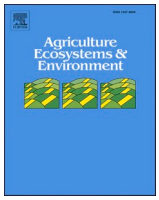
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Mountain grassland SOC stocks decline for 30 years with low N mineral fertilisation, independent of yield size and temperature increase

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ABSTRACT

The carbon (C) stocks of grassland soils represent one of the largest potential sinks for the greenhouse gas (GHG) CO_2. This makes knowledge of the changes in the soil organic C (SOC) stock essential. In a long-term experiment, we studied mountain grassland yields and topsoil SOC stocks in a one-level N and six-level PK-mineral fertiliser trial between 1990 and 2022, following the cessation of farmyard manure (FYM) fertilisation. To distinguish C-input from C-output pathways, we quantified the CO_2 exchange and the net ecosystem C balance (NECB) in 2022. During 33 years of NPK fertilisation, mean plant yield declined at a rate of 0.03 t C ha^{-1} yr^{-1}, and SOC stocks declined at 0.5 t C ha^{-1} yr^{-1}. In response to NPK treatments, plant yields showed a 1.6-fold difference, but the corresponding SOC stocks did not differ. In 2022, reference plots under continuous FYM fertilisation, still had the same SOC stocks as NPK plots in the zero year (1989). Short-term changes in SOC stock were not correlated with any climate indices or plant yields, but extreme weather conditions in 2022 coincided with abrupt changes in SOC stock. We conclude that in our experiment, grassland yield and long-term temperature increase were not modulators of SOC stock decline. Only under C and N import conditions, through FYM application, were historical SOC stocks maintained. In single years, hot and dry weather may cause large SOC stock losses of ca. 5 t C ha^{-1} yr^{-1} in the form of CO_2.

1. Introduction

In mountain areas worldwide, climatic factors and topography make arable crop production unfeasible. Instead, grasslands, used for mowing and grazing, constitute either the major or even the only form of agronomic land use. In areas traditionally used as grasslands, large amounts of soil organic carbon (SOC) have accumulated over centuries, largely due to minimal disturbance from agricultural management. As a consequence, grassland soils contain the highest C stocks of all agriculturally used mineral soils per area unit. In Switzerland, for example, 74% of the agricultural land is permanent grasslands, containing 144.5 Mt SOC on 1124,800 ha, including 538,000 ha of mountain pastures and meadows (Leifeld et al., 2005). In cold mountain climates, the low temperatures also protect soil C stocks against decomposition, in addition to physico-chemical soil properties such as pH and clay mineral content (Bahn et al., 2008; Bonfanti et al., 2025; Leifeld et al., 2009). This temperature effect favours the accumulation of a large fraction of particulate organic carbon (POC) and makes mountain soil C storage highly vulnerable to climate warming. The large SOC stock underpins several ecosystem functions, including soil health (Lal, 2016) and the long-term storage of the greenhouse gas (GHG) CO_2 as organic carbon (OC; Schimel et al., 1994). The high SOC stocks and the low degree of protection, compared to lowland SOC, make them prone to C losses (Garcia-Franco et al., 2024) and thus represent a large potential GHG source. The abovementioned characteristics make mountain grasslands a relevant and most suitable research object: The constant, low disturbance management creates only very small confounding side effects compared to more intensively used grassland or tilled cropland.

All OC in soils originally derives from plant products, which remain in the ecosystem for periods ranging from days to millennia (Trumbore, 2000), depending on the degree of exposure to microbial decomposition. Plant production and the decomposition rate depend on pedoclimatic

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factors and nutrient availability. As a consequence, both the production and the antagonistic decomposition mechanisms in mountain grasslands are favoured by soil moisture, increasing nutrient availability and temperature (Volk et al., 2021, 2022), in a wide range of environmental conditions. Usually, higher productivity increases OC input via both aboveground litterfall and belowground root/rhizodeposition (Villarino et al., 2021). Therefore, higher plant yield in grasslands (e.g., Mitchell et al., 2021; Bai and Cotrufo, 2022; Cavender-Bares et al., 2022) and optimised management (Conant et al., 2017) are suggestive of SOC stock accrual. Despite this evidence supporting a positive linkage, the relationship is frequently disrupted by nutrient-driven allocation shifts, environmental gradients, and asymmetrical responses to global change drivers. For example, Keller et al. (2023) found that in nine grasslands, aboveground and belowground responses to fertilization were not positively correlated, despite strong aboveground stimulation. Schipper et al. (2013) and Stoner et al. (2021) showed that, e.g., phosphorus fertilisation-driven productivity increases of very different sizes may all lead to the same soil C accumulation rate in previously SOC-depleted grassland. This effect of lower C 'capture efficiency' was attributed to increased decomposition rates. Beyond soil C input as organic matter, SOC storage also depends on the difference between the current SOC stock and the maximum SOC storage capacity (Bai and Cotrufo, 2022; Georgiou et al., 2025), as well as on the effective SOC stabilisation capacity (Stewart et al., 2007). Moreover, in many traditional agronomic grassland management systems, large amounts of OC are returned via organic manure.

As a consequence, the balance of OC in situations that favour plant yield is not easy to predict. However, with respect to GHG storage for climate change mitigation and soil health for agricultural production, we deem it necessary to identify optimised management practices that favour a large SOC stock (Bossio et al., 2020), based on process understanding. To evaluate the effects of different management options on SOC resources, we investigated the influence of plant yield and the cessation of organic manuring on SOC stocks in mountain grassland topsoil in a long-term trial (1990–2022). Using low-N + P + K fertiliser applications, we generated six distinct yield levels in a hay meadow at 1200 m asl. in the Swiss Alps. To quantify the antagonistic effects of gross primary productivity (GPP) and ecosystem respiration (ER) on changes in ecosystem C stock, we also measured CO_2 exchange. We established the net ecosystem C balance (NECB) in 2022. This year was the warmest to date in Switzerland (MeteoSchweiz, 2023), since the start of continuous temperature measurements in 1864, and allowed us to observe the effect of extreme weather conditions on SOC.

