Effects of land use and climate on carbon and nitrogen pool partitioning in European mountain grasslands

Seeber, Julia

2022-05-20

Seeber , J , Tasser , E , Rubatscher , D , Loacker , I , Lavorel , S , Robson , T M , Balzarolo , M , Altimir , N , Droesler , M , Vescovo , L , Gamper , S , Barancok , P , Staszewski , T , Wohlfahrt , G , Cernusca , A , Sebastia , M-T , Tappeiner , U & Bahn , M 2022 , ' Effects of land use and climate on carbon and nitrogen pool partitioning in European mountain grasslands ' , Science of the Total Environment , vol. 822 , 153380 . https://doi.org/10.1016/j.scitotenv.2022.153380

http://hdl.handle.net/10138/343481
https://doi.org/10.1016/j.scitotenv.2022.153380

unspecified
submittedVersion

Effects of land use and climate on carbon and nitrogen pool partitioning in European mountain grasslands

Julia Seeber[ab§], Erich Tasser[b§], Dagmar Rubatscher[a], Ingrid Loacker[a], Sandra Lavorel[c], T Matthew Robson[d], Manuela Balzarolo[e], Nuria Altimir[f,k], Matthias Drösler[g], Loris Vescovo[h], Sonja Gamper[a], Peter Barančok[i], Tomasz Staszewski[j], Georg Wohlfahrt[a], Alexander Cernusca[a], M.-Teresa Sebastia[f,l], Ulrike Tappeiner[ab] and Michael Bahn[a*]

[a] Department of Ecology, University of Innsbruck, Sternwartestrasse 15, 6020 Innsbruck, Austria

[b] Institute for Alpine Environment, Eurac Research, Drususallee 1, 39100 Bozen/Bolzano, Italy

[c] Laboratoire d'Ecologie Alpine, CNRS, Université Grenoble Alpes, Université Savoie-Mont Blanc, 38000 Grenoble, France

[d] Organismal and Evolutionary Biology, Viikki Plant Science Centre (ViPS), University of Helsinki, 00014 Helsinki, Finland.

[e] PLECO (Plants and Ecosystems), Department of Biology, University of Antwerp, 2610 Wilrijk, Belgium

[f] Laboratory of Functional Ecology and Global Change (ECOFUN), Forest Sciences Centre of Catalonia (CTFC), Solsona, Spain

[g] Institute of Ecology and Landscape University of Applied Sciences Weihenstephan-Triesdorf Am Hofgarten 1, 85354 Freising

[h] Sustainable ecosystems & bioresources department, Research and Innovation Center, Fondazione Edmund Mach, San Michele all'Adige, 38010, (TN), Italy

[i] Institute of Landscape Ecology, Slovak Academy of Sciences, Štefánikova 3, P.O.Box 254, 814 99 Bratislava, Slovakia

[j] deceased; formerly: Institute for Ecology of Industrial Areas, 6 Kossutha St., 40-844 Katowice, Poland

[k] Institute for Atmospheric and Earth System Research (INAR), University of Helsinki, 00014 Helsinki, Finland

[l] Group GAMES, Department of Horticulture, Botany and Landscaping, School of Agrifood and Forestry Science and Engineering, University of Lleida, Lleida, Spain

[§] these authors contributed equally as first authors

[*] Corresponding author: Michael.Bahn@uibk.ac.at

Abstract

European mountain grasslands are increasingly affected by land-use changes and climate, which have been suggested to exert important controls on grassland carbon (C) and nitrogen (N) pools. However, so far there has been no synthetic study on whether and how land-use changes and climate affect the partitioning of these pools amongst the different grassland compartments. We analyzed the partitioning of C and N pools of 36 European mountain grasslands differing in land-use and climate with respect to above- and belowground phytomass, litter and topsoil (top 23 cm). We found that a reduction of management intensity and the abandonment of hay meadows and pastures increased above-ground phytomass, root mass and litter as well as their respective C and N pools, concurrently decreasing the fractional contribution of the topsoil to the total organic carbon pool. These changes were strongly driven by the cessation of cutting and grazing, a shift in plant functional groups and a related reduction in litter quality. Across all grasslands studied, variation in the impact of land management on the topsoil N pool and C/N-ratio were mainly explained by soil clay content combined with pH. Across the grasslands, below-ground phytomass as well as phytomass- and litter C concentrations were inversely related to the mean annual temperature; furthermore, C/N-ratios of phytomass and litter increased with decreasing mean annual precipitation. Within the topsoil compartment, C concentrations decreased from colder to warmer sites, and increased with increasing precipitation. We conclude that site-specific conditions need to be considered for understanding the effects of land-use and of current and future climate changes on grassland C- and N-pools. As soils can lose C faster and more easily than they are able to gain it, particular care must be taken in identifying appropriate management measures to minimise soil C losses from grasslands.

Keywords: Climate controls; Intensification; Abandonment; Plant functional groups; Litter; Root; Phytomass partitioning; Plant and soil C/N ratios; Soil organic carbon pool

Introduction

Grassland ecosystems cover about 15% of the European land area (FAO, data from 2014), where they are usually managed by cutting or grazing and are important for fodder production and preserving soil and water resources, as well as biodiversity (Carlier et al., 2009; Jäger et al., 2020; Tasser et al., 2020). They are also able to store a large amount of carbon (C), the actual amount of C depending on the current and historical land use, soil properties including pH and moisture content, N availability as well as the composition of the vegetation and the soil microbiome (Conant et al., 2017; Grigulis et al., 2013; Poeplau et al., 2018; Smith, 2014; Soussana et al., 2006). Currently, European grasslands predominantly act as carbon sinks (Berninger et al., 2015; Schulze et al., 2010), however, the ability of grasslands to sequester C is strongly dependent on land management (Poeplau and Don, 2013; Poulton et al., 2018; Reed et al., 2021; Smith, 2014; Stumpf et al., 2018; Ward et al., 2016). The long-term C sink strength of terrestrial ecosystems relies on their productivity and the turnover of C in the different plant and soil C pools (Carvalhais et al., 2014; Li et al., 2018; Wu et al., 2020). While grassland intensification generally increases productivity, it also tends to increase the turnover of C when nitrogen (N) availability is increased and thus grassland areas can also become a source (Wohlfahrt et al. 2008; Marcolla et al. 2011). Conversely, decreasing management intensity and abandonment of grasslands generally leads to decreased productivity and C and N turnover (Chang et al., 2021; Leifeld et al., 2015). However, there are still large uncertainties as to the consequence of altered grassland management and abandonment on the size of the different above- and below-ground C and N pools (Fornara et al., 2020).

Besides land management, climate may have a significant impact on the C balance of grasslands (Chang et al. 2015, Wang et al. 2021). Global mostly model-based analyses highlight that grassland-related land-use change plays a more important role than climate in altering soil organic carbon (Li et al. 2017) and the greenhouse gas balance (Chang et al. 2021). Similarly, a recent field-based study in Northern China suggests that land use is the main driver for soil organic carbon stock changes, while the effects of climate may differ regionally. To date there is a general lack of studies testing how the effects of land management and land-use change on above- and belowground C and N pools are altered by background climatic conditions.

Grasslands are an important component of traditional mountain agriculture and shape the resulting diverse cultural landscapes in European mountain regions. They serve as summer pastures and supplementary fodder suppliers for the winter months, and have been particularly affected by widespread changes in management and land use, including intensification and, more frequently, abandonment during the past decades (Kozak et al., 2017; Tasser et al., 2005). Despite a variety of agricultural and environmental policy support measures, the change in mountain agriculture in the Alps, which started in the middle of the last century, could not be stopped (Fleury et al., 2013; Hinojosa et al., 2019). Low incomes, a lower degree of innovation compared to other economic sectors, limited flexibility, global competition and the unfavourable topographical site conditions mean pose severe constraints on the economic competitiveness of mountain agriculture. In some Alpine regions this has led to an intensification of agricultural management or a change to more productive land-use types such as fruit and wine cultures, while in other regions there has been a collapse of agricultural structures and land use (Egarter Vigl et al., 2017). Especially, the abandonment of cutting and grazing activities supports the emergence of woody plants (Vidal et al., 2020) and leads to a decrease in tissue N concentrations and a slowing down of C fluxes and N cycling, and an accumulation of above- and below-ground phytomass (Bahn et al., 2006; Gamper et al., 2007; Grigulis et al., 2013; Harris et al. 2018; Legay et al., 2014; Robson et al., 2010; Schmitt et al., 2010; Szukics et al., 2019; Tasser et al., 2021; Zeller et al., 2000). However, it is less clear whether and to what extent land management and land-use changes in mountain grasslands alter soil C accumulation (Meyer et al., 2012; Poeplau and Don, 2013), and their consequences for the partitioning of C and N between the major dynamic pools in phytomass, litter and topsoil are not yet well understood (Garcia-Pausas et al., 2017). Furthermore, there is a lack of understanding whether and how climatic conditions alter the effects of land use on C and N pool partitioning in mountain grasslands.

Based on a unique data set, collected using a harmonized approach, we analyzed the C and N pools in the above- and belowground phytomass, litter and topsoil from 36 European grasslands along land management and climatic gradients. We tested the hypotheses that with decreasing intensity of land use (i) grassland C and N pools increase, while tissue N concentrations decline, and (ii) the partitioning of C and N pools shifts from above-ground pools to litter and below-ground pools. We also expected that (iii) climate alters land-use effects on C and N pools, colder and wetter climates increasing belowground C and N pools, but decreasing C and N tissue concentration, with consequences for land use effects on C and N pools and their partitioning.

Methods

Study sites

We collected data from twelve mountain locations across Europe, consisting of grasslands differing in management intensity as well as abandoned grasslands (Table 1, Fig. 1). Altogether, our study comprised 36 grasslands (18 hay meadows, 10 pastures, 8 abandoned grasslands), encompassing a latitudinal range from 42 to 49° N, and an elevational range from 530 to 1966 m a.s.l.. The study sites are located in different biomes (Beck et al., 2018): the sites Alinya, Lautaret and Amplero are located in the transition zone from temperate, dry and hot summer climate to cold, mesic and warm summer climate. All other areas are in the cold climate zone with warm summers and without a dry season. The areas higher up in the Alpine region are characterized by cool summers. Mean annual air temperature and mean annual precipitation of the sites ranges from 2.5 to 10.0°C and 730 to 1900 mm, respectively. The soils are mainly Cambisols and Leptosols with a bulk density between 0.59 and 1.47 g cm^{-3}.

