^{-1} yr^{-1})	0.795/0.090/ 0.013	0.795/0.090/ 0.013	0.795/0.090/ 0.013
Cutting frequency (times per year)	2	2	2
Intensive management			
Fertilizer application rate (C/N/ P_2O_5 t ha^{-1} yr^{-1})	1.598/0.167/ 0.025	1.717/0.182/ 0.027	1.717/0.182/ 0.027
Cutting frequency (times per year)	4–5	4–5	4–5

* Initial soil conditions are corresponding with the values obtained before starting the experiment before any perturbation of the soil (implementation of mesocosms into the soil, translocations, and management practices) in 2016 (Garcia-Franco et al., 2020).

** During 4 years after the plant-soil mesocosms translocations (+1K, +2K, +3K, Control 1260 and Control 860) and the immediately implementation of extensive and intensive management practices.

intensive management, i.e., differing in frequency of cutting and cattle slurry application events (Table 1). After four years in July 2020, soil samples from three replicated plant-soil mesocosm per treatment were collected from two soil depths (0–5 and 5–15 cm), with replicates always originating from the three different sampling plots per site. The soil samples were taken from the centre of each translocated mesocosm to minimize edge effects. In total, 60 undisturbed metal soil cylinders with a volume of 98.175 cm^3, and a height of 4 cm were taken to study soil aggregation (5 climate conditions x 3 mesocosms x 2 management practices x 2 soil depths). From the same mesocosms a total of 180 undisturbed metal soil cylinders (5 climate conditions x 3 mesocosms x 3 replicates per mesocosm x 2 management practices x 2 depths) were taken for bulk density measurements. In the same way, soil samples were additionally taken for determination of SOC and tN and basic soil properties.

2.2. Soil analyses

2.2.1. Determination of basic soil properties

The soil samples were air-dried, sieved to < 2 mm, and analysed in the laboratory in triplicates. The pH and electrical conductivity (EC) were determined in a soil–water suspension (1:5). Soil bulk density was calculated from the oven-dry mass (105 °C, 24 h) and corrected for the content of coarse fragments > 2 mm.

2.2.2. Separation of water-stable soil aggregates

To separate aggregate-size classes a modified wet sieving procedure adapted from Elliott (1986) was conducted and four aggregate classes were separated: (i) > 2000 µm (LM: large macroaggregates), (ii) 250–2000 µm (SM: small macroaggregates), (iii) 63–250 µm (m: microaggregates), and (iv) < 63 µm (s + c: silt + clay-sized particles). The mean weight diameter (MWD), calculated by summing up the product of aggregate fractions (Xi) and mean diameter for each class (Wi), was used to express aggregate size distribution (Kemper and Rosenau 1986):

$$MWD = \sum_{i=1}^{n} Xi^{*}Wi$$

2.2.3. Organic c and total N determination

The total C (TC) and total N (tN) concentrations of bulk soils and aggregate size classes were determined using an Elemental Analyzer (Elementar, VarioMax cube, Langenselbold, Germany). Inorganic C (IC) was determined in the same way after heating the samples in a muffle furnace (Carbolite, ELF 11/6B, Germany) at 550 °C for 4 h to remove OC. Finally, the SOC content was calculated as the difference between the TC and IC content. The samples were analysed in triplicates. The SOC and N stocks (t/ha) were calculated using following equation:

$$\text{SOC} = \sum_{n}^{i=1} \text{SOCci*BDi*thi*}\left\{1 - \frac{\text{CPi}}{100}\right\}$$

where i represents each sampled depth of the soil profile, SOCc is the organic carbon concentration (g kg^{-1}) of the fine earth (<2 mm), BD is the soil bulk density (g cm^{-3}), thi is the thickness (m) of each sampled depth, and CP is the rock fragment content (volume percentage of particles > 2 mm). In 2020, four years after the beginning of the experiment, we calculated SOC and N stocks from BD and SOC/tN concentration using the equivalent soil mass (ESM) method according to (Wendt and Hauser (2013) and von Haden et al. (2020). The ESM method was applied to avoid/correct for potential soil perturbation as result of the translocation of mesocosms and the change in land-use intensity. For the ESM method, we used the re-located plant-mesocosms as references (Supplementary Table 1A).

2.3. Statistical analyses

All data were analysed using the IBM SPSS statistics 23.0 software (SPSS Inc., Chicago, Illinois). Prior to the analyses, normal distribution of the data was assessed using the Kolgomorov-Smirnov test and the homogeneity of variances with the Levene test. To assess differences of soil variables associated with different climate conditions, one-way analyses of variance (ANOVA) were conducted considering the translocation of mesocosms from high- to mid- and to low-elevation (Esterberg) and from mid- to low elevation (Graswang) and soil depth as fixed factors. To compare the different management practices (intensive vs. extensive management) and soil depths, first, we considered management and depth as fixed factors., Betweenelevations and depths were identified at the 0.05 probability level of significance using Tukey's test. When the data did not follow a normal distribution, we used the non-parametric Kruskal-Wallis's test followed by a pairwise comparison of groups to compare elevations and depths (0.05 probability level).

3. Results

3.1. Re-located control plant-soil mesocosms

3.1.1. High elevation site (Esterberg; 1,260 m a.s.l.)

Compared to initial conditions, after four years, the re-located plant-soil mesocosms at the high elevation (Esterberg, 1,260 m a. s. l.) showed a significant decrease of the bulk density by 16 % (0–5 cm) to 40 % (5–15 cm), and a significant decrease of MWD under both extensive