To test the effects of plant yield changes and climate warming on mountain grassland SOC, we hypothesised that

1) in the long term, the different yields of the NPK fertilisation treatments would generate different amounts of OC substrate input to the soil, which in turn would be reflected in different present-day SOC stocks. We also assumed that SOC stocks would be the highest at the reference site receiving traditional farmyard manure fertilisation, due to the large OC input to the soil.
2) interannual dynamics of the SOC stock are correlated with weather conditions. SOC accumulation may be increased by favourable weather for plant production, leading to a higher OC input to the soil. Alternatively, the same weather conditions may lead to even greater OC decomposition and, consequently, smaller SOC stocks.

2. Materials and methods

2.1. Experimental site and treatments

The research site is at 1200 m a.s.l. (46.690537° N, 9.517382° E) near the village of Muldain, municipality Obervaz, canton of the Grisons (Map S1). Mean annual precipitation was 932 mm, and mean annual temperature was 7.1 °C during the experiment. It was maintained from 1989 until 2023 under continuous NPK fertilisation management. For several decades prior to the experiment, the site had been under traditional FYM fertilisation management. In sync with the local cutting regime, all plots were mown at the end of May, the end of July, and the end of September. Each plot is 2 × 5 m, with the inner 6.25 m^2 used for yield assessment. The hay-meadow represents a *Polygono-Trisetion* (Br.-Bl. et Tx. ex Marschall 1947 nom. inv.) alliance on a gently sloping (ca. 7°), south-facing plateau above the gulch of the Albula creek (ca. 750 m a.s.l.). The soil was defined as a Gleyic Fluvisol (IUSS Working Group WRB, 2022), with a sandy loam texture (27% clay, 26% silt, 40% sand) and a pH of 6.95. Soil organic C stocks and C/N values at the beginning of the experiment are shown in Figs. 4 and 5 as REF zero-year 1989.

The 24 grassland plots used in this study were a subset of the original 64-plot design (Figure S1) that received 16 different NPK fertilisation treatments in a randomised complete block design. The original design was set up to investigate the effects of P and K fertilisation on yield, together with low N fertilisation. Because our study aimed to examine plant yield effects on SOC dynamics, we selected a subset of 6 NPK fertilisation treatments that spanned the full range of plant yields associated with the full set of 16 NPK fertilisation levels. The subset of fertilisation treatments was chosen prior to the 2022 SOC and CO_2 exchange measurements. NPK treatment levels are named after the mean yield during the decade preceding our NEE measurement campaign (2013 – 2022). Nitrogen (N) is applied evenly in all treatments at 25 kg ha^{-1} $year^{-1}$, as prescribed by the fertilisation norm (Richner et al., 2017; Table 1). Phosphorus (P) and potassium (K) are applied at different rates, from factor 0–1.5, compared to the fertilisation norm.

Three additional plots, located in the surrounding grassland 15 m from the main plots in E, S, and W directions, served as reference sites for farmyard manure (FYM) management. During the experiment, they continued to receive the traditional FYM fertilisation for a medium intensity mountain meadow, consisting of two slurry and one solid manure applications. Based on the farm type, this represents an import of ca. 133 kg N_{total} ha^{-1} yr^{-1} (equivalent to 62 kg plant available N) and 2.2 t C ha^{-1} yr^{-1} (Richner et al., 2017).

2.2. Meteorological parameters

MeteoSwiss provided meteorological data specific to the experimental site at Muldain. Local time series were generated from station data using spatial interpolation onto a regular grid, followed by bilinear interpolation and local linear regression with altitude (MeteoSwiss, Grid-Data Products: Local Time Series). For the 1990–2022 period, data on daily minimum and maximum temperatures, daily relative sunshine duration, and daily precipitation were collected. For the NEE flux parameterisation period (2022 and 2023), air temperature and global radiation were provided as hourly means.

Table 1
NPK fertilisation treatment level names, rates of annual N, P and K application and recent mean annual yields (sum of three cuts) of respective treatment levels. Treatment names combine mean annual yield (4.5–7.0 t DM ha^{-1}) and the respective NPK application rates (0–1.5 × fertilisation norm). Fertiliser input rates are given as elemental atomic masses.

NPK treatment name	Fertiliser application (kg ha^{-1} yr^{-1})	Yield (2013–2022 mean; t DM ha^{-1})
4.5 N1 P0 K0	N = 25; P = 0; K = 0	4.51 ± 0.190
4.9 N1 P0 K1	N = 25; P = 0; K = 216	4.89 ± 0.207
6.4 N1 P0.5 K1	N = 25; P = 36; K = 216	6.42 ± 0.237
6.6 N1 P1.5 K1	N = 25; P = 108; K = 216	6.63 ± 0.230
6.8 N1 P1 K1	N = 25; P = 72; K = 216	6.76 ± 0.252
7.0 N1 P1 K1.5	N = 25; P = 72; K = 324	7.04 ± 0.242

2.3. Plant dry matter yield and C and N content

The grassland canopy was mown at a height of 5 cm using a finger-bar motor mower. Plant biomass was oven-dried at 105 °C to constant mass and weighed. Total C and N concentrations were determined analogously to the soil C-N analysis (c.f. below). Plant dry matter contained 46.4 (± 0.2) % C and 2.67 (±0.08) % N on average, with no significant difference between treatments.