Each location comprised at least one land-use type that could be attributed to each of the three land-use types ’hay meadow‘ [M], ’pasture‘ [P] and ’abandonment‘ [A]. The M were divided into two management intensity classes, which are differentiated by fertilisation, namely into fertilized [MF] and unfertilized [MU] meadows. Fertilized hay meadows were fertilized with natural and/or artificial manure at least once a year and mown two to four times per year (see Table 1a). In contrast, unfertilized managed hay meadows [MU] were mown once every one or two years and were fertilized only once every few years. Both types were occasionally grazed at the end of the growing season. Pastures were mostly lightly managed, with sheep or cattle grazing during the summer months with less than 0.9 livestock units (LU) per hectare. Nevertheless, we distinguished between two intensity classes: low intensity class with a short grazing period (< 3 months) and/or low number of animals (< 0.9 LU ha^{-1}) and high intensity class with a long grazing period (> 3 months) and/or high number of animals (> 0.9 LU ha^{-1}). Abandoned sites were previously arable land or mown or grazed grasslands and had been abandoned for less [A1] or more than 30 years [A2]. Site, climate and soil characteristics are given in Tables 1a and 1b.

Sampling

In all the grassland ecosystems studied, samples were taken following a standardised procedure following the same protocol. Above-ground phytomass was clipped to the ground surface (n=2-4 replicates per site, 30 x 30 cm) when peak biomass was reached (typically in June or July) and was separated into functional groups (grasses, leguminous and non-leguminous forbs, dwarf shrubs, cryptogams) and dead phytomass. The above-ground phytomass of trees with a height > 0.2 m was not considered. Below-ground phytomass was collected to a depth of ≤23 cm, using a core sampler with a diameter of 7.7 cm. At the sites at Passeiertal, Stubaital, and Berchtesgaden below-ground phytomass was further separated into classes of different diameter (fine roots: <2 mm; coarse roots: >2 mm). Finally, the litter was harvested twice, at the beginning and the end of the growing season.

The dry weight of the above- and below-ground phytomass was measured after drying at 80°C until constant weight. Topsoil (0-23 cm depth) was sieved (<2mm) and dried at 105°C. C and N concentrations of the above- and below-ground phytomass and the topsoil were measured with elemental analysers. Soil standards (Leco 502-308, Leco, St Joseph, Michigan, U.S.A.) and "Orchard Leaves" (Leco 502-055, Leco, St Joseph, Michigan, U.S.A.) were used as references for elemental analysis.

Statistical analysis

We applied linear mixed effects models to test for the effect of land use, climate and topsoil parameters (fixed effects) on C- and N-concentrations as well as on C/N within each pool (phytomass, litter, roots and topsoil). Due to a nested sampling design, site was included as a random effect to account for site specific variations. To avoid multicollinearity between predictors, we evaluated correlation matrices (Fig. S1) between all available site, climate, and soil parameters (see Table 1a and 1b) and functional groups (Table S1). As threshold for multicollinearity we used a correlation coefficient of $r = 0.5$ between predictors. The following predictors were then chosen for the full model: land-use, mean temperature and mean precipitation as climate parameters, clay content, N-concentration, and pH as topsoil parameters. We applied stepwise backward selection procedures to obtain the best model for each dependent variable (starting from the full model the predictor with the highest *p*-value was deleted, until only significant predictors remained). As criteria for the best model we used the Baysian information criterion (BIC, the model with the lowest BIC is considered the best one, Claeskens and Hjort 2008) and model deviance (a measure of goodness of fit).

To analyse whether climate (mean temperature and mean precipitation) had differential effects on C- and N-concentrations of different land-use types, we calculated linear models with land-use, mean temperature and mean precipitation as explanatory variables. All analyses were conducted using the open-source statistical programming language R (version 3.5.2, R Core Team, 2018) in R Studio (version 1.1.447, RStudio, 2018). Linear mixed effects models were analysed with the R package *lme4* (Bates et al., 2015).

Results

Phytomass components and plant functional groups

Across all sites studied, grasslands abandoned less than 30 years ago (A1) held the largest amount of above-ground phytomass (Fig. 2, Table 1). While above-ground phytomass (excluding trees) declined in older abandoned grasslands (A2), the litter layer increased compared to other sites. Across all sites, the smallest phytomass and highest soil organic C pools were generally found in pastures. The proportion of above-ground phytomass varied considerably between land-use types, ranging from 41% (MU) to 10% (A1) of the total phytomass. Grasses and forbs were the most prevalent phytomass components on meadows (MF, MU), while on abandoned sites dwarf shrubs, necromass (A1, A2) and cryptogams (A1) made up the largest proportion of phytomass.

The mean amount of litter increased significantly from intensively mown and grazed sites (MF, P) to extensively managed (MU) and abandoned grasslands (A1). Abandonment for more than 30 years (A2) resulted in by far the highest litter accumulation (80 times greater than in MF).

Across sites, the below-ground phytomass was lowest on intensively managed areas (MF), and was similar on MU, P and A1, while highest on A2.

The main factors significantly affecting the amount of total phytomass were abandonment (Table 2) and climate. While the above-ground phytomass was negatively correlated and the litter material was positively correlated with mean annual precipitation, the below-ground phytomass was positively correlated with mean annual temperature. Remarkably, the changes in land use affected above-ground phytomass much less than below-ground phytomass.

Sites with higher leaf N pools were associated with a higher abundance of dwarf shrubs, which increased above-ground phytomass, and a higher N pool in the litter. The amount of below-ground phytomass was negatively related to the topsoil pH.

Carbon and nitrogen pools

The total C and N pools differed significantly between land-use types (Fig. 3). Topsoil pools (top 23 cm) were the largest for both C and N, followed by below-ground phytomass and litter. The C pool was lowest in the intensively used (MF) meadows, intermediate for the lightly used unfertilized meadows (MU), the pasture (P) and the recently abandoned area (A1) and highest for the old abandoned area (A2).

N pools were largest in the lightly used unfertilized meadows (MU) and the old abandoned areas (A2), and significantly smaller in recently abandoned areas (A1) and intensively used meadows (MF), respectively.

The general trends for above- and belowground phytomass and litter were similar: with decreasing land-use intensity C concentrations and C/N ratios increased, while N concentrations decreased; with increasing time since abandonment, these trends reversed (Fig. 4). Our models showed that, next to land-use intensity, the main driver for these trends was mean annual precipitation, especially for the above-ground phytomass and the litter compartment (Table 2). Within the topsoil compartment the patterns were less clear; however, in grasslands abandoned for more than 30 years C and N concentrations significantly increased (Fig. 4), and the associated increase in topsoil C/N ratios was mainly driven by mean annual temperature, pH and clay content (Table 2).

Effects of climate on carbon and nitrogen concentrations

Climate factors, especially mean annual temperature, had diverging effects on C and N concentrations between land-use types (Tables 3, S2). For some models, the data availability was too low to depict clear patterns; however, we did find some general trends in our data. Across grasslands, increasing mean annual temperature resulted in lower C concentrations in above-ground phytomass and higher C concentrations in litter (Table 3). Temperature had no clear effects on N-concentrations in any of the compartments.

Mean annual precipitation was negatively related to C and N concentrations of the below-ground phytomass across land-use types (Table 3). At sites with higher mean annual precipitation, C concentrations in the litter were reduced and N concentrations were increased. Within the topsoil compartment, C and N concentrations as well as C/N ratios increased with an increase of precipitation, but decreased with increasing mean annual temperatures (Table 3). Overall, some climate-land use interaction effects were observed. An increase in temperature with a simultaneous reduction in land-use intensity mostly led to a decrease in the C and N concentrations in the above-ground phytomass and in the topsoil, while the C and N concentrations increased in the below-ground phytomass (exception: C concentration at A1) and in the litter. A higher amount of precipitation led to opposite effects when it was associated with a reduced land-use intensity: C and N concentrations decreased in the below-ground phytomass and in the litter but increased in the above-ground phytomass and in the topsoil.

Discussion

Our study shows that in European temperate mountain grasslands the combination of land use and climate significantly influences the partitioning of organic C and N pools between vegetation and topsoil and within phytomass compartments. Overall, the reduction of land-use intensity and the abandonment of managed grasslands increased especially the fraction of C and N in above-ground phytomass, the litter layer and in the topsoil, while it had much smaller effects on the fraction of C and N in the below-ground phytomass. In general, the fractional contribution of the topsoil to the total organic carbon pool decreased with decreasing management intensity and with increasing time since abandonment.

The increased proportion of C in phytomass and litter after abandonment could have been caused by several factors. On abandoned sites, a lower nitrogen availability (Robson et al., 2010; Zeller et al., 2000), a higher fraction of necromass and a compositional shift from grasses and forbs towards sedges and dwarf shrubs (Gamper et al., 2007; Mysterud et al., 2011) led to an increase in the C/N-ratio of the total above-ground phytomass. Generally, low leaf/stem-ratios and low tissue N concentrations, which are characteristic for grasslands dominated by species with a conservative resource use strategy such as sedges and dwarf-shrubs (Wright et al., 2004; Gamper et al., 2007; Grigulis et al., 2013), contributed to the high overall above-ground phytomass C/N-ratio at these sites. High C/N ratios are associated with reduced litter quality and slow down litter decomposition (Cortez et al., 2007; Liu et al., 2006; Steinwandter et al., 2019), which was confirmed experimentally at three of the study sites (Fortunel et al., 2009; Gamper et al., 2007). The reduced litter decomposition rate could be a consequence of soil microbial communities, with high fungi/bacteria ratios, typically associated with low primary productivity (Bardgett et al., 1996; De Deyn et al., 2008; Grigulis et al., 2013; Karlowsky et al., 2018; Legay et al., 2016).