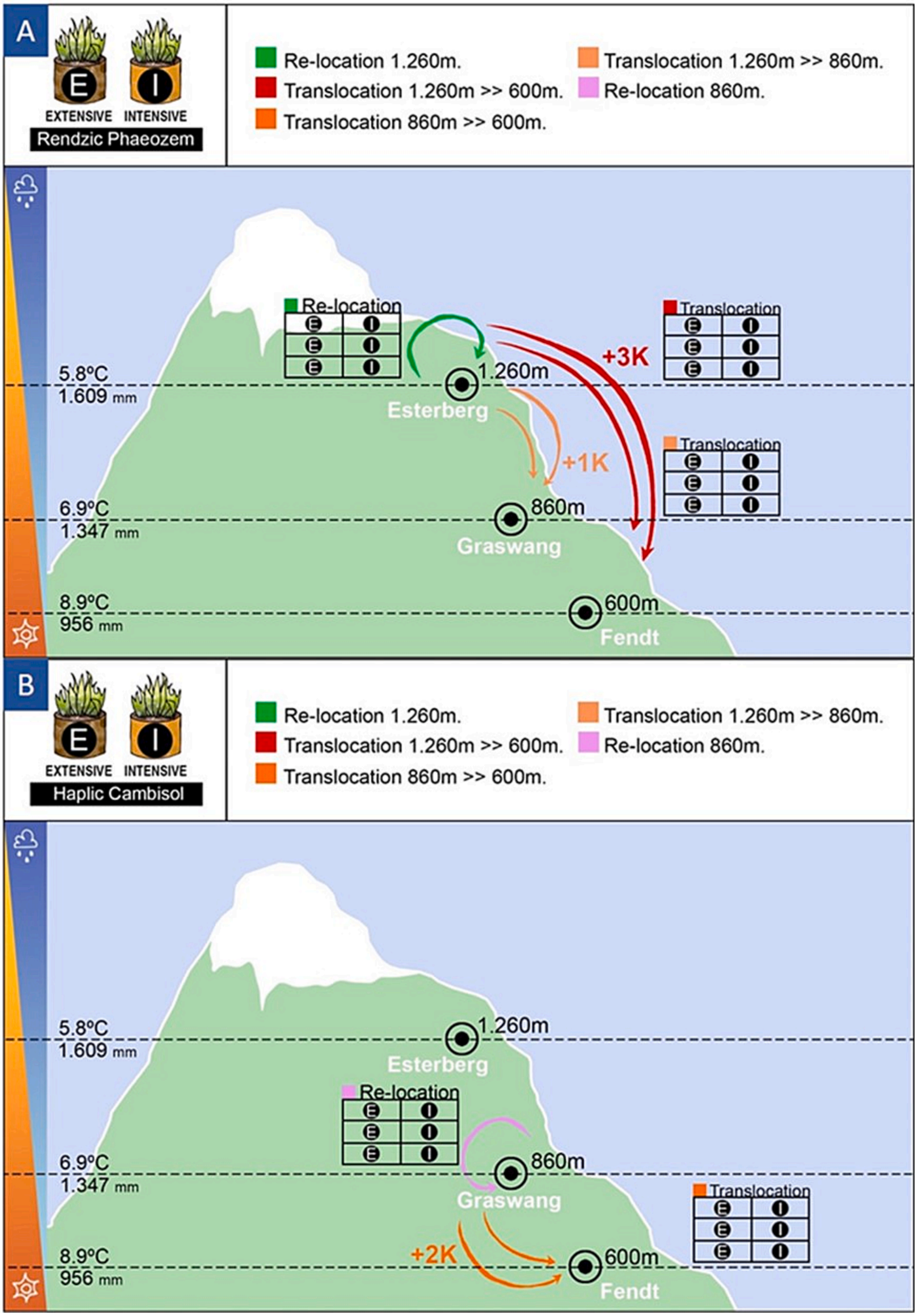

Fig. 1. A simplified scheme of the study design: **A)** Esterberg (1,260 m a. s. l.) where Rendzic Phaeozem plant-soil mesocosms were re-located (green color); and translocated from i) high (1260 m a. s. l.)- to mid-elevation (860 m a. s. l.) as + 1 K; in orange color; ii) and to low- elevation (600 m a. s. l.) as + 3 K; in red color; under extensive and intensive management practices. **B)** Graswang (860 m a. s. l.) where Haplic Cambisol plant-soil mesocosms were re-located (lila color); and translocated from i) mid (860 m a. s. l.)- to low-elevation (600 m a. s. l.) as + 2 K; in intensive orange color; under extensive and intensive management practices. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(36–55 %) and intensive (36–43 %) management, respectively (Supplementary Table 2A). No significant changes of SOC and tN concentrations were detected neither for intensive nor for extensive management at 0–5 cm soil depth. At 5–15 cm depth, the SOC concentration significantly increased by 28 % and 31 % under extensive and intensive management, respectively, while the tN concentration increased by 24 % under both management practices (Supplementary Table 2A). However, no differences were found in the C:N ratio at 0–5 and 5–15 cm soil depth. SOC stocks significantly decreased from 42.0 ± 1.2 to 37.2 ± 3.3 (extensive management) and to 34.7 ± 1.1 t ha^{-1} (intensive management) in the topsoil. The tN stocks showed the same trend as SOC stocks (Supplementary Table 2A). The proportion of LM significantly decreased by 23 % and 46 % at 0–5 cm soil depth under extensive and intensive management, respectively (Supplementary Fig. 1A-A). Below 5 cm soil depth no significant changes in the percentage of LM were detected. The proportions of SM and s + c fractions increased in both soil depths (Supplementary Fig. 1A-B). In the topsoil, the OC and tN concentrations of the s + c fraction increased for both management intensities compared to the initial status (Supplementary Fig. 3A-A). At 5–15 cm soil depth, the OC content in LM was significantly higher under extensive management compared to intensive management (Supplementary Fig. 3A-B). No changes in tN concentrations in aggregate size-classes were observed (Supplementary Fig. 3A–C and 3A-D).

3.1.2. *Mid elevation site (Graswang; 860 m a.s.l.)*

In contrast to re-located mesocosms at the high elevation (Esterberg, 1,260 m a.s.l.), the re-located mesocosm at the mid-elevation (Graswang, 860 m a.s.l.) showed an increase of bulk density by 25 % under extensive management and by 50 % under intensive management in the topsoil compared to the initial status at the beginning of the experiment (Supplementary Table 3A). At 5–15 cm soil depth, bulk density increased by 20 % under both management practices. The MWD decreased by 42–34 % under extensive management and by 39–32 % under intensive management at 0–5 and 5–15 cm soil depth, respectively. Moreover, a decrease of SOC concentration by 12 % and by 14 % was observed in topsoil under extensive and intensive management, respectively (Supplementary Table 3A). The tN concentration decreased by 8 % under intensive management, whereas under extensive management no significant changes were detected (Supplementary Table 3A). Regarding SOC and tN stocks, no significant changes were observed after four years of the re-location (Supplementary Table 3A). For aggregate-size classes, a decrease of OC concentration in the s + c fraction in the topsoil was detected, independent of the management intensity (Supplementary Fig. 4A-A). Moreover, OC concentration in the SM was higher under intensive management compared to extensive management in the topsoil (Supplementary Fig. 4A-A). At 5–15 cm soil depth (Supplementary Fig. 4A-B), we found the opposite trend in the OC content of SM than in the topsoil. The tN content of LM decreased in the re-located mesocosms at 0–5 cm soil depth under both extensive and intensive management (Supplementary Fig. 4A–C).

3.2. *Translocated Plant-Soil mesocosms from high elevation (+1K and + 3 K)*

3.2.1. *Bulk density, SOC, tN concentrations and stocks*

After four years of the plant-soil mesocosms translocation from high (Esterberg, 1,260 m a.s.l.) to mid (Graswang, 860 m a.s.l., +1K) and low elevation (Fendt, 600 m a.s.l., +3K), bulk density increased by 33–67 % under both intensive and extensive management at 0–5 cm soil depth (Table 2). At 5–15 cm soil depth bulk density decreased by 20 % at + 1 K warming under extensive management and increased by + 25 % at + 3 K warming under intensive treatment. In the topsoil, the SOC concentration under both management intensities was not significantly different compared to the control at + 1 K warming but decreased by 26 % and 13 % at + 3 K warming under extensive and intensive management,

Table 2
Soil properties of a Rendzic Phaeozem at 0–5 and 5–15 cm soil depth after four years of exposure to climate change (by translocation) and implementation of extensive vs intensive management practices from high (1260 m a. s. l.)- to mid-elevation (860 m a. s. l.) as + 1 K; and from high (1260 m a. s. l.)- to low-elevation (600 m a. s. l.) as + 3 K. As control we used plant-soil mesocosms that were re-located from Esterberg to Esterberg (Control 1260): BD (bulk density), concentrations of OC (organic C), tN (total N), C: tN ratios of bulk soil, MWD (Men weight diameter), and OC and tN stocks. Numerical values are means ± standard deviation. Different letters indicate significant differences between the plant-soil translocated mesocosms in each management practice. (Tukey's test, P < 0.05).

Soil properties	Extensive			Intensive		
	Control 1260	Translocation		Control 1260	Translocation	
		+ 1 K	+ 3 K		+ 1 K	+ 3 K
0–5 cm						
BD (g cm^{-3})	0.3 ± 0.0b	0.4 ± 0.0a	0.4 ± 0.0a	0.3 ± 0.0b	0.4 ± 0.0ab	0.5 ± 0.0a
OC (mg g^{-1})	208.9 ± 11.0a	190.2 ± 11.3a	154.4 ± 10.4b	194.8 ± 5.9a	187.8 ± 6.9a	168.7 ± 5.9b
tN (mg g^{-1})	20.3 ± 1.1a	18.6 ± 1.2a	15.0 ± 0.9b	18.8 ± 0.8a	18.5 ± 0.6a	16.6 ± 0.6a
C: tN ratio	10.3 ± 1.3a	10.2 ± 1.4a	10.3 ± 1.5a	10.4 ± 1.0a	10.2 ± 1.3a	10.2 ± 1.7a
MWD	1.9 ± 0.3a	2.1 ± 0.3a	1.5 ± 0.3b	2.4 ± 0.0a	2.1 ± 0.2ab	1.9 ± 0.0b
OC stock (t/ha)	37.2 ± 2.5a	34.1 ± 1.7a	28.9 ± 3.0b	34.7 ± 1.1a	33.6 ± 1.5a	30.7 ± 0.1b
tN stock (t/ha)	3.6 ± 0.3a	3.3 ± 0.2ab	2.8 ± 0.3b	3.3 ± 0.1a	3.3 ± 0.2a	3.0 ± 0.1b
5–15 cm						
BD (g cm^{-3})	0.5 ± 0.0a	0.4 ± 0.0a	0.5 ± 0.0a	0.4 ± 0.0a	0.4 ± 0.0a	0.5 ± 0.1a
OC (mg g^{-1})	165.9 ± 14.3a	167. 5 ± 14.2a	138.7 ± 5.6b	169.9 ± 9.6a	162.1 ± 3.8a	152.5 ± 10.0a
tN (mg g^{-1})	17.1 ± 2.2a	17.1 ± 1.5a	13.9 ± 0.6b	17.2 ± 1.2a	17.7 ± 0.6a	15.4 ± 1.0a
C: tN ratio	9.7 ± 1.1a	9.8 ± 0.8a	10.0 ± 1.1a	9.9 ± 1.0a	9.2 ± 1.0a	9.9 ± 0.9a
MWD	2.7 ± 0.2a	2.4 ± 0.2a	2.4 ± 0.1a	2.7 ± 0.1a	2.4 ± 0.2a	2.3 ± 0.2a
OC stock (t/ha)	71.7 ± 11.3a	72.3 ± 5.3a	65.7 ± 3.7a	73.6 ± 4.1a	70.2 ± 5.1a	71.2 ± 3.4a
tN stock (t/ha)	7.4 ± 1.5a	7.4 ± 0.7a	6.6 ± 1.0a	7.5 ± 0.6a	7.7 ± 0.8a	7.2 ± 0.4a

respectively. At 5–15 cm soil depth, the SOC concentration decreased by 16 % at + 3 K warming under extensive management. Under intensive management no significant changes of the SOC concentration in the 5–15 cm soil depth were found (Table 2). The tN concentration only decreased at + 3 warming under extensive management in both soil depths. SOC stocks decreased by 8 % at + 1 K warming and by 23 % at + 3 K warming under extensive management (Table 2). Under intensive management SOC stocks significantly decreased by 12 % at + 3 K warming in the topsoil. At 5–15 cm soil depth, no significant differences in SOC stocks were observed. With regard to tN stocks, a decrease of 25 % was detected under extensive management at + 3 K warming, while under intensive management a decrease of 9 %was observed in the topsoil (Table 2). At 5–15 cm soil depth no significant changes of tN stocks were found under both management intensities.