2.4. Soil sampling and analysis

In November 2022, two soil cores per plot were obtained in all 24 NPK fertilisation and 3 FYM fertilisation plots, approximately at 1.7 m and 3.3 m distance along the 0–5 m central axis of the plot. A 5 cm inner-diameter Humax impact probe (Martin Burch AG, Rothenburg, Switzerland) with a PVC insert sleeve was hammered perpendicularly to the surface into the ground to produce an intact 20 cm soil core. This core was split into two 10 cm depth increments in the lab. All samples were dried and sieved (2 mm). Using 2.65 g cm^{-3} for rock fragment density, fine soil bulk density ($BD_{fine\ soil}$) was determined individually for every single increment sample according to:

$$BD_{fine\ soil} = \frac{mass_{sample} - mass_{rock\ fragments}}{volume_{sample} - \frac{mass_{rock\ fragments}}{\rho_{rock\ fragments}}}$$

We measured total C and N contents in bulk soil by elemental analysis (oxidation of C-CO_2 and N-NO_2 in an O_2 stream and subsequent reduction of NO_2-N_2 by a copper–tungsten granule). Separation of CO_2 and N_2 was accomplished by gas chromatography–thermal conductivity detector (GC-TCD), and quantification was performed using acetanilid as an external standard (Hekatech Euro EA 3000, Wegberg, Germany). Calcium carbonate ($CaCO_3$, C_{min}) was determined for all plots individually using a calcimeter (Agroscope institutional repository: https://link.ira.agroscope.ch/de-CH/publication/45887), based on the reaction of $CaCO_3$ with hydrogen chloride (HCl), in which the volume of CO_2 generated is proportional to the carbonate content of the sample. C_{min} was later subtracted from the elemental analyser total C values to obtain soil organic C concentrations.

SOC stock per depth increment ($SOCstock_i$) was then calculated according to:

$$SOCstock_i = SOCcon_{fine\ soil} \times BD_{fine\ soil} \times depth_i$$

where $SOCcon_{fine\ soil}$ is the concentration of organic C in the fine soil (%), and $depth_i$ is the depth of the respective soil layer (cm).

2.5. Long-term SOC stock changes

Using the protocol described above, we also analysed the SOC concentration of 792 archived soil samples (1989 – 2021) from all 24 plots. Every year at the end of October, seven cores (0 – 20 cm depth, 4 cm diameter) per plot were collected with the Edelmann drill and lumped (qualitative sampling without known sample masses or bulk density (BD) assessment). In the zero-year (1989) of the experiment, the SOC concentrations of the research plots did not differ between assigned treatment level groups. To estimate historical SOC stocks, we used soil BD and stone content values obtained for those plots during the SOC stock sampling campaign (quantitative sampling with bulk density assessment) in November 2022. For a discussion of the implications of using the 2022 BD values to estimate historical SOC stocks, please compare Section 4. Discussion

2.6. Net ecosystem productivity (NEP)

Between June 2022 and June 2023, during 12 day-and-night measurement campaigns, NEE was measured approximately biweekly. Starting in mid-April and finishing in early November, we thus covered the entire growing season. As a result of this high-frequency coverage, the dynamic development of vegetation phenology and drought events was well represented for the parameterization of NEE fluxes. NEE-day was measured under clear sky, midday conditions. NEE-night was measured not earlier than 1 h after sunset to avoid light-enhanced dark respiration (Atkin et al., 1998; Bruhn et al., 2024) and was assumed to represent ecosystem respiration (ER). We utilized dynamic CO_2 concentration, non-flow-through, transparent acrylic chambers (30 × 40 × 35 cm) that were fitted to a permanently installed polyethene ground frame to support the chambers during measurements. Chambers were sufficiently large to include the fully developed canopy (Volk et al., 2011). Each of the 24 NPK fertilisation plots contained two ground frames for parallel measurements. We tested all CO_2 concentration increase/decrease measurements for linearity and omitted those with $R^2 < 0.95$. Parallel measurements were averaged per plot if both matched this quality standard. Altered assimilation or respiration due to chamber effects (CO_2 substrate depletion, overheating, reduced diffusion gradient) during the measurement (2 min) could therefore be safely excluded.

We calculated the temperature response of ER based on NEE-night flux data (8 – 23 °C soil temperature range) during no-drought conditions, using an exponential function after Lloyd and Taylor (1994) and Ammann et al. (2007). GPP was derived as NEE-day plus ER. The light response curve of GPP was measured at fully developed canopies for 4.5 P0K0 and 7.0 P1K1.5 treatments. The shapes of both curves were not significantly different.

For a year-round CO_2 flux parameterisation between the 12 measurement campaigns during the growing season, we used soil temperature at 10 cm depth to estimate ER and global radiation to estimate GPP, following Volk et al. (2011), (2016). NEP then resulted as GPP minus ER for a given time unit.

During wintertime, when no NEE measurements were available, GPP was considered negligible. Effects of potential substrate limitation of ER during winter were considered very small, since respiration rates were extremely low at very low temperatures. Accordingly, temperature-normalized ER during wintertime was modelled to remain constant from the last fall measurement to the first measurement of the new growing period.

2.7. Net ecosystem carbon balance (NECB)

For 2022, the annual rate of ecosystem C accumulation (or C loss) was computed as NECB (Chapin et al., 2006):

$$NECB = GPP - ER - C_{harvested\ plant\ material}$$

where NECB is the net ecosystem C balance, GPP is gross primary productivity, ER is ecosystem respiration and $C_{harvested\ plant\ material}$ is organic C, exported with the annual plant harvest. All terms are expressed as annual sums of C in t ha^{-1}. Fluxes of non-CO_2 GHGs, dissolved organic and inorganic C and the lateral transport of particulate C were considered negligible and omitted, because this grassland on mineral soil is well drained and under low-N, mineral fertilisation.

This NECB contains no term for aboveground plant material (c.f. above). We assumed the ecosystem OC mass between the soil surface and cutting height to be relatively constant. Depending on the season, the perennial plants would be either green stalks and leaves or dead but not yet decomposed organic material.

2.8. Statistics

Effects of six NPK fertiliser treatment levels (4 plots per treatment level) on SOC, DM plant yield, CO_2 fluxes (NEP) and net ecosystem C balance (NECB) were analysed, using an analysis of covariance (ANCOVA). Four blocks in the array of grassland plots, oriented perpendicular to the gentle slope and each containing all treatment

levels, were entered as covariate to test for slope-dependent effects of soil properties (e.g. water content, nutrients, depth, texture). Between-treatment level differences were then tested using pairwise multiple comparisons (Holm – Sidak). If no evidence of the covariate to affect the dependent variable was found and the equal slopes assumption was met, a single factor analysis of variance (ANOVA) design was chosen. Models were run in Sigmastat 14.5 (Systat Software, Inc.). Results are presented as means ± 1 standard error. Reported differences between means are statistically significant with $P \leq 0.05$, unless stated otherwise.