N limitation does not automatically reduce C turnover in the topsoil (Kirschbaum et al., 2008), and nutrient availability is generally unrelated to soil organic matter accumulation rates (Rees et al., 2005). Nevertheless, many studies as also this study highlight the decreasing soil organic matter through agricultural fertilization or through higher atmospheric nitrogen deposition (Dawson and Smith, 2007; Guo and Gifford, 2002; Jones et al., 2017), though these effects remain controversial and depend on local soil and climate context (Whitehead 2020). Our results revealed highest C and N pools on abandoned areas and on extensively used hay meadows, where due to one cut per year or even a cut every 2-3 years only a part of the phytomass is removed by management. It is generally assumed that cutting of hay meadows leads to a biomass removal of 80%, while 20% of the biomass are harvest losses (Rotz and Muck 1994; van der Linden et al. 2015). Biomass removal of predominantly grazed areas has been estimated to be ca. 50% due to a high share of non-productive areas (weed-infested areas, dwarf shrubs, stones) and a high part of non-grazed biomass (Buchgraber 2018; Egger et al. 2004). Thus, extensive grazing in particular promotes C gains more than C losses, leading to comparatively high carbon stocks in lightly managed pastures (Conant et al., 2017; Dawson and Smith, 2007; Rees et al., 2005; Viglizzo et al., 2019). This is also partly related to a more rapid annual turnover of shoot material and changes in species composition towards conservative grasses producing a denser and fibrous root system (Roumet et al., 2016). However, more intense grazing has been shown to distinctly reduce above- and below-ground C pools (Zhou et al., 2019).

Rhizodeposition, a further potential carbon source, has been suggested to be of minor importance for the input of organic carbon to grassland topsoils compared to root turnover (but see Pausch and Kuzyakov, 2018), since root litter tends to be more recalcitrant to degradation (Rees et al., 2005; Soussana et al., 2006, but see Schmidt et al., 2011). We found a significantly higher fractional contribution of fine roots on managed hay meadows but a distinctly higher mass of both fine and coarse roots on the abandoned, as compared to the meadow and pasture sites. Gill and Jackson (2000) suggested that in shrub-invaded ecosystems a lower proportion of root biomass would turn over and die annually compared to grass-dominated ecosystems, which would likewise hold true for our dwarf-shrub-dominated abandoned mountain grasslands, characterised by high C/N-ratios. In contrast, pastures are characterised by comparatively short root turnover times (Leifeld et al., 2015, 2009; Stewart and Frank, 2008), resulting in an increased input of C and N into the soil profile as fine root stocks were rapidly decomposed (Iversen et al., 2008).

As changes in the topsoil carbon pool are very slow (Jones and Donnelly, 2004; Rees et al., 2005), especially in the case of low-quality plant- and root litter, the contribution of the topsoil to the total organic carbon pool on abandoned sites might increase with time. Results from the literature are manifold (as summarized by Deng et al., 2016), suggesting that abandonment leads to a significant carbon and nitrogen accrual (McKinley and Blair, 2008) and an accumulation or a release of topsoil carbon depending on site conditions (Soussana et al., 2006); some studies also indicate that woody plant encroachment does not alter soil carbon stocks in grassland (Ortiz et al., 2016; Poeplau and Don 2013; Risch et al., 2008; Schedlbauer and Kavanagh, 2008) and even caused a decrease in soil carbon and nitrogen stocks by 15 and 20% following land-use change from pasture to conifer plantation (Guo et al., 2007). Our study indicates a minor increase in the topsoil carbon stocks and a decrease in the topsoil nitrogen stocks due to abandonment. This is consistent with findings from a detailed study using radiocarbon-based estimates of soil C turnover, which suggests that abandonment of mountain grassland leads to a transient storage of C in the labile particulate organic matter pool, which is likely not sequestered in the long term (Meyer et al., 2012). Guidi et al. (2014) demonstrated that natural forest succession on abandoned grasslands led to a decline in physical soil organic carbon stability in the mineral soil, suggesting that carbon may become more susceptible to management and environmental change.

Despite the consistent general trends discussed above, variations between individual grasslands were also found, which are most likely related to land-use history and specific management practices, but also to background climatic conditions. Even though our data was not sufficient to reveal general climate-related patterns for each land-use type, our results suggest that mean annual temperature and precipitation affect the response of C and N pools to land-use change, often resulting in different response trajectories in the single land-use types. The importance of local site-specific effects has been demonstrated also in other studies (Dawson and Smith, 2007; Guo and Gifford, 2002; Homann et al., 2007; Soussana et al., 2006; Vos et al., 2019 for agricultural sites in general).

Fertilizing with animal dung increase the plant-available mineral nitrogen, whereby the increase is strongly related to net nitrogen mineralization and nitrification (NNM). These processes are the key processes in making organic nitrogen available to plants (Zeller et al., 2001; Auyeung et al., 2012) and many studies have found that they are highly dependent on climatic conditions. For example, Rustad et al. (2001) and Larsen et al. (2011) were able to show that mineralization and nitrification increased with warming. Reduced soil moisture because of changed precipitation has generally decreased N mineralization rates and frequently also nitrification (Larsen et al., 2011). On the other hand, there is also evidence that that warming and changes in precipitation can have little to no effect on N cycling in some ecosystems (Niboyet et al., 2011; Auyeung et al., 2012). The same applies to the interaction effects, which, however, have only been investigated in a few studies so far. Here, too, results are inconsistent. Some studies have shown that drought attenuates the positive effect of warming on N mineralisation (Larsen et al., 2011); however, other studies have not demonstrated any interactive effects of warming and altered precipitation at all (Niboyet et al., 2011). So, it depends to a large extent on the ecosystem which processes take place and how. In the case of permanent grassland, our results show that climate effects are recognizable. In general, permanent grassland areas are currently concentrated in Central Europe in climatically and topographically rather unfavourable zones. They generally have an annual average temperature of 5-6 ° C, a high rainfall of more than 700 mm and are found in higher and steeper areas (Trnka et al., 2018). After Smit et al., (2008), the productivity and the spatial distribution of the grassland is strongly correlated with annual precipitation and less with the annual temperature sum and the length of the growing season. Our results underline, on the contrary, that in grassland, fertilization with simultaneous warming leads to an increase in the C concentration in the above-ground phytomass (in agreement with Gardarin et al., 2014). However, this does not directly apply to N concentration as well, where our results do not demonstrate a consistent relationship. Furthermore, reduced land use intensity and increasing mean annual temperatures lead according to our results to a reduction of C and N concentrations in the topsoil of grassland, while they increased in the below-ground phytomass and in the litter. Increasing mean annual precipitation led to a decrease in C and N concentrations in the belowground phytomass and litter and to an increase in C and N concentrations in the aboveground phytomass and topsoil. Thus, in grassland the correlation varies on the one hand depending on the compartment and that the increase in temperature and the increase in precipitation often show opposite effects. As already pointed out, our results also show that the C and N pools increase significantly due to the increase in phytomass along the land-use transect from the intensive hay meadow to the abandoned land and that climate only has a modulating, generally small effect. Similar results were also reached by Chen et al. (2020) on the Tibetan Plateau and also in a recent meta-analysis from Zhou et al. (2019).

Overall, however, it can be stated that more comprehensive long-term studies are needed to decipher land-use – climate interaction effects on C and N partitioning in mountain grasslands, whereby seasonal analyses could possibly help to gain further insights.

Conclusions

In the context of the current climate crisis, particular care must be taken in identifying appropriate management measures to minimise C losses (Whitehead et al., 2018). Such approaches require knowledge on which land management strategy and which site conditions allow a grassland to act as a source or a sink for carbon and greenhouse gases. Across mountain grasslands in the region covered by our study, fertilization resulted in high above-ground phytomass, however, this did not translate to an increase in C stocks, as the highest C and N pools were present in extensively used meadows and the abandoned grasslands. This was mainly due to the increasing proportion of these pools allocated to the soil under reduced land-use intensity or complete abandonment. Climate conditions, such as mean annual temperature and precipitation, had smaller and contradicting effects on C and N pools between land-use types and individual compartments of the ecosystems. An increase in temperature leads to a decrease in C and N concentrations in the aboveground phytomass and in the soil, and an increase in the belowground phytomass and in the litter, respectively. An increase in precipitation tends to have exactly the opposite effect. This implies that a comprehensive multi-site approach, combining C and N cycling and jointly considering land-use and climate effects, is required for understanding and projecting future changes in soil C and N stocks in mountain grasslands and for providing the knowledge required to advise on future mitigation strategies and agricultural policy.

Authors' contributions

DR, MB, JS, ET and AC conceived the study, all authors contributed data, JS analysed the data, ET prepared the Figures, JS, ET, DR and MB wrote the paper, and all authors (except TS) commented on the manuscript.

Acknowledgements

This study was based on investigations from the EU FP5 project CarboMont (EVK2-2001-00125), co-ordinated by Alexander Cernusca. The authors gratefully acknowledge Elisabeth Breitenlechner, Katharina Munk and Jürgen Buchner for the field and laboratory work conducted in Stubaital. The funding partners that have supported this research include also the project ClimAgro (Autonome Provinz Bozen – Südtirol, Abteilung Bildungsförderung, Universität und Forschung), the Austrian National Science Fund (FWF, project number P17560-B03), the Austrian Academy of Sciences (ESS-program), the Austrian Federal Ministry of Science, the Research and Economy with the HRSM – cooperation project KLIMAGRO and the Scientific Grant Agency of the MESRaS of the Slovak Republic and SAS – VEGA no. 2/0132/18. JS, MB, UT and GW are members of the 'Mountain Regions' research focus at the University of Innsbruck.

References

Auyeung, D.S.N., Suseela, V., Dukes, J.S., 2013. Warming and drought reduce temperature sensitivity of nitrogen transformations. Glob Change Biol 19, 662-676. https://doi.org/10.1111/gcb.12063

Bahn, M., Knapp, M., Garajova, Z., Pfahringer, N., Cernusca, A., 2006. Root respiration in temperate mountain grasslands differing in land use: grassland root respiration. Glob. Change Biol. 12, 995–1006. https://doi.org/10.1111/j.1365-2486.2006.01144.x

Bardgett, R.D., Hobbs, P.J., Frostegård, Å., 1996. Changes in soil fungal:bacterial biomass ratios following reductions in the intensity of management of an upland grassland. Biol. Fertil. Soils 22, 261–264. https://doi.org/10.1007/BF00382522

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. J. Stat. Softw. 67. https://doi.org/10.18637/jss.v067.i01

Beck, H.E., Zimmermann, N.E., McVicar, T.R., Vergopolan, N., Berg, A., Wood, E.F., 2018. Present and future Köppen-Geiger climate classification maps at 1-km resolution. Sci. Data 5, 180214. https://doi.org/10.1038/sdata.2018.214

Berninger, F., Susiluoto, S., Gianelle, D., Bahn, M., Wohlfahrt, G., Sutton, M., Garcia-Pausas, J., Gimeno, C., Sanz, M.J., Dore, S., Rogiers, N., Furger, M., Eugster, W., Balzarolo, M., Sebastià, M.T., Tenhunen, J., Staszewski, T., Cernusca, A., 2015. Management and site effects on carbon balances of European mountain meadows and rangelands. Boreal Environ. Res. 20, 748–760.