3.2.2. *Aggregate-size class distribution*

After four years of translocation, a general decrease of LM at + 1 K and + 3 K warming was observed at 0–5 cm soil depth under both management intensities, except under + 1 K warming under extensive intensity (Fig. 2A and C). This decrease of LM was more pronounced at + 3 K than + 1 K and under intensive (46 %) than under extensive management (30 %) (Fig. 2A and 2C). In contrast, the proportions of SM increased by 24 % and 46 % at + 1 K and + 3 K warming, respectively,

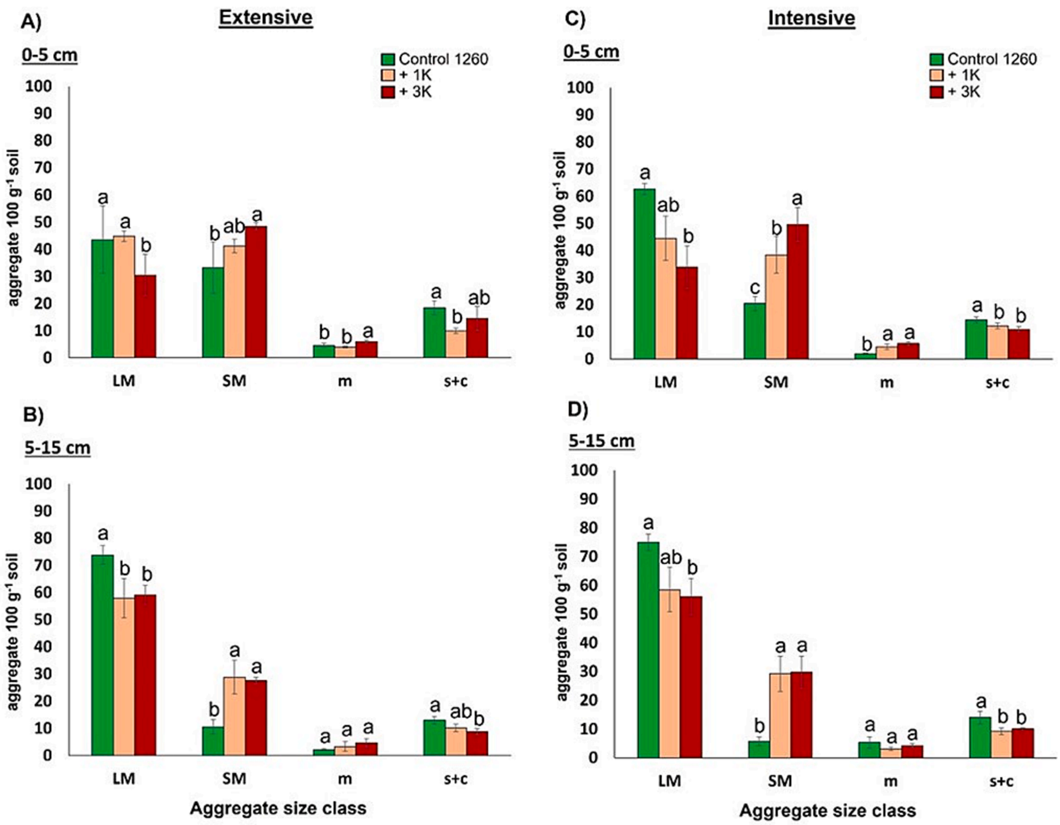

Fig. 2. Water-stable aggregate size distribution (g aggregate 100 g^{-1} soil): LM (>2000 μm), SM (250–2000 μm), m (63–250 μm), and s + c (<63 μm) for the translocated Rendzic Phaeozem plant-soil mesocosms from the high (1260 m a. s. l.)- to mid-elevation (860 m a. s. l.) as + 1 K; and from high (1260 m a. s. l.)- to low-elevation (600 m a. s. l.) as + 3 K. As control we used plant-soil mesocosms that were re-located from Esterberg to Esterberg (Control 1260). **A)** 0–5 and **B)** 5–15 cm soil depth under extensive management practice; and **C)** 0–5 and **D)** 5–15 cm soil depth under intensive management practice. Numerical values are means ± standard deviation. Different letters in bars indicate significant differences between the translocated plant-soil mesocosms for each aggregate size class (Tukey's test, $P < 0.05$).

under extensive management (Fig. 2A and C). For intensive management, an increase of SM by 88 % and 142 % at + 1 K and + 3 K warming was observed, respectively. The proportion of microaggregates showed a strong increase of 130 and 185 % under intensive management at both warming gradients (+1K and + 3 K). The s + c sized fraction showed a higher decrease under extensive compared to intensive management at + 1 K warming (46 % and 16 %, respectively) while at + 3 K warming the decrease of 26 % was observed intensive management. At 5–15 cm soil depth, LM in soils under extensive management decreased by 21 % and 20 % at + 1 K and + 3 K warming, respectively, (Fig. 2B), while under intensive management a decrease of LM of 22 % and 25 % at + 1 K and + 3 K warming was observed, respectively (Fig. 2D). In contrast, the proportion of SM and m under both management practices increased at both warming gradients at 0–5 cm soil depth (Fig. 2B). Changes is aggregate size class distribution where also reflected in changes of MWD which generally decreased (by 13–21 %) at 0–5 cm soil depth at + 3 K warming, while at 5–15 cm soil depth no significant changes were observed.

3.2.3. *OC, N, and C:N ratios of aggregate-size classes*

The OC content of each aggregate size class generally decreased with warming under extensive management in the topsoil with higher decreases found in SM and m at + 1 K warming and in m and s + c at + 3 warming (Table 3). Under intensive management, the OC content of LM decreased by 18 % at + 3 K warming. With regard to the tN content, we observed a decrease in microaggregates by 13 % and 28 % at + 1 K and + 3 K, respectively, under extensive management; and by 3 % and 12 % at + 1 K and + 3 K, respectively, under intensive management (Table 3). At 5–15 cm soil depth, no significant differences of the OC content of each aggregate size class at + 1 K warming under both management intensities was observed (Table 3). At 5–15 cm soil depth, tN contents decreased with aggregate size (LM > SM > m > s + c) at + 1 K and + 3 K warming under extensive and intensive management (Table 3). The C:N ratios were similar in each aggregate size class for both management intensities and soil depths.

3.2.4. *SOC stocks of aggregate-size classes*

The SOC and tN stock changes of aggregate-size classes (Table 4) were normalized per year using re-located control mesocosms as reference (t/ha yr^{-1}) to display the changes after four years of the translocated mesocosms from high- to mid- and low-elevation (Fig. 4). We observed a fluctuation in both extensive and intensive management practices after 4 years of the translocation (Fig. 4). We observed a significant mean increase of OC stock in s + c fraction at + 3 K warming under extensive management at 0–5 cm soil depth and decrease of the OC stock in LM and in s + c and an increase of OC stock in SM at + 1 K warming, whereas at + 3 K warming, the OC stock increased in both LM and SM under intensive management at 0–5 and 5–15 cm soil depth (Fig. 4). Below 5 cm soil depth the OC stock in LM decreased, while the OC stock in SM increased under extensive management (Fig. 4). Regarding the normalized tN stock changes per year we found not significant fluctuations (<1.0 t ha^{-1} $year^{-1}$).

Table 3
Concentrations of OC (organic C), tN (total N) (mg g^{-1} aggregate) and C: tN ratios of aggregates (large macroaggregates (LM) > 2000 μm, small macroaggregates (SM) 250–2000 μm, microaggregates (m) 63–250 μm, silt + clay fraction (s + c) < 63 μm) at 0–5 and 5–15 cm soil depth, after four years of exposure to climate change (by translocation of Rendzic Phaeozem); and the implementation of extensive vs intensive management practices: from high (1260 m a. s. l.)- to mid-elevation (860 m a. s. l.) as + 1 K; and from high (1260 m a. s. l.)- to low-elevation (600 m a. s. l.) as + 3 K. As control we used plant-soil mesocosms that were re-located from Esterberg to Esterberg (Control 1260). Numerical values are means ± standard deviation. Different letters in rows indicate significant differences between each translocation in each management practice for each aggregate size (Tukey's test, P < 0.05).