Changes in dry matter yield, SOC stock, and C/N ratio over time were analysed using linear mixed-effects models (Pinheiro and Bates, 2000). Dry matter yield, SOC stock, and C/N ratio were each regressed on the fixed predictors year (continuous) and mineral fertilisation category (factor with 6 levels). Block (factor with 4 levels) and Plot were random factors (random intercepts), and a continuous, AR-1 autoregressive correlation structure was imposed on the residuals to account for repeated meabesurements over time. We used the second-order Akaike Information Criterion (AICc; Burnham and Anderson, 2002) to assess whether the year × mineral fertilisation category interaction needed to be included, and it was omitted from all three models. The linear mixed-effects models were run in R, version 4.2.5 (R Core Team, 2025), using the nlme package (Pinheiro et al., 2024). The R code and analysis output are available in the supplementary information section.

3. Results

3.1. Time effects on plant yield and soil C and N stocks

During 33 years, the mean plant yield across fertilisation treatments declined by 22%, from a five-year mean of 7.2 (± 0.19) t DM ha^{-1} yr^{-1} (1990–1994) to 5.6 (± 0.24) t DM ha^{-1} yr^{-1} (2018 – 2022). This is equivalent to an average decline rate of 0.03 t C ha^{-1} annually (Fig. 1).

In the same period, the average annual decline of the SOC stock (Fig. 2) in NPK fertilisation plots was 0.5 t C ha^{-1} yr^{-1}, resulting in a 12% drop between five-year means (97.7 t C ha^{-1} 1989–1993 mean vs. 86.4 t C ha^{-1} 2018 – 2022 mean). The 2021 – 2022 SOC stock change even resulted in a dramatic 5.4 (± 2.39) t C ha^{-1} loss. The corresponding soil N stock declined in parallel by 10% from a five-year mean of 11.20 t N ha^{-1} to 10.04 t N ha^{-1}. This synchronous decline left the resulting C/N ratio of soil organic material almost unchanged (Fig. 2).

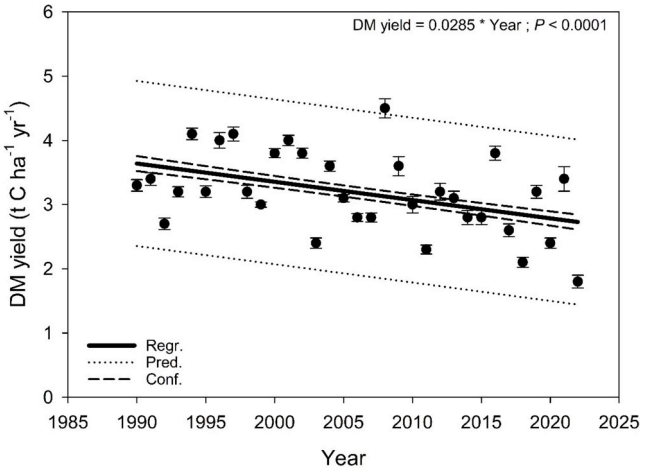


Fig. 1. Annual mean plant yield of six NPK fertiliser treatments during the long-term experiment. Linear regression followed by ANOVA on ranks shows that for all treatment levels combined, annual yield declines by ca. 0.03 t C ha^{-1} yr^{-1} since 1990. Error bars indicate ±1 SE.

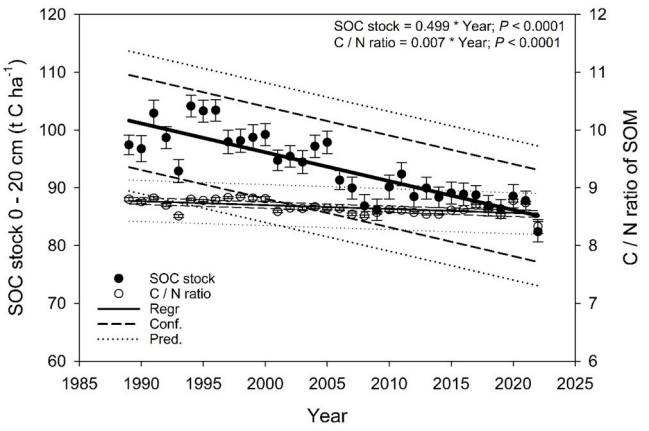


Fig. 2. The SOC stock and C/N ratio averaged over all six NPK fertilisation treatment levels. Linear regression shows that independent of the treatment level, soil OC stock declines by ca. 0.5 t C ha^{-1} yr^{-1} since 1989. The N stock declines with a similar slope (data not shown). As a result, the C/N ratio remains almost unchanged. Error bars indicate ±1 SE.

3.2. Fertilisation treatment effects on plant yield and soil C and N stocks

By the end of the experiment in 2022, an extremely warm and dry year, grassland DM yields between NPK treatment levels varied by factor 2 (from 1.1 t C ha^{-1} to 2.2 t C ha^{-1}; $P < 0{,}001$), despite all treatments receiving the same amount of N (Fig. 3). For comparison, the ten-year average difference between treatments was similarly distributed, but smaller overall (factor 1.6; c.f. Table 1).

In contrast, the 2022 SOC stocks (from 83.3 t C ha^{-1} to 89.4 t C ha^{-1}) and C/N ratios (from 7.7 to 8.6) were not statistically different between NPK fertilisation treatment levels (Figs. 4 and 5 Panel B). Notably, the 2022 SOC stock of the FYM fertilisation sites and of the zero-year of the NPK fertilisation experiment were equal to each other, but significantly higher than the mean of the 2022 NPK fertiliser plot SOC stocks (Fig. 4 Panel A). The soil C/N ratio was higher in the Reference zero-year 1989 compared to the NPK fertiliser plots in 2022 (Fig. 5 Panel A; $P = 0.002$). Linear regression showed that, between NPK treatments, SOC stocks were not correlated with the C/N ratio (data not shown).