Buchgraber, K., 2018. Zeitgemässe Grünland-Bewirtschaftung. 3., völlig neu bearb. Aufl. Stocker, Graz

Carlier, L., Rotar, I., Vlahova, M., Vidican, R., 2009. Importance and Functions of Grasslands. Not. Bot. Horti Agrobot. Cluj-Napoca 37, 25–30. https://doi.org/10.15835/nbha3713090

Carvalhais, N., Forkel, M., Khomik, M., Bellarby, J., Jung, M., Migliavacca, M., Mu, M., Saatchi, S., Santoro, M., Thurner, M., Weber, U., Ahrens, B., Beer, C., Cescatti, A., Randerson, J.T., Reichstein, M., 2014. Global covariation of carbon turnover times with climate in terrestrial ecosystems. Nature 514, 213–217. https://doi.org/10.1038/nature13731

Chang, J., Ciais, P., Gasser, T., Smith, P., Herrero, M., Havlík, P., Obersteiner, M., Guenet, B., Goll, D.S., Li, W., Naipal, V., Peng, S., Qiu, C., Tian, H., Viovy, N., Yue, C., Zhu, D., 2021. Climate warming from managed grasslands cancels the cooling effect of carbon sinks in sparsely grazed and natural grasslands. Nat. Commun. 12, 118. https://doi.org/10.1038/s41467-020-20406-7

Chen, T., Bao, A., Jiapaer, G., Guo, H., Zheng, G., Jiang, L., Chang, C., Tuerhanjiang, L., 2019. Disentangling the relative impacts of climate change and human activities on arid and semiarid grasslands in Central Asia during 1982–2015. Sci. Total Environ. 653, 1311-1325. https://doi.org/10.1016/j.scitotenv.2018.11.058.

Chen, Y., Feng, J., Yuan, X., Zhu, B., 2020. Effects of warming on carbon and nitrogen cycling in alpine grassland ecosystems on the Tibetan Plateau: A meta-analysis. Geoderma 370, 114363. https://doi.org/10.1016/j.geoderma.2020.114363

Chen, B., Zhang, X., Tao, J., Wu, J., Wang, J., Shi, P., Zhang, Y., Yu, C., 2014. The impact of climate change and anthropogenic activities on alpine grassland over the Qinghai-Tibet Plateau. Agric. For. Meteorol. 189–190, 11-18. https://doi.org/10.1016/j.agrformet.2014.01.002

Claeskens, G., Hjort, N.L., 2008. Model Selection and Model Averaging. Cambridge University Press. https://doi.org/10.1017/CBO9780511790485

Conant, R.T., Cerri, C.E.P., Osborne, B.B., Paustian, K., 2017. Grassland management impacts on soil carbon stocks: a new synthesis. Ecol. Appl. 27, 662–668. https://doi.org/10.1002/eap.1473

Cortez, J., Garnier, E., Pérez-Harguindeguy, N., Debussche, M., Gillon, D., 2007. Plant traits, litter quality and decomposition in a Mediterranean old-field succession. Plant Soil 296, 19–34. https://doi.org/10.1007/s11104-007-9285-6

Dawson, J.J.C., Smith, P., 2007. Carbon losses from soil and its consequences for land-use management. Sci. Total Environ. 382, 165–190. https://doi.org/10.1016/j.scitotenv.2007.03.023

De Deyn, G.B., Cornelissen, J.H.C., Bardgett, R.D., 2008. Plant functional traits and soil carbon sequestration in contrasting biomes. Ecol. Lett. 11, 516–531. https://doi.org/10.1111/j.1461-0248.2008.01164.x

Deng, L., Zhu, G., Tang, Z., Shangguan, Z., 2016. Global patterns of the effects of land-use changes on soil carbon stocks. Glob. Ecol. Conserv. 5, 127–138. https://doi.org/10.1016/j.gecco.2015.12.004

Egarter Vigl, L., Tasser, E., Schirpke, U., Tappeiner, U., 2017. Using land use/land cover trajectories to uncover ecosystem service patterns across the Alps. Reg. Environ. Change. 17, 2237–2250. https://doi.org/10.1007/s10113-017-1132-6

Egger, G., Angerman, K., Aigner, S., Buchgraber, K., 2004. GIS-gestützte Ertragsmodellierung zur Optimierung des Weidemanagements auf Almweiden. BAL-Veröffentlichungen Nr. 40. BAL, Irdning

Flury, C., Huber, R., Tasser, E., 2013. Future of Mountain Agriculture in the Alps. In: Mann S. (eds) The Future of Mountain Agriculture. Springer Geography. Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-33584-6_8

Fornara, D.A., Flynn, D., Caruso, T., 2020. Effects of nutrient fertilization on root decomposition and carbon accumulation in intensively managed grassland soils. Ecosphere 11. https://doi.org/10.1002/ecs2.3103

Fortunel, C., Garnier, E., Joffre, R., Kazakou, E., Quested, H., Grigulis, K., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Doležal, J., Eriksson, O., Freitas, H., Golodets, C., Jouany, C., Kigel, J., Kleyer, M., Lehsten, V., Lepš, J., Meier, T., Pakeman, R., Papadimitriou, M., Papanastasis, V.P., Quétier, F., Robson, M., Sternberg, M., Theau, J.-P., Thébault, A., Zarovali, M., 2009. Leaf traits capture the effects of land use changes and climate on litter decomposability of grasslands across Europe. Ecology 90, 598–611. https://doi.org/10.1890/08-0418.1

Gardarin, A., Garnier, E., Carrère, P., Cruz, P., Andueza, D., Bonis, A., Colace, M.P., Dumont, B., Duru, M., Farrugia, A., Grigulis, K., Kernéïs, E., Lavorel, S., Louault, F., Loucougaray, G., Mesléard, F., Yaverkowski, N., Kazakou, E., 2014. Plant trait-digestibility relationships across management and climate gradients in French permanent grasslands. Journal of Applied Ecology 51, 1207-1217

Gamper, S.M., Tasser, E., Tappeiner, U., 2007. Short-time effects of land-use changes on O-horizon in subalpine grasslands. Plant Soil 299, 101–115. https://doi.org/10.1007/s11104-007-9366-6

Garcia-Pausas, J., Romanyà, J., Montané, F., Rios, A.I., Taull, M., Rovira, P., Casals, P., 2017. Are Soil Carbon Stocks in Mountain Grasslands Compromised by Land-Use Changes?, in: Catalan, J., Ninot, J.M., Aniz, M.M. (Eds.), High Mountain Conservation in a Changing World, Advances in Global Change Research. Springer International Publishing, Cham, pp. 207–230. https://doi.org/10.1007/978-3-319-55982-7_9

Gill, R.A., Jackson, R.B., 2000. Global patterns of root turnover for terrestrial ecosystems: RESEARCH Root turnover in terrestrial ecosystems. New Phytol. 147, 13–31. https://doi.org/10.1046/j.1469-8137.2000.00681.x

Grigulis, K., Lavorel, S., Krainer, U., Legay, N., Baxendale, C., Dumont, M., Kastl, E., Arnoldi, C., Bardgett, R.D., Poly, F., Pommier, T., Schloter, M., Tappeiner, U., Bahn, M., Clément, J.-C., 2013. Relative contributions of plant traits and soil microbial properties to mountain grassland ecosystem services. J. Ecol. 101, 47–57. https://doi.org/10.1111/1365-2745.12014

Guidi, C., Magid, J., Rodeghiero, M., Gianelle, D., Vesterdal, L., 2014. Effects of forest expansion on mountain grassland: changes within soil organic carbon fractions. Plant Soil 385, 373–387. https://doi.org/10.1007/s11104-014-2315-2

Guo, L.B., Gifford, R.M., 2002. Soil carbon stocks and land use change: a meta analysis: soil carbon stocks and land use change. Glob. Change Biol. 8, 345–360. https://doi.org/10.1046/j.1354-1013.2002.00486.x

Guo, L.B., Wang, M., Gifford, R.M., 2007. The change of soil carbon stocks and fine root dynamics after land use change from a native pasture to a pine plantation. Plant Soil 299, 251–262. https://doi.org/10.1007/s11104-007-9381-7

Hinojosa, L., Tasser, E., Rüdisser, J., Leitinger, G., Schermer, M., Lambin, E.F., Tappeiner, U., 2019. Geographical heterogeneity in mountain grasslands dynamics in the Austrian-Italian Tyrol region. Appl. Geography 106, 50-59. https://doi.org/10.1016/j.apgeog.2019.03.006.

Homann, P.S., Kapchinske, J.S., Boyce, A., 2007. Relations of mineral-soil C and N to climate and texture: regional differences within the conterminous USA. Biogeochemistry 85, 303–316. https://doi.org/10.1007/s10533-007-9139-6

Ingrisch, J., Karlowsky, S., Hasibeder, R., Gleixner, G., Bahn, M., 2020. Drought and recovery effects on belowground respiration dynamics and the partitioning of recent carbon in managed and abandoned grassland. Glob. Change Biol. 26, 4366–4378. https://doi.org/10.1111/gcb.15131

Iversen, C.M., Ledford, J., Norby, R.J., 2008. CO_2 enrichment increases carbon and nitrogen input from fine roots in a deciduous forest. New Phytol. 179, 837–847. https://doi.org/10.1111/j.1469-8137.2008.02516.x

Jäger, H., Peratoner, G., Tappeiner, U., Tasser, E., 2020. Grassland biomass balance in the European Alps: current and future ecosystem service perspectives. Ecosyst. Serv. 45, 101163. https://doi.org/10.1016/j.ecoser.2020.101163

Jones, M.B., Donnelly, A., 2004. Carbon sequestration in temperate grassland ecosystems and the influence of management, climate and elevated CO2: Tansley review. New Phytol. 164, 423–439. https://doi.org/10.1111/j.1469-8137.2004.01201.x