Depth	OC concentration (mg g⁻¹ aggregate)					
	Extensive			Intensive		
	Control 1260	Translocation		Control 1260	Translocation	
		+ 1 K	+ 3 K		+ 1 K	+ 3 K
0–5 cm						
LM	207.7 ± 1.0a	194.4 ± 2.3b	177.3 ± 1.8c	198.3 ± 0.9a	192.8 ± 3.8a	163.4 ± 6.3b
SM	198.0 ± 4.1a	162.4 ± 2.2b	169.8 ± 4.2b	188.0 ± 0.3a	181.3 ± 5.3a	169.4 ± 3.3b
m	199.5 ± 5.1a	157.2 ± 2.2b	156.2 ± 8.1b	197.7 ± 1.3a	180.9 ± 7.9ab	166.4 ± 5.8b
s + c	142.6 ± 4.8a	124.9 ± 2.9b	94.1 ± 0.3c	143.6 ± 3.1a	141.2 ± 10.7a	118.3 ± 10.0a
5–15 cm						
LM	181.2 ± 18.8a	173.3 ± 16.6a	151.7 ± 4.3a	183.7 ± 4.5a	171.8 ± 11.0a	160.7 ± 4.4a
SM	157.2 ± 31.1a	179.7 ± 15.4a	137.4 ± 2.4a	152.9 ± 14.5a	160.9 ± 5.7a	144.8 ± 5.2a
m	155.5 ± 32.8a	171.4 ± 13.5a	107.9 ± 26.5a	150.5 ± 17.0a	162.0 ± 4.5a	168.2 ± 7.0a
s + c	92.4 ± 32.0a	97.8 ± 15.0a	77.1 ± 20.0a	110.1 ± 16.7a	97.4 ± 2.2a	115.3 ± 5.7a

Depth	**tN concentration (mg g⁻¹ aggregate)**					
	Extensive			**Intensive**		
	Control	**Translocation**		**Control**	**Translocation**	
	1260	**+ 1 K**	**+ 3 K**	**1260**	**+ 1 K**	**+ 3 K**
0–5 cm						
LM	20.9 ± 0.7a	19.4 ± 1.0a	20.2 ± 2.4a	20.0 ± 0.8a	18.8 ± 1.2a	15.9 ± 0.3b
SM	19.9 ± 1.6a	18.0 ± 2.6a	13.7 ± 2.8a	19.2 ± 0.4a	18.5 ± 0.5ab	17.4 ± 0.1b
m	19.8 ± 1.5a	17.2 ± 1.9ab	14.3 ± 1.5b	19.0 ± 1.1a	18.5 ± 0.6a	16.7 ± 0.8a
s + c	15.0 ± 0.7a	10.9 ± 0.7b	10.6 ± 1.3b	12.4 ± 0.7a	14.7 ± 1.8a	11.9 ± 1.0a
5–15 cm						
LM	18.2 ± 3.1a	19.3 ± 0.9a	14.6 ± 1.3a	18.5 ± 1.4a	17.7 ± 0.1a	16.0 ± 0.3a
SM	16.6 ± 3.3a	17.0 ± 2.8a	14.3 ± 0.5a	16.2 ± 2.0a	16.8 ± 0.4a	13.6 ± 1.9a
m	15.1 ± 3.2a	15.9 ± 2.7a	10.7 ± 2.5a	15.8 ± 2.2a	17.4 ± 0.1a	15.3 ± 1.1a
s + c	9.7 ± 3.3a	8.4 ± 2.3a	7.9 ± 2.0a	12.1 ± 2.5a	9.6 ± 0.1a	11.0 ± 0.8a

Depth	**C: tN ratio**					
	Extensive			**Intensive**		
	Control	**Translocation**		**Control**	**Translocation**	
	1260	**+ 1 K**	**+ 3 K**	**1260**	**+ 1 K**	**+ 3 K**
0–5 cm						
LM	10.0 ± 0.3a	10.1 ± 0.6a	8.9 ± 1.1a	9.9 ± 0.4a	10.3 ± 0.9a	10.3 ± 0.2a
SM	10.0 ± 0.6a	9.2 ± 1.1a	13.0 ± 2.9a	9.8 ± 0.2a	9.8 ± 0.0a	9.8 ± 0.1a

Table 3 (*continued*)

Depth	OC concentration (mg g⁻¹ aggregate)					
	Extensive			Intensive		
	Control 1260	Translocation		Control 1260	Translocation	
		+ 1 K	+ 3 K		+ 1 K	+ 3 K
m	10.1 ± 0.6a	9.2 ± 0.9a	11.1 ± 1.5a	10.4 ± 0.6a	9.8 ± 0.1a	10.0 ± 0.2a
s + c	9.5 ± 0.3a	11.5 ± 0.9a	9.0 ± 1.1a	11.6 ± 0.7a	9.8 ± 2.0a	9.9 ± 0.0 a
5–15 cm						
LM	10.1 ± 0.8a	9.0 ± 0.5a	10.4 ± 0.9a	10.0 ± 0.7a	9.7 ± 0.7a	10.0 ± 0.5a
SM	9.5 ± 0.1a	10.8 ± 1.6a	9.6 ± 0.1a	9.5 ± 0.3a	9.6 ± 0.2a	10.9 ± 1.9a
m	10.3 ± 0.7a	11.0 ± 0.9a	10.0 ± 0.1a	9.6 ± 0.6a	9.3 ± 0.3a	11.1 ± 0.9a
s + c	9.5 ± 0.1a	11.9 ± 1.3a	9.8 ± 0.1a	9.2 ± 1.0a	10.2 ± 0.3a	10.6 ± 1.0a

3.3. *Translocation of Plant-Soil mesocosms from mid-elevation (+2K)*

3.3.1. *Bulk density, SOC, tN concentrations and stocks*

Four years of warming of + 2 K resulted in an increase of bulk density by 20 % at 0–5 cm soil depth under extensive management practices, whereas under intensive management practices we observed no significant changes (Table 5). At 5–15 cm soil depth, bulk density did not change under extensive management, whereas an increase of 33 % was detected under intensive management (Table 5). The SOC and tN contents generally decreased by 11–15 % under both management practices and in both soil depths (Table 5). The SOC stocks decreased by 14 % after four years warming by + 2 K under extensive management at 0–5 soil depth, but not under intensive management (Table 5). At 5–15 cm soil depth, no significant changes of SOC stocks were found. The tN stocks showed no significant changes in the topsoil (Table 5).

3.3.2. *Aggregate-size class distribution*

After four years of warming at + 2 K no significant changes were detected in the proportions of any aggregate size class under extensive management at 0–5 and 5–15 cm soil depth (Fig. 3A). In contrast, under intensive management a significant increase of LM of 6 % and a significant decrease of SM of 4 % was detected in the topsoil (Fig. 3C). At 5–15 cm soil depth a decrease of LM of 14 % and an increase of SM of 36 % was observed under intensive management (Fig. 3D). In fact, the MWD showed no significant changes under both management practices and in both soil depths (Table 5).

3.3.3. *OC, N, and C/tN ratios of aggregate-size classes*

In the topsoil the OC content of each aggregate size class generally decreased four years after warming at + 2 K both under extensive management (by 9.5 % in LM, 18 % in SM, 10 % in m, 17 % in s + c) and intensive management (by 13 % in LM, 32 % in SM, 29 % in m, 18 % in s + c) (Table 6). At 5–15 cm soil depth, no changes of the OC content of LM, SM, and s + c were observed under extensive management. However, under intensive management, a significant decrease of the OC content of LM (15 %), SM (14 %), and s + c (23 %) (Table 7) was detected. With regard to the tN content, a significant decrease was detected for LM at 0–5 cm soil depth under extensive management. A decrease of tN contents was also observed for each aggregate size class under intensive management. The C:N ratio showed no not significant changes in each aggregate size class under both management practices and in both soil depths (Table 6).

3.3.4. *SOC stocks of aggregate-size classes*

Similar to that the section 3.1.5, the SOC and tN stock of aggregate-size classes (Table 7) were normalized per year (t/ha yr^{-1}) to display the

Table 4
OC and tN stocks (t/ha) of aggregates (large macroaggregates (LM) > 2000 μm, small macroaggregates (SM) 250–2000 μm, microaggregates (m) 63–250 μm, silt/clay fraction (s + c) < 63 μm) at 0–5 and 5–15 cm soil depth, after four years of exposure to climate change (by translocation of Rendzic Phaeozem) and the implementation of extensive vs intensive management practices: from high (1260 m a. s. l.)- to mid-elevation (860 m a. s. l.) as + 1 K; and from high (1260 m a. s. l.)- to low-elevation (600 m a. s. l.) as + 3 K. As control we used plant-soil mesocosms that were re-located from Esterberg to Esterberg (Control 1260). Numerical values are means ± standard deviation. Different letters in rows indicate significant differences between each translocation in each management practice for each aggregate size (Tukey's test, P < 0.05).

Depth	OC stocks (t/ha)					
	Extensive			Intensive		
	Control 1260	Translocation		Control 1260	Translocation	
		+ 1 K	+ 3 K		+ 1 K	+ 3 K
0–5 cm						
LM	16.5 ± 2.6ab	19.1 ± 4.7a	9.9 ± 3.0b	22.5 ± 0.6a	17.3 ± 3.8ab	11.5 ± 3.8b
SM	16.9 ± 5.2a	12.0 ± 3.8a	16.7 ± 0.2a	7.4 ± 1.2b	13.0 ± 2.2a	14.5 ± 1.5a
m	2.4 ± 0.7a	1.1 ± 0.3a	2.8 ± 1.9a	0.8 ± 0.1b	1.6 ± 0.5a	1.7 ± 0.2a
s + c	1.6 ± 0.4a	2.8 ± 1.0a	3.2 ± 1.0a	4.0 ± 0.2a	2.7 ± 0.1b	2.1 ± 0.3b
5–15 cm						
LM	57.3 ± 9.5a	45.4 ± 11.3a	46.4 ± 3.0a	59.5 ± 2.7a	46.1 ± 8.0ab	44.4 ± 4.7b
SM	17.5 ± 3.0a	22.9 ± 5.2a	19.6 ± 2.0a	3.9 ± 1.9b	21.5 ± 5.2a	21.6 ± 6.9a
m	2.8 ± 0.3a	2.4 ± 1.8a	2.4 ± 0.3a	3.3 ± 1.0a	2.3 ± 0.5a	3.6 ± 0.9a
s + c	2.6 ± 0.5a	4.4 ± 1.0a	3.4 ± 0.6a	6.9 ± 2.8a	4.1 ± 0.7a	5.8 ± 0.9a