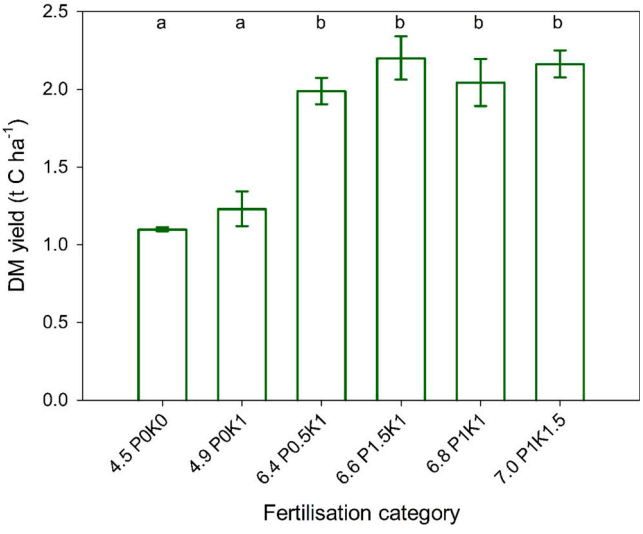


Fig. 3. Final year (2022) dry matter plant yields in t C ha^{-1}, observed in the six NPK fertilisation treatments. Different lowercase letters above the bars indicate statistically significant differences of the means. Error bars indicate ±1 SE.

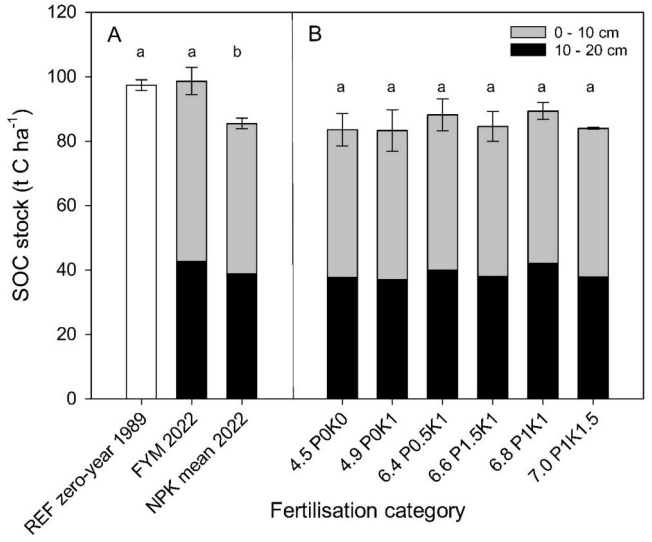


Fig. 4. Panel A) SOC stocks of the 1989 reference zero-year (REF zero-year 1989, mean of the 24 NPK plots before the experiment), the 2022 traditional FYM fertilisation plots (FYM 2022) and the 2022 NPK fertilisation treatment plots (NPK mean 2022, mean of the 24 NPK plots after the experiment). Panel B) SOC stocks of NPK fertilisation plots (4.5 P0K0 … 7.0 P1K1.5). Within each panel, different lowercase letters above the bars indicate statistically significant differences of the means. Error bars indicate ±1 SE.

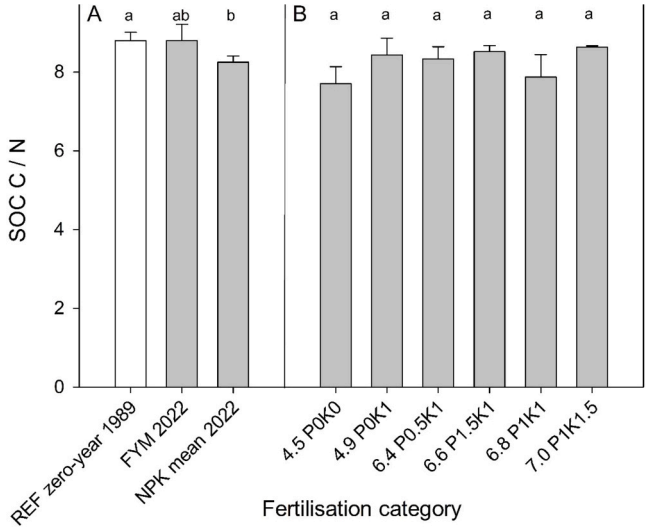


Fig. 5. Panel A) Soil organic matter C/N ratios for the 1989 reference zero-year (REF zero-year 1989, mean of the 24 NPK plots before the experiment), the 2022 traditional FYM fertilisation plots (FYM 2022) and the 2022 NPK fertilisation treatment plots (NPK mean 2022) mean of the 24 NPK plots after the experiment. Panel B) SOC C/N ratios are not different between NPK treatment levels (4.5 P0K0 … 7.0 P1K1.5). Within each panel, different lowercase letters above the bars indicate statistically significant differences in the means. Error bars indicate ±1 SE.

3.3. Weather effects

At the experimental site, the ten-year average growing season temperature (April – September mean temperature ± 1 SE) rose from 11.8 °C ± 0.17 (1991 – 2000) to 12.4 °C ± 0.27 (2001 – 2010) and to 13.0 °C ± 0.21 (2011 – 2020). Similarly, the whole year means increased (6.6 °C ± 0.152, 6.8 °C ± 0.185, and 7.8 °C ± 0.170, respectively). Across all years, we found that plant yield was negatively correlated with warmth during the growing season (growing degree days from April to September, $GDD_{April\text{-}Sept}$, Fig. 6). In the extremely warm, final year 2022 we registered an unusually small annual DM mean yield of 1.8 (± 0.10) t C ha^{-1}, that was only 53% of the 2021 yield (c.f. Fig. 1). In that same year the SOC stock dropped by 5.4 t C ha^{-1} (± 2.39), compared to 2021 (c.f. Fig. 2). Despite this, year-to-year SOC stock changes were not significantly correlated with $GDD_{April\text{-}Sept}$ in the long-term (Fig. 6). Other available climate indices (temperature means, aridity), different time frames for climate indices (e.g. GDD April - July) or a longer lag phase for the presumed SOC response (not end of same season, but end of the following season) did not produce significant correlations with the SOC stock changes either.