Jones, S.K., Helfter, C., Anderson, M., Coyle, M., Campbell, C., Famulari, D., Di Marco, C., van Dijk, N., Tang, Y.S., Topp, C.F.E., Kiese, R., Kindler, R., Siemens, J., Schrumpf, M., Kaiser, K., Nemitz, E., Levy, P.E., Rees, R.M., Sutton, M.A., Skiba, U.M., 2017. The nitrogen, carbon and greenhouse gas budget of a grazed, cut and fertilised temperate grassland. Biogeosciences 14, 2069–2088. https://doi.org/10.5194/bg-14-2069-2017

Karlowsky, S., Augusti, A., Ingrisch, J., Hasibeder, R., Lange, M., Lavorel, S., Bahn, M., Gleixner, G., 2018. Land use in mountain grasslands alters drought response and recovery of carbon allocation and plant-microbial interactions. J. Ecol. 106, 1230–1243. https://doi.org/10.1111/1365-2745.12910

Kirschbaum, M.U.F., Guo, L.B., Gifford, R.M., 2008. Why does rainfall affect the trend in soil carbon after converting pastures to forests? For. Ecol. Manag. 255, 2990–3000. https://doi.org/10.1016/j.foreco.2008.02.005

Kozak, J., Gimmi, U., Houet, T., Bolliger, J., 2017. Current practices and challenges for modelling past and future land use and land cover changes in mountainous regions. Reg. Environ. Change 17, 2187–2191. https://doi.org/10.1007/s10113-017-1217-2

Larsen, K.S., Andresen, L.C., Beier, C. et al., 2011. Reduced N cycling in response to elevated CO_2, warming, and drought in a Danish heathland: synthesizing results of the CLIMAITE project after two years of treatments. Glob Change Biol 17, 1884–1899. https://doi.org/10.1111/j.1365-2486.2010.02351.x

Legay, N., Baxendale, C., Grigulis, K., Krainer, U., Kastl, E., Schloter, M., Bardgett, R.D., Arnoldi, C., Bahn, M., Dumont, M., Poly, F., Pommier, T., Clément, J.C., Lavorel, S., 2014. Contribution of above- and below-ground plant traits to the structure and function of grassland soil microbial communities. Ann. Bot. 114, 1011–1021. https://doi.org/10.1093/aob/mcu169

Legay, N., Lavorel, S., Baxendale, C., Krainer, U., Bahn, M., Binet, M., Cantarel, A.A.M., Colace, M., Foulquier, A., Kastl, E., Grigulis, K., Mouhamadou, B., Poly, F., Pommier, T., Schloter, M., Clément, J., Bardgett, R.D., 2016. Influence of plant traits, soil microbial properties, and abiotic parameters on nitrogen turnover of grassland ecosystems. Ecosphere 7. https://doi.org/10.1002/ecs2.1448

Leifeld, J., Meyer, S., Budge, K., Sebastia, M.T., Zimmermann, M., Fuhrer, J., 2015. Turnover of Grassland Roots in Mountain Ecosystems Revealed by Their Radiocarbon Signature: Role of Temperature and Management. PLOS ONE 10, e0119184. https://doi.org/10.1371/journal.pone.0119184

Leifeld, J., Zimmermann, M., Fuhrer, J., Conen, F., 2009. Storage and turnover of carbon in grassland soils along an elevation gradient in the Swiss Alps. Glob. Change Biol. 15, 668–679. https://doi.org/10.1111/j.1365-2486.2008.01782.x

Li, W., Ciais, P., Guenet, B., Peng, S., Chang, J., Chaplot, V., Khudyaev, S., Peregon, A., Piao, S., Wang, Y., Yue, C., 2018. Temporal response of soil organic carbon after grassland-related land-use change. Glob. Change Biol. 24, 4731–4746. https://doi.org/10.1111/gcb.14328

Liu, P., Huang, J., Han, X., Sun, O.J., Zhou, Z., 2006. Differential responses of litter decomposition to increased soil nutrients and water between two contrasting grassland plant species of Inner Mongolia, China. Appl. Soil Ecol. 34, 266–275. https://doi.org/10.1016/j.apsoil.2005.12.009

Marchi, M., Castellanos-Acuna, D., Hamann, A., Wang, T., Ray, D. Menzel, A. 2020. ClimateEU, scale-free climate normals, historical time series, and future projections for Europe. Scientific Data 7, 428. https.//doi.org/10.1038/s41597-020-00763-0

Marcolla, B., Cescatti, A., Manca, G., Zorer, R., Cavagna, M., Fiora, A., Gianelle, D., Rodeghiero, M., Sottocornola, M., Zampedri, R., 2011. Climatic controls and ecosystem responses drive the inter-annual variability of the net ecosystem exchange of an alpine meadow. Agric. For. Meteorol. 151, 1233-1243. https://doi.org/10.1016/j.agrformet.2011.04.015

McKinley, D.C., Blair, J.M., 2008. Woody Plant Encroachment by Juniperus virginiana in a Mesic Native Grassland Promotes Rapid Carbon and Nitrogen Accrual. Ecosystems 11, 454–468. https://doi.org/10.1007/s10021-008-9133-4

Meyer, S., Leifeld, J., Bahn, M., Fuhrer, J., 2012. Free and protected soil organic carbon dynamics respond differently to abandonment of mountain grassland. Biogeosciences 9, 853–865. https://doi.org/10.5194/bg-9-853-2012

Mysterud, A., Hessen, D.O., Mobæk, R., Martinsen, V., Mulder, J., Austrheim, G., 2011. Plant quality, seasonality and sheep grazing in an alpine ecosystem. Basic Appl. Ecol. 12, 195–206. https://doi.org/10.1016/j.baae.2011.03.002

Niboyet, A., Le Roux, X., Dijkstra, P., Hungate, B.A., Barthes, L., Blankinship, J. C., Brown, J. R., Field, C. B., Leadley, P. W., 2011. Testing interactive effects of global environmental changes on soil nitrogen cycling. Ecosphere 2, 1–24. https://doi.org/10.1890/ES10-00148.1

Ortiz, C., Vázquez, E., Rubio, A., Benito, M., Schindlbacher, A., Jandl, R., Butterbach-Bahl, K., Díaz-Pinés, E., 2016. Soil organic matter dynamics after afforestation of mountain grasslands in both a

Mediterranean and a temperate climate. Biogeochemistry 131, 267–280. https://doi.org/10.1007/s10533-016-0278-5

Pausch, J., Kuzyakov, Y., 2018. Carbon input by roots into the soil: Quantification of rhizodeposition from root to ecosystem scale. Glob. Change Biol. 24, 1–12. https://doi.org/10.1111/gcb.13850

Poeplau, C., Don, A., 2013. Sensitivity of soil organic carbon stocks and fractions to different land-use changes across Europe. Geoderma 192, 189–201. https://doi.org/10.1016/j.geoderma.2012.08.003

Poeplau, C., Zopf, D., Greiner, B., Geerts, R., Korvaar, H., Thumm, U., Don, A., Heidkamp, A., Flessa, H., 2018. Why does mineral fertilization increase soil carbon stocks in temperate grasslands? Agric. Ecosyst. Environ. 265, 144–155. https://doi.org/10.1016/j.agee.2018.06.003

Poulton, P., Johnston, J., Macdonald, A., White, R., Powlson, D., 2018. Major limitations to achieving "4 per 1000" increases in soil organic carbon stock in temperate regions: Evidence from long-term experiments at Rothamsted Research, United Kingdom. Glob. Change Biol. 24, 2563–2584. https://doi.org/10.1111/gcb.14066

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Reed, C.C., Merrill, A.G., Drew, W.M. et al. (2021) Montane Meadows: A Soil Carbon Sink or Source? Ecosystems 24, 1125–1141. https://doi.org/10.1007/s10021-020-00572-x

Rees, R.M., Bingham, I.J., Baddeley, J.A., Watson, C.A., 2005. The role of plants and land management in sequestering soil carbon in temperate arable and grassland ecosystems. Geoderma 128, 130–154. https://doi.org/10.1016/j.geoderma.2004.12.020

Risch, A.C., Jurgensen, M.F., Page-Dumroese, D.S., Wildi, O., Schütz, M., 2008. Long-term development of above- and below-ground carbon stocks following land-use change in subalpine ecosystems of the Swiss National Park. Can. J. For. Res. 38, 1590–1602. https://doi.org/10.1139/X08-014

Robson, T.M., Baptist, F., Clement, J.-C., Lavorel, S., 2010. Land use in subalpine grasslands affects nitrogen cycling via changes in plant community and soil microbial uptake dynamics: Land-use gradients affect N cycle via plants and microbes. J. Ecol. 98, 62–73. https://doi.org/10.1111/j.1365-2745.2009.01609.x

Rotz, C.A., Muck, R.E., 1994. Chapter 20: Changes in forage quality during harvest and storage. In: Fahey GC (ed) Forage quality, evaluation, and utilization. American Society of Agronomy, Madison, WI, pp 828-868.

Roumet, C., Birouste, M., Picon-Cochard, C., Ghestem, M., Osman, N., Vrignon-Brenas, S., Cao, K. F., Stokes, A., 2016. Root structure-function relationships in 74 species: evidence of a root economics spectrum related to carbon economy. New Phytol 210, 815-826. https://doi.org/10.1111/nph.13828

RStudio Team (2020). RStudio: Integrated Development for R. RStudio, PBC, Boston, MA URL http://www.rstudio.com/.

Rustad, L.E., Campbell, J.L., Marion, G.M. et al., 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and above-ground plant growth to experimental ecosystem warming. Oecologia 126, 543–562. https://doi.org/10.1007/s004420000544

Schedlbauer, J.L., Kavanagh, K.L., 2008. Soil carbon dynamics in a chronosequence of secondary forests in northeastern Costa Rica. For. Ecol. Manag. 255, 1326–1335. https://doi.org/10.1016/j.foreco.2007.10.039

Schmidt, M.W.I., Torn, M.S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I.A., Kleber, M., Kögel-Knabner, I., Lehmann, J., Manning, D.A.C., Nannipieri, P., Rasse, D.P., Weiner, S., Trumbore, S.E., 2011. Persistence of soil organic matter as an ecosystem property. Nature 478, 49–56. https://doi.org/10.1038/nature10386

Schmitt, M., Bahn, M., Wohlfahrt, G., Tappeiner, U., Cernusca, A., 2010. Land use affects the net ecosystem CO<sub>2</sub> exchange and its components in mountain grasslands. Biogeosciences 7, 2297–2309. https://doi.org/10.5194/bg-7-2297-2010

Schulze, E.D., Ciais, P., Luyssaert, S., Schrumpf, M., Janssens, I.A., Thiruchittampalam, B., Theloke, J., Saurat, M., Bringezu, S., Lelieveld, J., Lohila, A., Rebmann, C., Jung, M., Bastviken, D., Abril, G., Grassi, G., Leip, A., Freibauer, A., Kutsch, W., Don, A., Nieschulze, J., Börner, A., Gash, J.H., Dolman, A.J., 2010. The European carbon balance. Part 4: integration of carbon and other trace-gas fluxes. Glob. Change Biol. 16, 1451–1469. https://doi.org/10.1111/j.1365-2486.2010.02215.x

Smit, H.J., Metzger, M.J., Ewert, F., 2008. Spatial distribution of grassland productivity and land use in Europe. Agric. Syst. 98, 208-219. https://doi.org/10.1016/j.agsy.2008.07.004.