Depth	tN stocks (t/ha)					
	Extensive			Intensive		
	Control 1260	Translocation + 1 K	+ 3 K	Control 1260	Translocation + 1 K	+ 3 K
0–5 cm						
LM	1.8 ± 0.4a	1.8 ± 0.4a	1.0 ± 0.2a	2.2 ± 0.1a	1.6 ± 0.2b	1.1 ± 0.3b
SM	1.1 ± 0.4a	1.2 ± 0.5a	1.2 ± 0.3a	0.7 ± 0.1b	1.6 ± 0.1a	1.6 ± 0.1a
m	0.1 ± 0.0a	0.1 ± 0.0a	0.2 ± 0.1a	0.1 ± 0.0b	0.2 ± 0.0a	0.2 ± 0.0a
s + c	0.6 ± 0.3a	0.2 ± 0.1a	0.3 ± 01a	0.3 ± 0.0a	0.3 ± 0.0a	0.2 ± 0.0a
5–15 cm						
LM	5.9 ± 1.1a	4.7 ± 0.5a	4.1 ± 0.3a	6.0 ± 0.3a	4.8 ± 1.2a	4.4 ± 0.5a
SM	0.8 ± 0.4a	2.1 ± 1.0a	1.9 ± 0.2a	0.4 ± 0.2b	2.2 ± 0.4a	1.9 ± 0.2a
m	0.2 ± 0.0a	0.2 ± 0.1a	0.9 ± 0.1a	0.3 ± 0.1a	0.2 ± 0.0a	0.3 ± 0.0a
s + c	0.5 ± 0.2a	0.4 ± 0.1a	0.3 ± 0.1a	0.8 ± 0.3a	0.4 ± 0.0a	0.5 ± 0.0a

changes after 4 years of the translocated Haplic Cambisol plant-soil mesocosms from the mid- (860 m a. l. s) to the low-elevation (600 m a. s. l). We observed opposite fluctuations (increase or decrease or not changes) of SOC stock between extensive vs. intensive management (Fig. 5). It means that while the SOC stock in SM significantly decreased at + 2 K warming at 0–5 cm soil depth under extensive management, we not observed significant changes of SOC stock in SM after 4 years under intensive management, although the SOC stock in s + c fraction significantly decreased under intensive management practices. Below 5 cm depth, we have still observed opposite trends between extensive and intensive management practices. Interestedly, under intensive management we found a significant increase of OC stock in LM and SM and still a significant decrease of OC stock in s + c fraction (Fig. 5).

Table 5
Soil properties of a Haplic Cambisol at 0–5 and 5–15 cm soil depth after four years of exposure to climate change (by translocation) and the implementation of extensive vs. intensive management practices, from mid-elevation (860 m a. s. l.) to low-elevation as + 2 K. As control we used plant-soil mesocosms that were re-located from Graswang to Graswang (Control 860). BD (bulk density), OC (organic carbon concentration), tN (total nitrogen concentration), C: tN (carbon nitrogen ratio), and OC and tN stocks. Numerical values are means ± standard deviation. Different letters in rows indicate significant differences between treatments (Kruskal-Wallis's test, P < 0.05).

Soil properties	Extensive		Intensive	
	Control 860	Translocation +2K	Control 860	Translocation +2K
0–5 cm				
BD (g cm^{-3})	0.5 ± 0.0b	0.6 ± 0.0a	0.6 ± 0.0a	0.6 ± 0.0a
OC (mg g^{-1})	118.2 ± 9.5a	100.9 ± 4.7b	115.3 ± 4.9a	99.6 ± 5.9a
tN (mg g^{-1})	12.2 ± 0.9a	10.6 ± 0.5b	12.2 ± 0.7a	10.5 ± 0.7b
C: tN ratio	9.7 ± 1.0a	9.5 ± 1.0a	9.5 ± 1.2a	9.5 ± 1.0a
MWD	1.8 ± 0.0 a	2.1 ± 0.2a	1.9 ± 0.5a	2.0 ± 0.2a
OC stock (t/ha)	28.5 ± 0.8a	24.5 ± 2.3b	31.6 ± 1.6a	27.9 ± 0.4b
tN stock (t/ha)	2.9 ± 0.1a	2.6 ± 0.3a	3.3 ± 0.3a	3.0 ± 0.3a
5–15 cm				
BD (g cm^{-3})	0.6 ± 0.0a	0.6 ± 0.0a	0.6 ± 0.0b	0.8 ± 0.0a
OC (mg g^{-1})	98.1 ± 9.1a	87.9 ± 5.2b	94.2 ± 2.5a	80.0 ± 7.4b
tN (mg g^{-1})	10.9 ± 0.8a	9.2 ± 1.2a	9.2 ± 0.4a	8.3 ± 0.8a
C: tN ratio	9.0 ± 1.1a	9.6 ± 1.3a	10.2 ± 1.2a	9.6 ± 1.3b
MWD	2.5 ± 0.3a	2.4 ± 0.3a	2.6 ± 0.3a	2.3 ± 0.6a
OC stock (t/ha)	59.3 ± 4.6a	58.3 ± 1.1a	55.9 ± 6.0a	53.1 ± 6.5a
tN stock (t/ha)	6.6 ± 0.3a	5.7 ± 1.0a	6.3 ± 0.8a	5.5 ± 0.5a

4. Discussion

4.1. Soil perturbation induced by re-location of Plant-Soil mesocosms

Soil perturbation induced by excavation, transportation and re-introduction of plant-soil mesocosms may accompany the destined effects of management and climate change in mesocosm experiments. The mesocosm re-location significantly affected bulk density and MWD (Supplementary Table 2A and 3A). However, soils of the mid elevation (Haplic Cambisol) responded in a different way compared to soils of the high elevation (Rendzic Phaeozem). In the re-located Cambisols, bulk density increased and MWD decreased, whereas in the re-located Rendzic Phaeozem bulk density generally decreased. In addition, relevant effects were found regarding aggregate-size distribution with a general loss of macroaggregation in the re-located Rendzic Phaeozem mesocosms that was associated with OC changes of aggregate-size classes (Fig. 2). In contrast, for the re-located Haplic Cambisol mesocosm no changes in aggregate distribution were observed (Fig. 3). Obviously, soil perturbation induced by excavation, transportation and re-introduction of mesocosm is soil type specific. The stronger perturbation effect in OC-rich Rendzic Phaeozems compared to Haplic Cambisols could be attributed to the high proportion of large macroaggregates, which are prone to disturbance (Kühnel et al., 2019; Garcia-Franco et al., 2021). In contrast, Haplic Cambisols are characterized by a lower OM amount, but also with higher amount of IC, which is associated with a higher aggregate stability (Garcia-Franco et al., 2021). Our results indicated that climate manipulation experiments based on mesocosm approaches may be biased if they do not consider effects of soil perturbation during the translocation process.

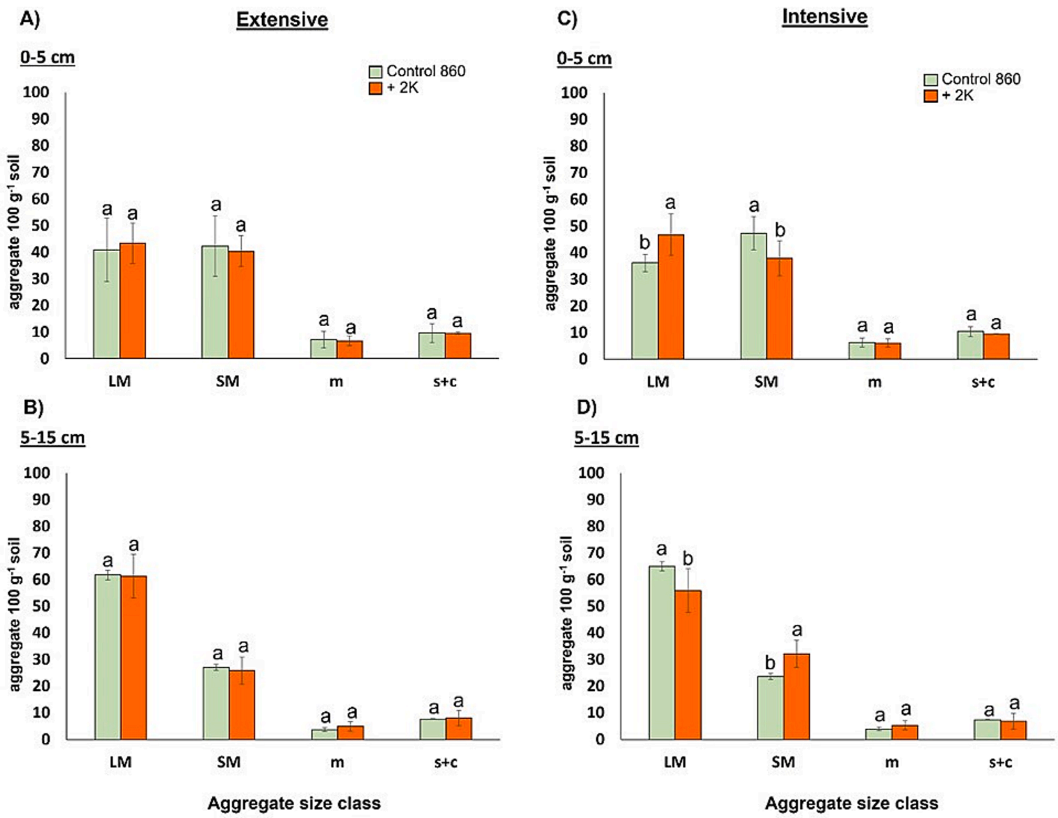

Fig. 3. Water-stable aggregate size distribution (g aggregate 100 g^{-1} soil): LM (>2000 µm), SM (250–2000 µm), m (63–250 µm), and s + c (<63 µmfor the translocated Haplic Cambisol plant-soil mesocosms from the mid (860 m a. s. l.)- to low-elevation (600 m a. s. l.) as + 2 K. As control we used plant-soil mesocosms that were re-located from Graswang to Graswang (Control 860). A) 0–5 and B) 5–15 cm soil depth under extensive management practice; and C) 0–5 and D) 5–15 cm soil depth under intensive management practice. Numerical values are means ± standard deviation. Different letters in bars indicate significant differences between the translocated plant-soil mesocosms for each aggregate size class (Kruskal-Wallis's test, $P < 0.05$).