3.4. Net ecosystem C balance

The mean calculated NECB loss in the year 2022 was 5.3 t C ha^{-1}, averaged over NPK fertilisation treatments (Fig. 7), and nearly equal to the dramatic SOC stock loss of 5.4 t C ha^{-1} between the season means of 2021 and 2022. This implies that the NECB estimate is a quantitative proxy for the ecosystem C budget and suggests that the NECB loss is primarily due to C loss from the SOC stock. On the other hand, the significant between-treatment differences of NECB do not match the lack of between-treatment differences of the SOC stock (Fig. 4B). Also, the CO_2 flux-derived components of NECB (i.e. GPP and ER) are not significantly different between treatments. Thus, NECB differences are apparently driven by plant harvest C export. A visual comparison of ER means suggests a between-treatment difference, but the statistical power is too low to detect it.

4. Discussion

4.1. Limitations of historical SOC stock assessment

Lacking weight and volume data for the archived soil samples from 1989 to 2021, no independent bulk density (BD) values for these years could be calculated. Instead, we used the BD values obtained during our sampling campaign in 2022. This implies that the accuracy of our long-term SOC stock time series depends on constant BDs during this time. The largest potential source of BD variability is expected to result from the management change, after dedicating part of the FYM-fertilised area to the mineral fertilisation experiment. Changing from organic fertilisers to mineral fertilisers may lead to increased BD, because organic fertilizers promote aggregate formation and increase soil organic matter,

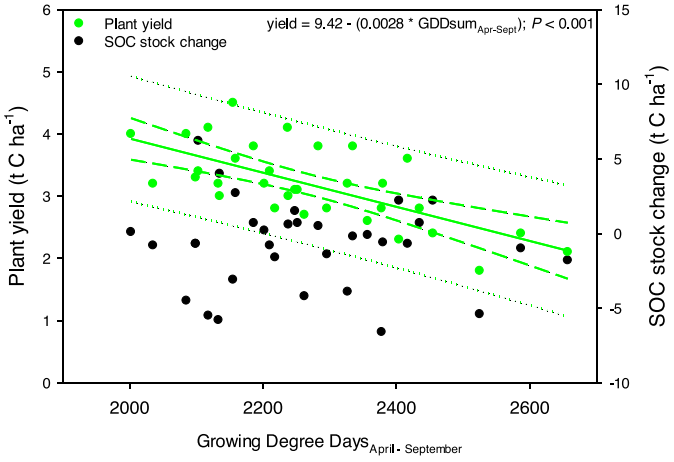


Fig. 6. Year 1990 to 2022 annual plant yield (green circles) and SOC stock change (SOC stock compared to the previous year's SOC stock; black circles). Values are the means of the six NPK fertilisation treatments, plotted against temperature sum (Growing degree days $GDD_{April\ -\ September}$). Green lines indicate linear regression model, confidence-, and prediction intervals (95%) for plant yield over $GDD_{April\text{-}Sept}$.

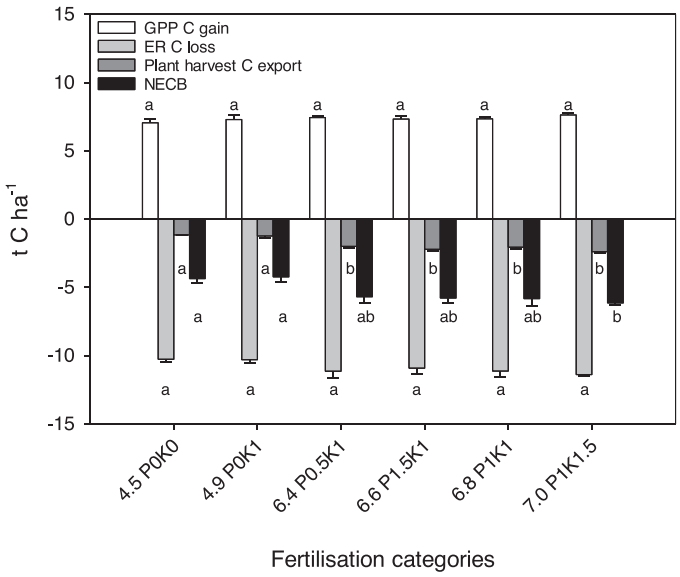


Fig. 7. The net ecosystem C balance (NECB: black bars) for 2022 by NPK fertilisation treatment, resulting from the sum of the CO_2 fluxes GPP (positive, white bars) and ER (negative, light grey bars), and organic C exported with the plant harvest (negative, dark grey bars). Different lowercase letters above bars of the same C-flux category indicate statistically significant differences. Error bars indicate ±1 SE.

which directly lowers bulk density (Acar et al., 2025). Because mineral fertiliser was spread manually, three annual manure spreadings with a tractor were omitted (Keller et al., 2019), potentially leading to reduced soil compaction and lower BD in mineral fertilisation plots. The decline in mean yields across treatments may increase BDs, due to reduced root growth and litter input, resulting in lower OC additions from roots and residues and less root-induced soil displacement (Phalempin et al., 2021). Analogously, differences in yield levels between treatments, with associated changes in root growth and litter input, may have affected BD. To quantify the effects of changing management on BD, we compared BD values measured in 2022 for each of the six mineral fertilisation treatment groups with different yields (n = 4) with those of the traditionally FYM-treated plots (n = 3), located just outside the mineral fertilisation array. One Way ANOVA yielded no significant difference (P = 0.89). Mean BD in mineral fertilisation plots was 0.91 (± 0.031) and in FYM plots 0.88 (± 0.023). With a difference of ca. + 0.03 or + 3% in NPK plots, a management effect on BD resulting from the change from FYM to NPK mineral fertilisation can thus very likely be excluded.