Smith, P., 2014. Do grasslands act as a perpetual sink for carbon? Glob. Change Biol. 20, 2708–2711. https://doi.org/10.1111/gcb.12561

Soussana, J.-F., Loiseau, P., Vuichard, N., Ceschia, E., Balesdent, J., Chevallier, T., Arrouays, D., 2006. Carbon cycling and sequestration opportunities in temperate grasslands. Soil Use Manag. 20, 219–230. https://doi.org/10.1111/j.1475-2743.2004.tb00362.x

Steinwandter, M., Schlick-Steiner, B.C., Steiner, F.M., Seeber, J., 2019. One plus one is greater than two: mixing litter types accelerates decomposition of low-quality alpine dwarf shrub litter. Plant Soil 438, 405–419. https://doi.org/10.1007/s11104-019-03991-5

Stewart, A.M., Frank, D.A., 2008. Short sampling intervals reveal very rapid root turnover in a temperate grassland. Oecologia 157, 453–458. https://doi.org/10.1007/s00442-008-1088-9

Stumpf, F., Keller, A., Schmidt, K., Mayr, A., Gubler, A., Schaepman, M., 2018. Spatio-temporal land use dynamics and soil organic carbon in Swiss agroecosystems. Agric. Ecosyst. Environ. 258, 129–142. https://doi.org/10.1016/j.agee.2018.02.012

Szukics, U., Grigulis, K., Legay, N., Kastl, E.-M., Baxendale, C., Bardgett, R.D., Clément, J.-C., Lavorel, S., Schloter, M., Bahn, M., 2019. Management versus site effects on the abundance of nitrifiers and denitrifiers in European mountain grasslands. Sci. Total Environ. 648, 745–753. https://doi.org/10.1016/j.scitotenv.2018.08.039

Tasser, E., Gamper, S., Walde, J., Obojes, N., Tappeiner, U. (2021) Evidence for the importance of land use, site characteristics and vegetation composition for rooting in European Alps. Sci. Rep. 11, 11246. https://doi.org/10.1038/s41598-021-90652-2

Tasser, E., Schirpke, U., Zoderer, B.M., Tappeiner, U., 2020. Towards an integrative assessment of land-use type values from the perspective of ecosystem services. Ecosyst. Serv. 42, 101082. https://doi.org/10.1016/j.ecoser.2020.101082

Tasser, E., Tappeiner, U., Cernusca, A., 2005. Ecological Effects of Land-use Changes in the European Alps, in: Huber, U.M., Bugmann, H.K.M., Reasoner, M.A. (Eds.), Global Change and Mountain Regions, Advances in Global Change Research. Springer Netherlands, Dordrecht, pp. 409–420. https://doi.org/10.1007/1-4020-3508-X_41

Trnka, M., Eitzinger, J., Hlavinka, P., Dubrovský, M., Semerádová, D., Štěpánek, P., Thaler, S., Žalud, Z., Možný, M., Formayer, H., 2009. Climate-driven changes of production regions in Central Europe. Plant Soil Environ 55, 257-266.

van der Linden, A., Oosting, S.J., van de Ven, G.W., de Boer, I.J., van Ittersum, M.K., 2015. A framework for quantitative analysis of livestock systems using theoretical concepts of production ecology. Agric. Syst. 139, 100-109. https://doi.org/10.1016/j.agsy.2015.06.007

van Gestel, N., Shi, Z., van Groenigen, K.J., Osenberg, C.W., Andresen, L.C., Dukes, J.S., Hovenden, M.J., Luo, Y., Michelsen, A., Pendall, E., Reich, P.B., Schuur, E.A.G., Hungate B.A., 2018. Predicting soil carbon loss with warming. Nature 554, E4-E5. https://doi.org/10.1038/nature20150

Veneklaas, Villar., R., 2004. The worldwide leaf economics spectrum. Nature 428, 821-827. https://doi.org/10.1038/nature02403

Vidal, A., Schucknecht, A., Toechterle, P., Linares, D.R.A., Garcia-Franco, N., von Heßberg, A., Krämer, A., Sierts, A., Fischer, A., Willibald, G., Fuetterer, S., Ewald, J., Baumert, V., Weiss, M., Schulz, S., Schloter, M., Bogacki, W., Wiesmeier, M., Mueller, C.W., Dannenmann, M., 2020. High resistance of soils to short-term re-grazing in a long-term abandoned alpine pasture. Agric. Ecosyst. Environ. 300, 107008. https://doi.org/10.1016/j.agee.2020.107008

Viglizzo, E.F., Ricard, M.F., Taboada, M.A., Vázquez-Amábile, G., 2019. Reassessing the role of grazing lands in carbon-balance estimations: Meta-analysis and review. Sci. Total Environ. 661, 531–542. https://doi.org/10.1016/j.scitotenv.2019.01.130

Vos, C., Don, A., Hobley, E.U., Prietz, R., Heidkamp, A., Freibauer, A., 2019. Factors controlling the variation in organic carbon stocks in agricultural soils of Germany. Eur. J. Soil Sci. 70, 550–564. https://doi.org/10.1111/ejss.12787

Ward, S.E., Smart, S.M., Quirk, H., Tallowin, J.R.B., Mortimer, S.R., Shiel, R.S., Wilby, A., Bardgett, R.D., 2016. Legacy effects of grassland management on soil carbon to depth. Glob. Change Biol. 22, 2929–2938. https://doi.org/10.1111/gcb.13246

Whitehead, D., Schipper, L.A., Pronger, J., Moinet, G.Y.K., Mudge, P.L., Calvelo Pereira, R., Kirschbaum, M.U.F., McNally, S.R., Beare, M.H., Camps-Arbestain, M., 2018. Management practices to reduce losses or increase soil carbon stocks in temperate grazed grasslands: New Zealand as a case study. Agric. Ecosyst. Environ. 265, 432–443. https://doi.org/10.1016/j.agee.2018.06.022

Whitehead, D., 2020. Management of Grazed Landscapes to Increase Soil Carbon Stocks in Temperate, Dryland Grasslands. Frontiers in Sustainable Food Systems 4.

Wohlfahrt, G., Hammerle, A., Haslwanter, A., Bahn, M., Tappeiner, U., Cernusca, A., 2008. Seasonal and inter-annual variability of the net ecosystem CO_2 exchange of a temperate mountain grassland: Effects of weather and management, J. Geophys. Res. 113, D08110. https://doi.org/10.1029/2007JD009286

Wright, I., Reich, P., Westoby, M. et al., 2004. The worldwide leaf economics spectrum. Nature 428, 821–827. https://doi.org/10.1038/nature02403

Wu, E. J., Piao, D., Zhu, S., Wang, D., X., Ciais, P., Bastos, A., Xu, X., Xu, W., 2020. Accelerated terrestrial ecosystem carbon turnover and its drivers. Glob. Change Biol. 26, 5052–5062. https://doi.org/10.1111/gcb.15224

Zeller, V., Bardgett, R.D., Tappeiner, U., 2001. Site management effects on soil microbial properties of subalpine meadows: a study of land abandonment along a north-south gradient in the European Alps. Soil Biol Biochem 33, 639-649. https://doi.org/ 10.1016/S0038-0717(00)00208-X

Zeller, V., Bahn, M., Aichner, M., Tappeiner, U., 2000. Impact of land-use change on nitrogen mineralization in subalpine grasslands in the Southern Alps. Biol. Fertil. Soils 31, 441–448. https://doi.org/10.1007/s003740000200

Zhou, G., Luo, Q., Chen, Y., He, M., Zhou, L., Frank, D., He, Y., Fu, Y., Zhang, B., Zhou, X., 2019. Effects of livestock grazing on grassland carbon storage and release override impacts associated with global climate change. Glob. Change Biol. 25, 1119–1132. https://doi.org/10.1111/gcb.14533

Effect of land use on carbon and nitrogen pool partitioning in European mountain grasslands

Tables

Table 1a. Site and land-use characteristics of the study sites. The coordinates are given in m (projection: ETRS_1989_LAEA), die Growing degree-days > 5°C (DDG) and the frost-free period (FFP) were adopted from Marchi et al. (2020).