4.2. Decline of SOC and tN stocks and DETERIORATION OF MACROAGGREGATION induced by warming

Mountainous grassland soils are regional and global hotspots for SOC storage as a result of high mean annual precipitation and low mean annual temperature leading to comparably high primary productivity and C inputs and relatively low SOM decomposition (Leifeld et al., 2009). Physical protection of mainly root-derived C inputs within soil aggregates is particularly relevant in mountainous grassland soils (Conant et al., 2001; Li et al., 2016). Translocation induced changes in both abiotic and biotic environmental conditions allow to examine the net effect of both direct and indirect impacts of climate warming (Alexander et al., 2015; Yang et al., 2018). Our warming experiment demonstrates the sensitivity of mountainous grassland soils to climate change under different management intensity. Four years of translocation-induced warming caused a rapid and massive decrease of SOC and N contents and stocks at + 3 K and + 2 K warming in the topsoil. The SOC losses were generally higher under extensive management (22 % and 14 % at + 3 K and + 2 K, respectively) than under intensive management (11 % at both + 3 K and + 2 K), which indicates that intensive grassland management with higher OC return slightly offset SOC losses. With regard to the effect of soil types, the normalized SOC losses under extensive management were higher in the translocated Rendzic Phaeozem mesocosms (22 %) than in the translocated Haplic Cambisol mesocosms (14 % management, respectively). However, under intensive management SOC losses were similar (11 %) for both study sites. (Table 2 and 5). The Rendzic Phaeozems in our study were very dark soils due the high amount of less decomposed organic matter from the vegetation with values of 188.9 mg g^{-1} and 18.8 mg g^{-1}, OC and tN respectively (Garcia-Franco et al., 2021). In addition, the high content of available calcium ions bound to soil particles, resulting in a very permeable and well aggregated structure (IUSS Working Group WRB, 2015). Whereas the Haplic Cambisols in our study had a thinner Ah horizon (compared with the Rendzic Phaeozems), and covered a wide range of inorganic carbon concentration (IC), of parent material (gravel, solid rock) and stage of pedogenesis (Kreyling et al., 2013).

We assumed that the observed warming-induced decline of SOC may generally be attributed to the combined effect of (i) climate change together with (ii) management soil practices. Climate change may increase the soil microbial activity throughout the year, particularly during the winter months (Kühnel et al., 2019); and the mineralization of SOM (Melillo et al., 2002; Puissant et al., 2015; Poeplau et al., 2020; Verbrigghe et al., 2022). At our study sites at mid and low elevations (Graswang, 860 m a. s. l; Fendt, 600 m a. s. l), the vegetation period was considerably longer (up to a month) compared to the study site at the highest elevation (Esterberg, 1,260 m a. s. l) (Bauer et al., 2020). Although there are uncertainties with regard to the temperature sensitivity of different fractions of SOM, physiological responses of vegetation and soil microorganisms, and the effects of physicochemical factors such as pH, soil moisture, oxygen, and nutrients (Conant et al., 2001; Davidson and Janssens, 2006; Von Lützow et al., 2008), indications for declining SOC stocks in grassland soils induced by climate change were reported in several previous studies (Puissant et al., 2017; Yang et al., 2018; Peplau et al., 2021; Poeplau, 2021; Volk et al., 2022). A loss of SOC of mountainous regions due to climate change, as reported here for our study sites in the pre-alpin/ alpine region of S-Germany, was also observed in the Himalaya (Schickhoff et al., 2022), the Swiss Jura (Volk et al., 2022) and the Pyrenees (Garcia-Pausas et al., 2007). Mountainous grasslands below (i.e., sub-alpine) or above (i.e., alpine) the tree line is typically characterized by slow process rates and element fluxes.

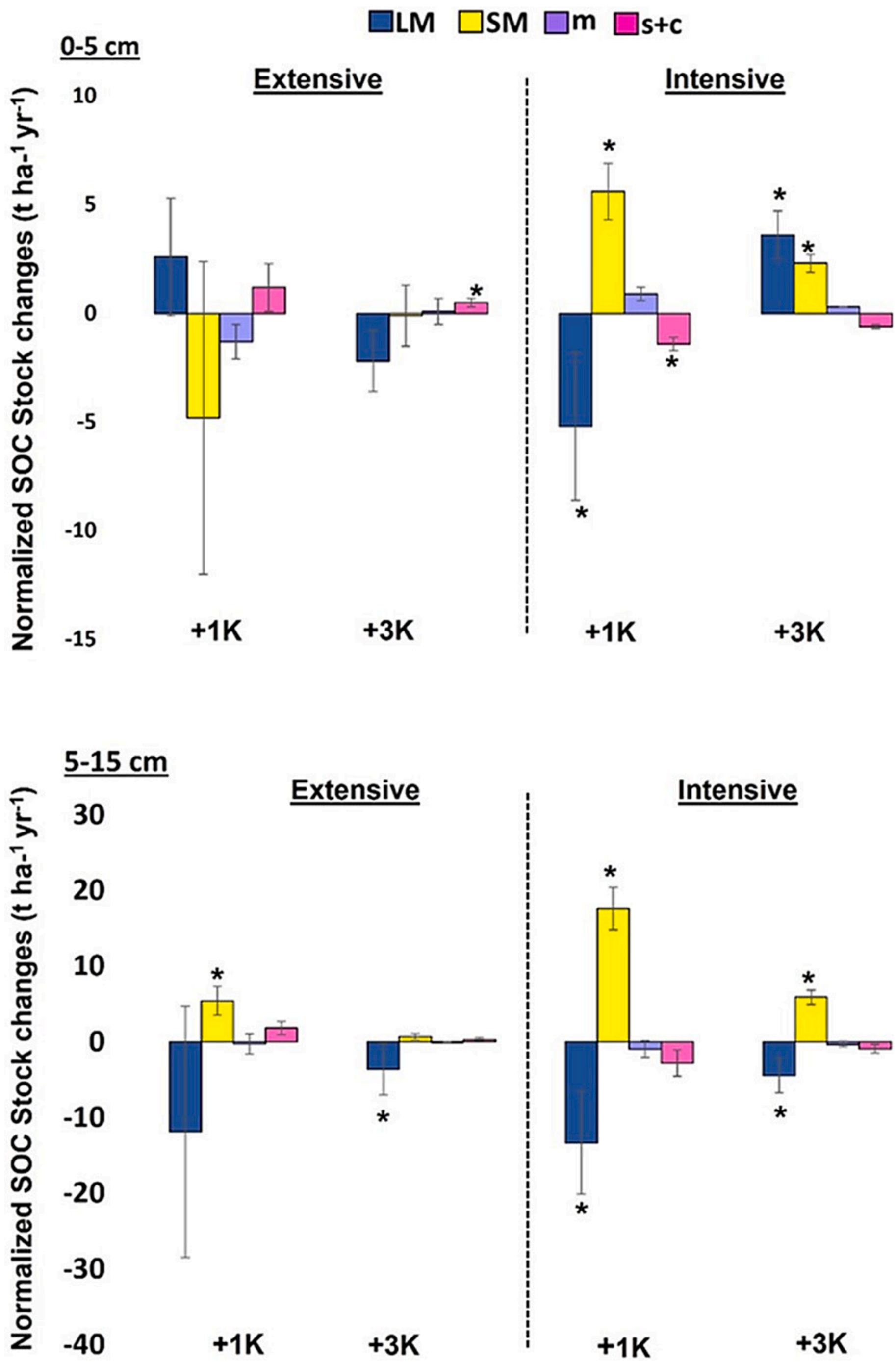

Fig. 4. Normalized OC stock changes in each aggregate-size class (t/ha yr-1): LM (>2000 μm), SM (250–2000 μm), m (63–250 μm), and s + c (<63 μm) for the translocated Rendzic Phaeozem plant-soil mesocosms from the high (1260 m a. s. l.)- to mid-elevation (860 m a. s. l.) as + 1 K; and from high (1260 m a. s. l.)- to low-elevation (600 m a. s. l.) as + 3 K. The "*" symbol indicates significant changes after 4 years.