We have no means to quantify a potential time effect on BD, which may have affected FYM and mineral fertilisation plots alike. However, we also have no reason to assume that the continuous, extensive grassland management that succeeded arable crop production approximately 80–90 years ago (Rosenzweig et al., 2016) still produced a time effect over the last 30 years. If the 12% SOC stock decline estimate were really in error, then this would require a BD increase of the same magnitude. Judging from the minute differences reported above, this seems unlikely.

4.2. Plant yield influence on SOC stock change

The high-montane location of the site suggests that plant growth is limited by temperature (Wang et al., 2013). Rising temperatures under climate change are likely to have positive effects on plant yield, as thermal energy becomes less limiting. However, contrary to our expectations, we observed declining mean annual yields with rising GDDs between 1990 and 2022 (Fig. 6), suggesting that water availability limitations had replaced thermal limitations (Möhl et al., 2022; Volk et al., 2022). Since we also observed a 12% average decline in SOC stock in total, or 0.5 t C ha^{-1} yr^{-1} (Fig. 2), this observation fully matched our expectations, as we hypothesised that SOC stock change would depend on plant yield change. Thus, in the long term, the parallel decline in plant yield and SOC stocks appeared to support the notion that SOC development is yield-dependent.

Every year, our NPK fertilisation treatment generated a large yield gradient between treatment levels. These fertilisation-driven yield differences were independent of the potentially climate-confounded, long-term plant yield development across decades. At the beginning of the experiment, we observed a uniform level of plant yield. We therefore assume that in the 1990s the nutrient supply from the soil was dominated by carry-over effects from past decades of traditional FYM application, because FYM builds organic matter and nutrient reserves that continue to release nitrogen and sustain productivity for several years after application ceases or mineral fertilisation is introduced (Riley, 2016; Schröder et al., 2007). After cessation of the FYM management, over the course of the experiment, soil nutrient availability increasingly reflected the respective NPK fertilisation treatment. As a result, different yield levels developed and the P- and K-supply driven difference between smallest and largest yield (Table 1) was factor 1.6 (ten-year mean) and factor 2 (the last year of the trial; Fig. 3). Contrary to our hypothesis, this yield gradient was not mirrored by the SOC stocks measured in 2022, at the end of the experiment (Fig. 4 B). We therefore conclude that in our experiment plant yield is not the driving factor for SOC stocks in the NPK-fertilised grassland.

4.3. Temperature influence on SOC stock change

Increasing temperatures may accelerate microbial C-turnover and thus favour SOC decomposition (Bellamy et al., 2005; Bond-Lamberty and Thomson, 2010). However, the temperature sensitivity of SOC decomposition has been shown to differ widely between organic compounds and to interact with other environmental constraints (e.g. Davidson and Janssens, 2006; Subke & Bahn, 2010; Conant et al., 2011; Schmidt et al., 2011). Despite this, a high sensitivity of apparently labile components during the very first years after warming is widely acknowledged (e.g. Lugato et al., 2021). Research on subalpine grassland has shown dramatic 14% SOC losses in turf monoliths subjected to a + 3.0 °C increase in growing-season temperature for 5 years (Volk et al., 2022).

Based on the evidence above, it is likely that the gradual increase in the mean temperature over decades adds another reason for declining SOC stocks in our field trial. Firstly, to distinguish potential long-term effects of temperature on SOC stock from the effect of switching from FYM fertilisation to low-N mineral fertilisation, we compared soil C analyses from the year before the experiment started (1989) with soil samples from the neighbouring, continuously FYM treated sites in 2022 (Fig. 4A). But these FYM sites showed no SOC stock difference, despite a 1.2 °C April – September mean temperature increase over time. This leads us to dismiss the assumption that the 1.2 °C warming in three decades would cause a SOC stock loss in our experimental grassland under FYM fertilisation. Next, we postulated that archived annual soil samples could be used for short-term (between-year) temperature-effect analysis. The year-to-year weather effect on SOC stock change can be positive or negative and is independent of the long-term trend of climate warming and decreasing soil N availability. Nevertheless, no significant correlation was found between temperature (GDDs) and SOC stock changes across years (Fig. 6). Neither test indicates a detectable temperature effect on SOC stock in our data.

Despite the lack of a temperature signal in the long-term SOC stock response, the extreme decline between 2021 and 2022 suggests that the decline in SOC stock was modulated by seasonal weather conditions, as 2022 was the warmest year on record to date (MeteoSchweiz, 2023). This result was supported by our NECB analysis, which showed a nearly identical C loss based on C flux measurements rather than SOC analyses.

4.4. NECB-sensitivity in the detection of SOC stock changes

Averaged over NPK treatments, the 2022 NECB (Fig. 7), derived from C fluxes, resulted in the same ecosystem C stock loss that was observed in the SOC stock between 2021 and 2022 (Fig. 1). Apparently, plant harvest and CO_2 exchange balanced in the NECB cover all quantitatively relevant C-fluxes in the perennial grassland of our study. We assume that in the 2022 NECB, exceptional weather conditions have caused large and immediate SOC stock losses, resulting in a release of ca. 5 t C ha^{-1} yr^{-1} in the form of CO_2 from the ecosystem to the atmosphere. If not compensated by similarly large ecosystem C gains under very favourable weather conditions, mountain grassland soils, like those on our study site, may develop into substantial GHG sources.

If, as concluded above, the NECB quantitatively reflects ecosystem C stock changes, then it should show no differences between NPK treatments, since there were none in SOC stock. However, NECB was significantly more negative at maximum yield than at the two low-yield levels. We excluded ecosystem C loss via harvest as a source of error: Cutting the grass canopy at a fixed height (ca. 5 cm) leads to a relative underestimation of yield in low canopies compared to high canopies, but it correctly estimates the total export of organic material.