Project sites	Land-use type	Plots (n)	Longitude	Latitude	Altitude (m a.s.l.)	Inclination (°)	Aspect	MAT (°C)	FFP (d)	DD>5 (°)	MAP (mm)	Mowing events (n y^{-1})	Grazing intensity (1/2)	Fertilization events (n y^{-1})	Abandoned (years)	Historical land use
Alinyà, Pyrenees (E)	P	6	3611501.15	2159655.58	1765	5	N	6.1	157.4	1487.3	1070	0	2 (0.5 LU ha^{-1})	0	9	A/H
	A1	6	3611459.12	2159619.80	1568	15	N	6.1	157.4	1487.3	988	0	0	0	15-20	A/H
Lautaret, French Alps (F)	MF	9	4032695.88	2443794.53	1880	15	SSW	6.0	155.9	1364.6	956	1	1	1	0	A/H
	MU	18	4032997.61	2443947.10	1920	18	SSW	6.0	164.9	1474.6	956	2	1	0	0	A/H
	P	9	4034887.76	2443170.04	1916	23	S/SSE	6.0	163.9	1450.6	956	0	1	0	0	A/H
	A1	9	4034046.93	2443899.52	1966	27	SSW	6.0	155.9	1394.6	956	0	0.5	0	0	A/H
Amplero, Abbruzzi (I)	MU	3-10	4621220.37	2096264.94	900	0	FLAT	10.0	234.0	2487.0	1463	2	1 (0,9 LU ha^{-1})	1	0	A
Monte Bondone (I)	MU	3-4	4402395.76	2544657.25	1550	3	E	5.3	154.0	1121.0	1244	1	0	0	0	-
	P	3	4402304.48	2544745.47	1560	5	NE	5.3	154.0	1121.0	1244	0	1	0	0	-
	A1	3	4402443.62	2544717.61	1550	6	ESE	5.3	154.0	1121.0	1244	0	0	0	20	H
Passeiertal (I)	MF	64	4418587.88	2636267.70	1770	20	SSW	3.6	145.0	1075.0	1041	1	0	1	0	-
	MU	20	4418743.11	2636296.54	1770	25	SSW	3.6	126.0	827.0	1041	0,3	0	0	0	-
	A1	48	4418794.44	2636330.76	1770	28	SSE	3.6	126.0	827.0	1041	0	0	0	10	H
	A2	12	4418860.47	2636241.04	1750	38	SSE	3.6	126.0	827.0	1041	0	0	0	30	H
Leutasch (A)	MF	3	4406204.82	2694433.30	1115	0	FLAT	4.8	153.0	1296.0	1308	2	0	1	0	-
Ötztal (A)	MF	3	4393789.43	2663619.95	1180	0	FLAT	5.8	156.0	1353.0	733	3	0	2	0	-
Stubaital (A)	MF	10	4421265.82	2667867.00	980	0	FLAT	6.3	170.0	1594.0	840	3	0	2	0	-
	MF	10	4420042.14	2669139.41	1750	12	SE	3.0	109.0	654.0	1500	1	1	1	0	-
	MU	10	4419773.30	2668968.71	1600	28	SE	3.0	109.0	654.0	1500	1	0	0	0	-
	P	10	4419836.62	2669158.16	1950	27	SE	3.0	109.0	654.0	1500	0	0	0.5	0	-
	A1	10	4418949.30	2668759.37	1960	17	SE	3.0	84.0	366.0	1500	0	0	0	10-20	P
	A2	13	4419258.39	2668812.90	1595	34	SE	3.0	84.0	366.0	1500	0	0	0	50	P
Zillertal (A)	MF	3	4460976.12	2697836.67	530	0	FLAT	8.1	179.0	1975.0	1013	4	0	3	0	-
Berchtesgaden (D)	P	6-18	4544237.06	2726663.59	620	1	FLAT	7.5	177.9	1704.7	1900	0	2	1	0	-
	P	15-27	4543971.44	2721994.95	1420	3	FLAT	4.1	120.0	997.0	1900	0	1	0	0	H
	A1	5-9	4543487.80	2721504.38	1750	34	NE	2.5	104.6	571.1	1900	0	0	0	3-4	P
Polana (SK)	MF	5	5027949.85	2894402.37	820	5	SW	5.8	166.0	1711.0	853	2	1	1	0	-
	MU	5	5032371.37	2892940.02	820	5	SW	5.8	166.0	1706.0	853	1	1	0	0	-
Brenna (PL)	MU	3-6	4965894.37	2994530.10	665	9	SW	7.0	175.0	1723.0	1100	2	0	0	0	-
	A1	3-6	4966063.93	2994147.16	670	9	SW	7.0	170.0	1623.0	1100	0	0	0	8	H

Land-use types: MF… intensively used fertilized meadows, MU… lightly used unfertilized meadows, P…grazed pastures, A1…abandoned grassland younger than 30 years, A2…abandoned grassland older than 30 years. MAT…mean annual temperature; MAP…mean annual precipitation; grazing intensity: 1…low intensity (short grazing period and/or low number of animals), 2… high intensity (long grazing period and/or high number of animals); historical land use: A…arable land, H…hay meadow, P…pasture.

Table 1b. Soil characteristics and total organic carbon- and nitrogen pools (for the uppermost 23 cm of the soil)

Project sites	**Land-use type**	**Soil type**	**Bed rock**	**Sand (%)**	**Silt (%)**	**Clay (%)**	**SOM (%)**	**pH**	**Bulk density (g m^{-3})**	**Total org. C pool (kg m^{-2})**	**Total org. N pool (kg m^{-2})**
Alinyà, Pyrenees (E)	P	Anthric Leptosol	C	27.0	43.0	30.0	n.a.	7.1	n.a	9.63 ± 0.80	0.75 ± 0.05
	A1	n.a.	C	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	4.35 ± 0.34	0.36 ± 0.03
Lautaret, French Alps (F)	MF	Cambisol	C	27.7	43.0	29.3	n.a.	7.9	1.47	20.73 ± 0.64	1.55 ± 0.02
	MU	Cambisol	C	23.6	45.2	31.2	n.a.	6.9	1.13	21.70 ± 2.05	1.62 ± 0.08
	P	Cambisol	C	32.4	41.1	26.5	n.a.	7.0	1.35	29.04 ± 0.49	1.66 ± 0.01
	A1	Cambisol	C	30.0	41.3	28.7	n.a.	6.2	1.12	15.89 ± 0.60	1.37 ± 0.01
Amplero, Abbruzzi (I)	MU	Haplic Phaeozem	C	12.7	32.4	54.8	38.0	6.3	1.03	8.95	1.23
Monte Bondone (I)	MU	Hapludalf	C	32.3	42.6	25.1	n.a.	5.2	0.79	9.11 ± 1.77	0.18 ± 0.07
	P	Hapludalf	C	1.1	86.1	12.8	24.8	4.5	0.83	n.a.	n.a.
	A1	Hapludalf	C	17.6	74.1	8.3	18.3	4.9	0.65	n.a.	n.a.
Passeiertal (I)	MF	Cambisol	S	41.1	38.1	20.8	14.9	4.5	0.63	10.63 ± 0.70	0.96 ± 0.10
	MU	Cambisol	S	49.7	30.7	19.6	21.5	3.8	0.60	10.18 ± 0.05	0.84 ± 0.00
	A1	Cambisol	S	42.8	34.8	22.4	15.1	3.8	0.64	13.27 ± 1.28	0.93 ± 0.11
	A2	Cambisol	S	41.9	39.6	18.5	17.4	3.5	0.60	13.08 ± 0.11	0.86 ± 0.00
Leutasch (A)	MF	Rendzic Leptosol	C	10.8	50.1	39.0	25.0	7.2	0.6	20.40 ± 0.71	n.a.
Ötztal (A)	MF	Gley Fluvisol	S	62.1	30.2	7.7	8.8	6.4	1.01	10.05 ± 0.21	n.a.
Stubaital (A)	MF	Fluvisol	S	55.7	36.0	8.3	5.1	6.2	1.27	5.72 ± 0.48	0.51 ± 0.04
	MF	Eutric Cambisol	S	42.9	29.8	27.3	11.6	5.6	0.82	8.01 ± 0.35	0.77 ± 0.04
	MU	Eutric Cambisol	S	39.1	46.6	14.4	14.2	4.1	0.69	19.27 ± 1.53	1.15 ± 0.15
	P	Eutric Cambisol	C	31.7	46.7	22.0	13.7	7.0	0.87	14.38 ± 1.97	0.66 ± 0.06
	A1	Dystric Cambisol	S	28.6	47.5	23.9	12.2	4.7	0.59	6.30 ± 0.78	0.45 ± 0.04

	A2	Dystric Cambisol	S	46.7	35.3	17.5	11.9	4.1	0.84	16.16 ± 2.01	0.87 ± 0.11
Zillertal (A)	MF	Gleyic Fluvisol	S	15.1	69.2	15.7	9.2	6.2	0.98	10.69 ± 0.39	n.a.
Berchtesgaden (D)	P	Cambisol	C	n.a.	n.a.	n.a.	n.a.	5.9	1.03	16.20 ± 6.74	1.04 ± 0.02
	P	Cambisol	C	n.a.	n.a.	n.a.	n.a.	6.3	0.69	9.64 ± 0.20	1.24 ± 0.28
	A1	Leptosol	C	n.a.	n.a.	n.a.	n.a.	5.9	0.87	13.87 ± 1.91	1.04 ± 0.13
Polana (SK)	MF	Eutric Cambisol	S	46.0	34.0	20.0	n.a.	4.7	1.198	8.17 ± 1.41	0.63 ± 0.04
	MU	Eutric Cambisol	S	46.0	34.0	20.0	n.a.	4.7	1.198	8.75 ± 0.43	0.62 ± 0.02
Brenna (PL)	MU	Albi-Dystric Cambisol	C	63.4	24.4	12.2	10.2	4.2	1.06	7.45	0.62
	A1	Albi-Dystric Cambisol	C	65.3	23.8	10.9	16.6	3.9	0.83	10.29	0.92

Land-use types: MF… intensively used fertilized meadows, MU… lightly used unfertilized meadows, P…grazed pastures, A1…abandoned grassland younger than 30 years, A2…abandoned grassland older than 30 years. Bed rock: C…carbonate, S…silicate. SOM…soil organic matter.

Table 2: Estimated means (± SE of model estimates) obtained from linear mixed effects models for above-, below-ground and litter dry weight (DW), the respective C- and N-concentrations (incl. topsoil) and their ratios. Units are kg m^{-2} for DW and % for carbon and nitrogen contents in the DW and soil. Significant estimates from the best model were obtained by stepwise backwards model selection (starting from the full model and removing the predictor with the highest *p*-value). For goodness of fit, the Bayesian information criterion (BIC) and deviance are reported for the best, the full and the null model (the model containing only the random effect). d.f. … degrees of freedom, MF… intensively used fertilized meadows, MU…lightly used unfertilized meadows, P… pastures, A1…grasslands abandoned for less than 30 years, A2… grasslands abandoned for more than 30 years.