Because of their high SOC concentrations and particularly high proportion of labile OM (Leifeld et al., 2009; Budge et al., 2011), these grasslands are prone to SOC losses induced by environmental disturbance and are alleged to be potential sources for CO_2 emissions (Sjögersten et al., 2011).

Our study suggests that changes in the physical protection of SOM via altered soil structure is a key process regarding the decline of SOC and tN. We observed a marked decrease of the proportion of large-macroaggregates and silt–clay-sized fractions, while the proportion of small-macroaggregates and microaggregates increased after four years of + 3 K warming, independent of the management intensity (Figs. 4 and 5). This could at least partly explain the changes in the SOC and tN stocks of the bulk soil and changes of the soil structure, as the increase of SM and m can be attributed to the combined effect of LM disruption together with the occlusion of silt–clay-sized OM into the SM and m. In a previous study on the initial status of the studied grassland soils, we found indications that carbonates and high SOM levels have a positive effect on aggregate size and stability, which in combination with slow SOM degradation rates may explain high OC contents in micro- and macroaggregates in these grassland soils (Garcia-Franco et al., 2021). However, our results evidenced that warming induced a depletion of SOM and a destabilization of macroaggregates. At the same time, a

Table 6
Concentrations of OC (organic C), tN (total N) (mg g-1 aggregate) and C/N ratios of aggregates (large macroaggregates (LM) > 2000 μm, small macroaggregates (SM) 250–2000 μm, microaggregates (m) 63–250 μm, silt + clay fraction (s + c) < 63 μm) at 0–5 and 5–15 cm soil depth, after four years of exposure to climate change (by translocation of Haplic Camsisols); and the implementation of extensive vs intensive management practices: from mid-elevation (860 m a. s. l.) to low-elevation as + 2 K. As control, we used plant-soil mesocosms that were re-located from Graswang to Graswang (Control 860). Numerical values are means ± standard deviation. Different letters in rows indicate significant differences between each translocation in each management practice for each aggregate size (Kruskal-Wallis's test, P < 0.05).

Depth	OC concentration (mg g^{-1} aggregate)			
	Extensive		Intensive	
	Control 860	Translocation +2K	Control 860	Translocation +2K
0–5 cm				
LM	109.8 ± 5.6a	99.4 ± 0.3b	113.8 ± 4.3a	99.2 ± 1.1b
SM	125.5 ± 0.5a	102.8 ± 1.8b	150.5 ± 3.3a	102.2 ± 0.5b
m	117.5 ± 5.3a	105.8 ± 2.3b	135.0 ± 2.7a	96.1 ± 4.5b
s + c	65.2 ± 2.1a	54.2 ± 2.3b	62.3 ± 3.4a	51.2 ± 1.4b
5–15 cm				
LM	105.7 ± 11.4a	93.6 ± 5.6a	98.6 ± 6.0a	83.9 ± 4.1b
SM	97.1 ± 9.5a	86.7 ± 11.7a	97.8 ± 2.0a	84.5 ± 3.3b
m	95.6 ± 6.7a	73.7 ± 7.6b	96.3 ± 10.3a	67.6 ± 13.8a
s + c	41.7 ± 6.3a	39.5 ± 7.4a	45.8 ± 1.8a	35.2 ± 3.6b

Depth	**tN concentration (mg g^{-1} aggregate)**			
	Extensive		**Intensive**	
	Control 860	**Translocation +2K**	**Control 860**	**Translocation +2K**
0–5 cm				
LM	12.5 ± 0.4a	9.9 ± 0.6b	12.0 ± 0.5a	9.7 ± 0.8b
SM	12.3 ± 0.9a	10.6 ± 0.7 a	13.6 ± 1.1a	11.4 ± 0.4b
M	12.1 ± 0.9a	10.1 ± 1.0 a	12.9 ± 0.6a	11.0 ± 0.6b
s + c	6.7 ± 0.2b	7.6 ± 0.6 a	6.7 ± 0.3a	5.0 ± 0.4b
5–15 cm				
LM	10.7 ± 1.3a	9.2 ± 1.5a	10.2 ± 1.1a	9.0 ± 0.8a
SM	10.7 ± 0.9a	9.8 ± 1.3a	10.7 ± 0.9a	9.3 ± 0.6a
M	9.3 ± 1.3a	7.7 ± 1.0a	10.5 ± 1.0a	7.3 ± 1.7a
s + c	4.9 ± 0.7 a	4.3 ± 0.7a	4.7 ± 0.5a	3.9 ± 0.6a

Depth	**C: tN ratio**			
	Extensive		**Intensive**	
	Control 860	**Translocation +2K**	**Control 860**	**Translocation +2K**
0–5 cm				
LM	8.8 ± 0.4a	10.1 ± 0.6a	9.5 ± 0.3a	10.3 ± 0.7a
SM	10.3 ± 0.8a	9.7 ± 0.4a	11.2 ± 1.2a	9.0 ± 0.3b
M	9.8 ± 0.3a	10.5 ± 0.9a	10.5 ± 0.4a	8.8 ± 0.8b
s + c	9.8 ± 0.6a	7.2 ± 0.9a	9.3 ± 0.1b	10.2 ± 0.9a
5–15 cm				
LM	9.9 ± 0.7a	10.4 ± 1.2a	9.7 ± 0.4a	9.5 ± 1.3a
SM	9.1 ± 0.1a	8.9 ± 0.3a	9.2 ± 0.7a	9.1 ± 0.3a
M	10.3 ± 0.7a	9.7 ± 0.7a	9.2 ± 0.2a	9.3 ± 0.5a
s + c	8.5 ± 1.1a	9.2 ± 0.7a	9.8 ± 1.0a	9.2 ± 0.6a

destabilization of macroaggregates may further cause a destabilization of SOC – a positive feedback loop (Lavee et al., 1996; Matthias C. Rilling, Sara F. Wright 2002; Poeplau, 2021). Puissant et al. (2017) also found an alteration of soil macroaggregate size distribution after four years of a climate manipulation experiment in alpine grasslands in Switzerland. The deterioration of the soil structure by warming was also supported by the observed decrease of MWD, which can be viewed as a soil structural stability indicator (Wiesmeier et al., 2019). Except for topsoils under extensive management, the breakdown of macroaggregates rich in OC led to a higher proportion of SOC stored in smaller aggregate size classes. Whereas under intensive management associated with higher application of organic fertilizer we observed more promoting the formation of small-macroaggregates as compared to extensive management. (Fig. 4).

Table 7
OC and tN stocks (t/ha) of aggregates (large macroaggregates (LM) > 2000 μm, small macroaggregates (SM) 250–2000 μm, microaggregates (m) 63–250 μm, silt/clay fraction (s + c) < 63 μm) at 0–5 and 5–15 cm soil depth, after four years of exposure to climate change (by translocation of Haplic Camsisols) and the implementation of extensive vs intensive management practices: from mid-elevation (860 m a. s. l.) to low-elevation as + 2 K. As control, we used plant-soil mesocosms that were re-located from Graswang to Graswang (Control 860). Numerical values are means ± standard deviation. Different letters in rows indicate significant differences between each translocation in each management practice for each aggregate size (Kruskal-Wallis's test, P < 0.05).

Depth	OC stocks (t/ha)			
	Extensive		Intensive	
	Control 860	Translocation +2K	Control 860	Translocation +2K
0–5 cm				
LM	10.0 ± 1.2a	11.9 ± 3.3a	12.2 ± a	12.6 ± a
SM	14.9 ± 2.2a	9.7 ± 0.9b	9.5 ± a	12.1 ± a
m	1.9 ± 0.5a	1.6 ± 0.3a	1.3 ± a	1.9 ± a
s + c	1.7 ± 0.3a	1.3 ± 0.1a	5.3 ± a	1.4 ± b
5–15 cm				
LM	38.8 ± 5.7a	38.4 ± 6.5	37.9 ± 3.5a	30.8 ± 3.0b
SM	16.3 ± 7.9a	15.2 ± 5.2a	5.7 ± 2.8b	18.4 ± 5.9a
m	2.2 ± 1.3a	2.5 ± 1.0a	1.4 ± 0.2a	2.3 ± 0.7a
s + c	2.0 ± 1.0aa	2.2 ± 1.2a	4.0 ± 1.8a	1.6 ± 0.8b

Depth	**tN stocks (t/ha)**			
	Extensive		**Intensive**	
	Control 860	**Translocation +2K**	**Control 860**	**Translocation +2K**
0–5 cm				
LM	1.1 ± 0.2a	1.2 ± 0.3a	1.4 ± 0.8a	1.2 ± 0.4a
SM	1.5 ± 0.3a	1.0 ± 0.1a	1.5 ± 0.5a	1.3 ± 0.2a
M	0.2 ± 0.1a	0.2 ± 0.0a	0.2 ± 0.1a	0.2 ± 0.1a
s + c	0.2 ± 0.0a	0.2 ± 0.0a	0.2 ± 0.1a	0.1 ± 0.0a
5–15 cm				
LM	4.3 ± 0.7a	3.6 ± 0.8a	4.2 ± 0.4a	3.2 ± 0.8a
SM	1.9 ± 0.8a	1.6 ± 0.6a	1.6 ± 0.4a	1.9 ± 0.3a
M	0.2 ± 0.1a	0.2 ± 0.1a	0.3 ± 0.0a	0.2 ± 0.0a
s + c	0.2 ± 0.1a	0.2 ± 0.1a	0.2 ± 0.0a	0.2 ± 0.0a