Also, the ER and the NEE-derived GPP value may have introduced an error into our NECB. Nighttime ER measurements, which were used to parameterise both night and day ER, and thus GPP, do not provide a precise estimate of diurnal ER dynamics (Heskel et al., 2013), but these shortcomings do not affect the NEP estimate. Consequently, we assume that our NEE measurements underestimated the difference in GPP between NPK treatments. Low-yield canopies may have been assessed at their maximum assimilation capacity, as intended by the protocol. Very high-yield canopies, on the other hand, may have suffered from reduced assimilation capacity, due to measurement-cuvette effects on canopy structure. As a result, the NECB is found to be sensitive enough to represent the extreme-year ecosystem C-fluxes correctly, averaged across fertiliser treatments, but fails to distinguish between fertiliser treatments.

4.5. Organic C input and N input as drivers of SOC stock change

Cessation of FYM fertilisation simultaneously led to a reduced C input of ca. 2.2 t C ha^{-1} yr^{-1} and reduced plant available N input from ca. 62 kg ha^{-1} yr^{-1} to 25 kg ha^{-1} yr^{-1} (Richner et al., 2017). These side effects of the NPK treatment experiment suggest a lack of substrate for soil OC formation, consistent with the observed annual decline in the SOC stock. Accordingly, the termination of organic matter input via FYM in 1989 is a sufficient reason for the new, lower SOC stocks observed in 2022 (Fig. 4A). By the same token, maintaining the traditional FYM management, thus importing large amounts of C and N, had resulted in unchanged SOC stocks after 33 years. In addition, the decline of N-supply may have contributed to declining SOC stocks, if low N-supply would have triggered N-mining processes, as discussed below.

Despite large differences in yield, SOC stocks were not different between NPK treatment levels after about 30 treatment years (Fig. 4B). Based on the extremely complex interactions among litter-N content, organic soil-N, fertiliser mineral-N and soil organic C dynamics (Neff et al., 2002; Knorr et al., 2005; Hobbie, 2005), we speculate that soil N availability might be limiting soil C storage. This may offer a plausible explanation for the observed pattern. Generally, microbial biomass is homeostatic in terms of elemental stoichiometry (Cleveland and Liptzin, 2007; Xu et al., 2013). This requires microorganisms to maintain their biomass stoichiometry independent of the stoichiometry of their substrate. One symptom of maintaining this stoichiometric homeostasis is a changing CUE (Manzoni et al., 2012; Riggs & Hobbie, 2016). We assume that the constant C/N ratio we observe in SOC, despite large C losses (Fig. 2), reflects the homeostatic behaviour of microbial biomass. A consequence of N-driven CUE changes and microbial homeostasis under decreasing N supply conditions is N-mining at the expense of accelerated SOC decomposition. For example, Spohn (2015) found that soil microorganisms respire more C, both in absolute terms and per unit microbial biomass C, when decomposing N-poor substrate and that, conversely, N fertilisation, rather than P or K fertilisation, increases microbial C use efficiency (Spohn et al., 2016). Also, Poeplau et al. (2018) find highly different SOC stocks associated with different N doses under NPK fertilisation. In similar mountain grasslands in the Swiss Alps, we compared the effects of N supply, representing typical management scenarios or increased atmospheric N deposition. For example, Volk et al. (2025) found that the same N supply rate in the form of FYM was associated with the same topsoil SOC stock (89.6 ± 4.2 t C ha^{-1}, 0–20 cm) that was found here. In both higher and lower FYM applications, smaller SOC stocks were observed. In a different, less productive subalpine pasture at 2200 m asl. there was a strong N-related increase in SOC stock at low deposition rates up to 10 kg N ha^{-1} yr^{-1} and smaller increases at high deposition rates up to 50 kg N ha^{-1} yr^{-1} (Volk et al., 2016). Yet, in another study with a maximum deposition treatment of 15 kg N ha^{-1} yr^{-1}, Volk et al. (2022) observed no SOC response, suggesting no mitigation of a (presumed) N limitation of microbial activity at this low N input level.

Despite lacking our own data on, e.g., microbial community composition, enzyme activities, or CUE, we speculate that low N availability led to N-mining and subsequently reduced SOC stocks over the decades (Craine et al., 2007). This process would then continue until the SOC stock has reached a new equilibrium that matches the new N availability. The identical N availability across the different NPK treatments is assumed to have acted as the limiting factor for soil C storage. The above arguments from the literature suggest that the fertilisation N input level may have determined the SOC stock observed in this experiment.

5. Conclusion

The long-term decline in mean plant yield is likely due to declining nutrient supply compared to pre-experimental conditions. Cessation of FYM fertilisation and the concurrent lack of OC and N input led to SOC stocks declining to the same level across different NPK treatments. This suggests that differences in grassland yield resulting from NPK fertilisation are not a significant modulator of SOC stock in our experimental setup. Instead, we speculate that the uniformly low N availability imposes stoichiometric limitations on microbial decomposition, explaining the uniform SOC stocks observed after 30 treatment years. It is plausible that increased OC substrate input from higher plant yields in high mineral fertilisation treatments is compensated for by antagonistically acting increased ecosystem respiration. Surprisingly, in the context of our experiment, no significant correlation of SOC stock decline with temperature was observed.

These findings suggest that management practices aiming at increased yield do not necessarily support larger SOC stocks. On the other hand, traditional FYM application management helps maintain SOC stocks. In conclusion, over the last three decades, the present-day mountain grassland SOC stock in our experiment was likely maintained through OC and N import via FYM, originating either from the same grassland or from external sources.

CRediT authorship contribution statement

Matthias Volk: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Elisa R.R. Filippini:** Investigation, Formal analysis. **Sonja G. Keel:** Writing – review & editing.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2026.110810.

Data availability

Data will be made available on request.

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