Several studies on grassland management effects on SOM found higher SOC contents with increasing levels of fertilization (Conant et al., 2001; Ammann et al., 2009). Furthermore, regarding fertilizer type, grassland soils that received cattle slurry showed higher SOC stocks compared to soils receiving mineral fertilizers (Soussana and Lüscher, 2007; Poeplau, 2021). This may at least partly explain the lower SOC and N losses in topsoil of intensively managed grasslands in our experiment that received substantially higher amounts of C and N (1.6 and 0.2 t ha^{-1} yr−1, respectively) via slurry compared to extensively managed grasslands (0.895 and 0.1 t ha^{-1} yr^{-1}, respectively). Similar to SOC stocks, N stocks decreased under climate change, but this effect was buffered under high management intensity (Table 2 and 5). In a previous study carried out on the same experimental sites, (Schlingmann et al., (2020) found that both intensified slurry application and climate change led to negative N balances. This suggests a risk of soil N mining in montane and subalpine grassland under climate change and land use intensification (Schlingmann et al., 2020). In fact, in a previous study Wang et al. (2021) found losses of 2–3 t ha^{-1} of C, derived from chamber based C flux measurements. However, Kühnel et al. (2019) examined long-term SOC dynamics in grassland soils of Bavaria, which are part of a long-term soil monitoring program, and found that the application of organic fertilizer was a prerequisite to maintain or increase SOC stocks of pre-alpine grassland soils within the observation period from 1986 to 2016. In a global meta-analysis carried out by Maillard and Angers (2014) the importance of continuous addition of animal manure to maintain or increase SOC stocks in grassland soils was emphasized. Several studies of SOC stocks in grassland soils under different management intensities and warming gradients recollected by Peplau et al.

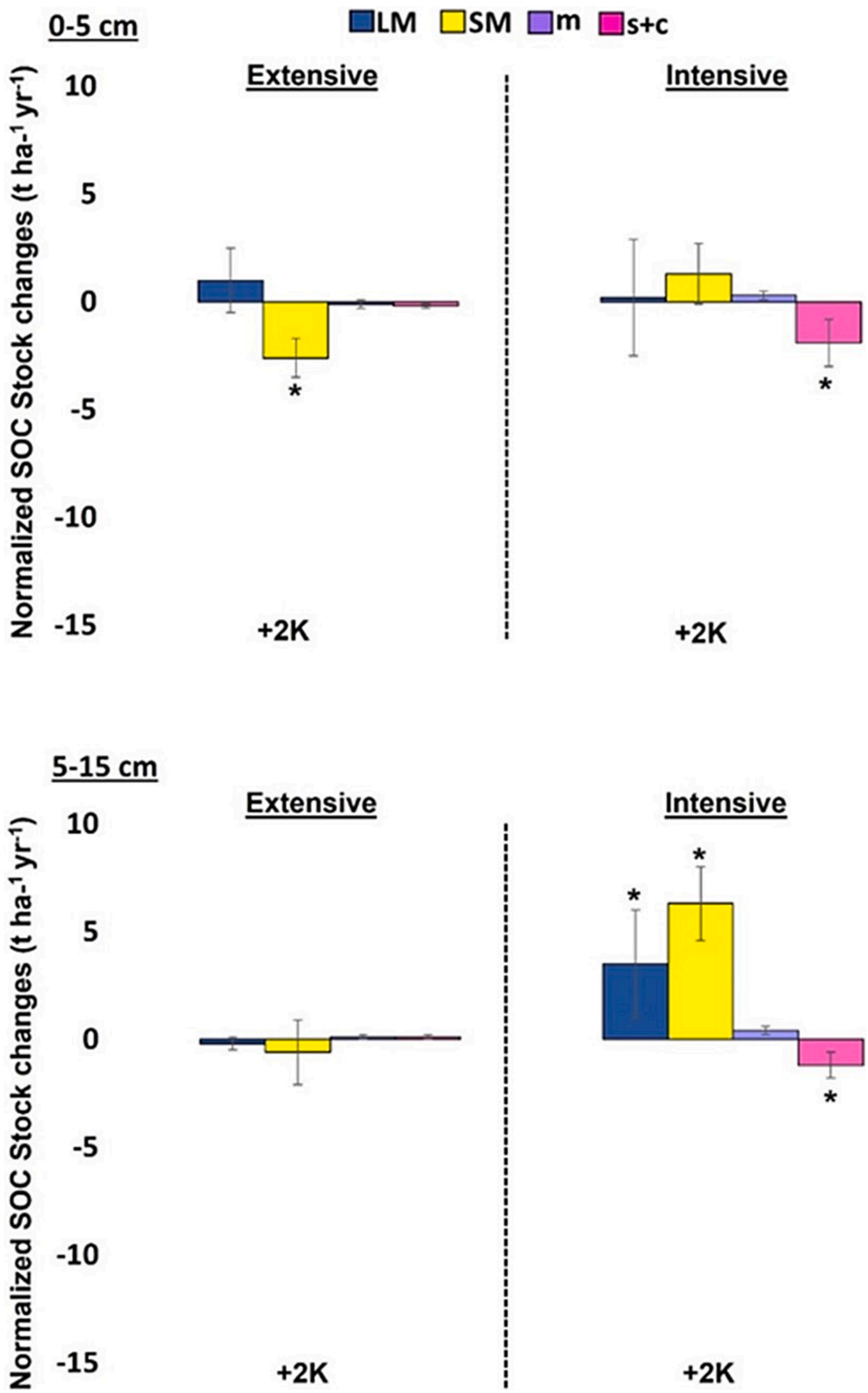

Fig. 5. Normalized OC stock changes in each aggregate-size class (t/ha yr-1): LM (>2000 μm), SM (250–2000 μm), m (63–250 μm), and s + c (<63 μm) for the translocated Haplic Cambisol plant-soil mesocosms from the mid- (1260 m a. s. l.)- to low-elevation (600 m a. s. l.) as + 2 K. The "*" symbol indicates significant changes after 4 years.

(2021) revealed that SOC stocks increased with an increase in cutting frequency and fertilization rate, even without external C inputs. Thus, sufficient return of exported biomass in form of organic fertilizers such as manure seems to be a prerequisite to maintain grassland SOC stocks or at least reduce SOC losses induced by climate change. In previous studies in the same experimental area, we observed that climate warming increases the length of growing seasons and thereby the productivity of the grasslands (Berauer et al., 2019,2020), which may facilitate increased management intensity (more cuts and fertilization events) by the farmers.

5. Outlook

Four years of simulated climate change induced by translocating plant-soil mesocosms along an elevation gradient in the Northern Limestone Alps of Germany resulted in a rapid and massive decrease of

SOC and tN stocks of SOM-rich grassland soils that was associated with a disruption of soil macroaggregates, particularly under extensive grassland management. Our study provided evidence that climate change may have severe consequences for the soil structure and thus for the physical protective capacity of mountainous grassland soils to store SOM. We propose large-macroaggregates as diagnostic fraction that could be used as early warning indicator for SOM and soil structure losses. Intensive management with higher manure C return slightly offset the losses of SOC and N through the formation of smaller aggregates. The loss of SOC not only causes a substantial release of CO_2 from these SOM-rich soils but may also deteriorate their ecosystem services in the long-term.

Funding

We are grateful to the German Ministry for Education and Research (BMBF) for funding the SUSALPS project ("Sustainable Use of Alpine and Pre-Alpine Grassland Soils in a Changing Climate"), which is part of the funding measure "Soil as a Sustainable Resource for the Bioeconomy-BonaRes" (FKZ 031B1067B; FKZ 031B0516A; BonaRes, Module A).

CRediT authorship contribution statement

Noelia Garcia-Franco: Writing – original draft, Formal analysis, Investigation, Methodology, Resources, Validation, Visualization, Data curation, Writing – review & editing. **Martin Wiesmeier:** Investigation, Supervision, Writing – original draft, Conceptualization, Resources, Writing – review & editing. **Vincent Buness:** Formal analysis, Writing – review & editing. **Bernd J. Berauer:** Methodology, Formal analysis, Writing – review & editing. **Max A. Schuchardt:** Methodology. **Anke Jentsch:** Methodology. **Marcus Schlingmann:** Methodology, Resources, Writing – original draft. **Diana Andrade-Linares:** Methodology, Writing – review & editing. **Benjamin Wolf:** Investigation, Methodology, Supervision. **Ralf Kiese:** Conceptualization, Investigation, Methodology, Resources, Supervision, Writing – original draft. **Michael Dannenmann:** Conceptualization, Investigation, Methodology, Resources, Supervision, Validation, Writing – original draft, Writing – review & editing. **Ingrid Kögel-Knabner:** Conceptualization, Investigation, Writing – original draft.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Noelia Garcia-Franco reports financial support and article publishing charges were provided by Technical University of Munich. Noelia Garcia-Franco reports a relationship with Technical University of Munich that includes: employment. Noelia Garcia-Franco has patent no patent pending to no patent. There is not If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

We thank Franziska Fella, Sigrid Hirsch, Monika Heilmeier, Gabi Albert for field and laboratory work, and Juan Martínez Garcia, Luis Carlos Colocho Hurtarte for help with the figure design.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geoderma.2024.116807.

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