	Above-ground phytomass				**Below-ground phytomass**			
	DW	**C**	**N**	**C/N**	**DW**	**C**	**N**	**C/N**
BIC null model	-87.6	-1558.1	-3415.9	2565.0	538.6	-724.4	-1612.7	1299.6
Deviance null model (d.f.)	-105.8 (426)	-1576.1 (395)	-3433.9 (395)	2547.0 (395)	522.0 (249)	-740.0 (178)	-1628.3 (178)	1284.0 (178)
BIC full model	-79.6	-1292.7	-2887.3	2227.4	457.6	-466.4	-1165.4	1004.4
Deviance full model (d.f.)	149.6 (330)	-1356.9 (331)	-2952.4 (331)	2163.2 (331)	399.3 (188)	-520.2 (122)	-1219.2 (122)	950.6 (122)
Fixed effects								
Intercept (A1)	0.69 ± 0.06	0.47 ± 0.01	0.015 ± 0.001	35.23 ± 2.24	1.22 ± 0.37	0.46 ± 0.03	0.01 ± 0.001	50.78 ± 2.15
land use A2	-0.27 ± 0.10	-0.04 ± 0.02		-7.90 ± 3.41				
land use MF	-0.24 ± 0.08	-0.04 ± 0.02	0.007 ± 0.001	-14.64 ± 2.95		-0.08 ± 0.03		-21.05 ± 2.30
land use MU	-0.31 ± 0.09	-0.05 ± 0.02		-6.00 ± 2.98				-10.55 ± 3.43
land use P	-0.21 ± 0.09	-0.04 ± 0.02				-0.11 ± 0.05		-10.82 ± 2.55
Temperature	-0.11 ± 0.04				0.36 ± 0.15			
Precipitation	-0.18 ± 0.03	0.01 ± 0.01	0.002 ± 0.001	-2.18 ± 1.07		-0.03 ± 0.01		-5.72 ± 1.01
pH				-3.51 ± 1.08	-0.62 ± 0.21	0.03 ± 0.02		
nitrogen conc.	-0.08 ± 0.02							
clay								5.47 ± 2.22
Random effect								
Site (st.dev.)	0.14	0.03	0.002	4.62	0.46	0.03	0.002	0.00
BIC	-75.2	-1541.2	-3409.7	2216.7	447.5	-474.4	-1597.4	995.3
Deviance (d.f.)	-135.1 (388)	-1589.1 (390)	-3457.6 (390)	2164.1 (333)	399.8 (190)	-518.4 (124)	-1633.8 (174)	951.3 (124)
Observations (n)	398	398	398	342	199	133	181	133
Groups (n)	29	29	29	27	23	20	22	20

Colour codes for significance and direction of effect:

increase with p<0.001 increase with p<0.01 increase with p<0.05 decrease with p<0.001 decrease with p<0.01 decrease with p<0.05

Table 2 continued

	Litter				Topsoil		
	DW	**C**	**N**	**C/N**	**C**	**N**	**C/N**
BIC null model	4558.7	-737.6	-2027.6	1460.3	-430.3	-978.2	378.9
Deviance null model (d.f.)	4541.8 (280)	-754.1 (243)	-2044.1 (242)	1443.7 (242)	-444.3 (102)	-992.2 (102)	364.9 (102)
BIC full model	3972.0	-725.6	-1977.2	1473.3	-393.1	-914.0	363.1
Deviance full model (d.f.)	3906.0 (231)	-786.1 (233)	-2037.6 (232)	1412.9 (232)	-443.7 (88)	-964.6 (88)	312.6 (88)
Fixed effects							
Intercept (A1)	0.53 ± 0.40	0.48 ± 0.01	0.016 ± 0.001	31.84 ± 2.13	0.088 ± 0.021	0.008 ± 0.001	13.23 ± 0.86
land use A2	1.38 ± 0.56	-0.09 ± 0.01		-7.79 ± 2.93	0.076 ± 0.030		2.51 ± 1.14
land use MF		-0.09 ± 0.01	0.005 ± 0.002	-13.66 ± 2.79			
land use MU		-0.08 ± 0.01					
land use P		-0.05 ± 0.02			0.070 ± 0.032		
Temperature		-0.03 ± 0.01		-2.87 ± 1.31			-1.15 ± 0.33
Precipitation	0.59 ± 0.26	-0.04 ± 0.01	0.002 ± 0.001	-6.26 ± 1.59			
pH							1.06 ± 0.38
nitrogen conc.	0.27 ± 0.01						
clay	0.41 ± 0.20					0.001 ± 0.000	-0.87 ± 0.28
Random effect							
Site (st.dev.)	0.70	0.01	0.002	3.79	0.05	0.003	1.48
BIC	3961.4	-735.9	-2008.9	1472.9	-419.7	-924.7	359.0
Deviance (d.f.)	3906.5 (233)	-785.4 (237)	-2052.9 (237)	1423.3 (236)	-452.2 (98)	-961.5 (91)	313.1 (89)
Observations (n)	243	246	245	245	105	99	99
Groups (n)	18	19	19	19	28	26	26

Colour codes for significance and direction of effect:

increase with p<0.001 | increase with p<0.01 | increase with p<0.05 | decrease with p<0.001 | decrease with p<0.01 | decrease with p<0.05

Table 3: Interaction effects of mean annual temperature (upper panel) and mean annual precipitation (lower panel) with land use type on carbon (C) and nitrogen (N) concentrations in the single compartments. Arrows depict direction of interaction: arrows pointing upwards indicate that response variables (C, N, C/N) increase with increasing climate parameter within land-use type, arrows pointing downwards indicate a decrease of response variable with increasing climate parameter. Color of arrow indicates whether interaction trend differs significantly from the trend within land-use type MF as reference: $p<0.001$ ⬆ (+), ⬇ (-); $p<0.01$ ⬈ (+), ⬋ (-); $p<0.05$ ⇗ (+), ⇙ (-). Cell blocks of the same shade indicate the same trends for all land-use types (increasing = blue shaded, decreasing = red shaded). MF… intensively used fertilized meadows, MU… lightly used unfertilized meadows, P…grazed pastures, A1… grasslands abandoned for less than 30 years, A2… grasslands abandoned for more than 30 years.

	Above-ground phytomass			**Below-ground phytomass**			**Litter**			**Topsoil**		
	C	N	C/N	C	N	C/N	C	N	C/N	C	N	C/N
MF x temperature	0.418	0.025	16.90	0.398	0.014	27.50	0.439	0.023	20.08	0.057	0.007	9.19
MU x temperature	n.s.	⬆	⬇	⇗	n.s.	n.s.	⬈	n.s.	n.s.	⬇	n.s.	⬇
P x temperature	⬇	⬇	⇗	⇗	n.s.	⬈	n.s.	NA	NA	n.s.	n.s.	⬇
A1 x temperature	⬇	⬆	⬇	⬋	⬆	⬇	n.s.	n.s.	⇗	⬇	⬋	⇙
A2 x temperature	n.s.	⬋	n.s.	⬈	n.s.	⬈	⬆	⬇	⬆	n.s.	n.s.	⇙
R-squared:	0.388	0.415	0.451	0.232	0.424	0.514	0.405	0.216	0.461	0.480	0.163	0.763
Adjusted R-squared:	0.374	0.401	0.438	0.192	0.393	0.489	0.384	0.189	0.443	0.431	0.083	0.740
F-statistic:	27.34	30.57	35.36	5.74	13.96	20.10	20.12	8.11	25.27	9.75	2.05	33.91
p-value:	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.042	<0.001
MF x precipitation	0.377	0.012	27.47	0.369	0.012	34.54	0.410	0.021	20.14	0.137	n.s.	16.29
MU x precipitation	n.s.	⇙	n.s.	⇙	n.s.	n.s.	⬋	n.s.	⬋	⇗	n.s.	⬆
P x precipitation	n.s.	⬆	⬋	⇙	n.s.	⬋	NA	NA	NA	n.s.	n.s.	⬆
A1 x precipitation	n.s.	⬈	⬋	n.s.	⇙	n.s.	n.s.	⬆	⬇	n.s.	n.s.	n.s.
A2 x precipitation	n.s.	n.s.	n.s.	⬋	n.s.	⇙	⬋	⬆	⬇	n.s.	n.s.	⇗
R-squared:	0.216	0.465	0.399	0.150	0.198	0.220	0.419	0.279	0.602	0.402	0.135	0.685
Adjusted R-squared:	0.198	0.453	0.385	0.105	0.156	0.179	0.199	0.254	0.589	0.346	0.053	0.655
F-statistic:	11.86	37.84	28.58	3.34	4.70	5.37	21.32	11.39	44.65	7.11	1.65	22.93
p-value:	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.1126	<0.001

Figures

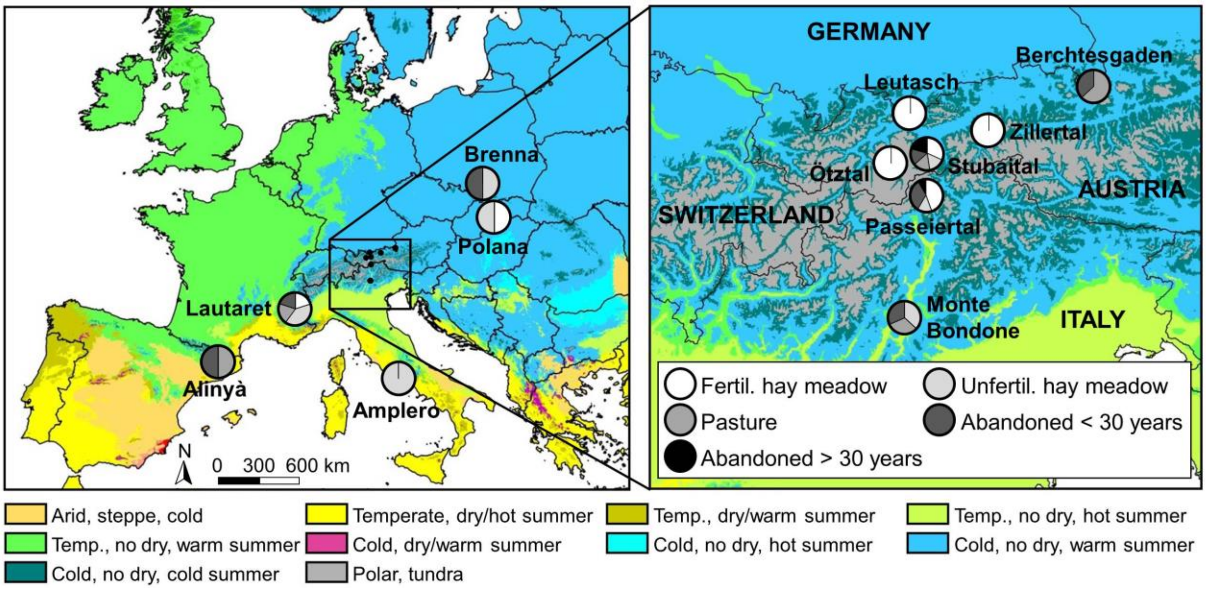

Figure 1: Study sites, analyzed land-use types and climate classification after Beck et al. (2018).

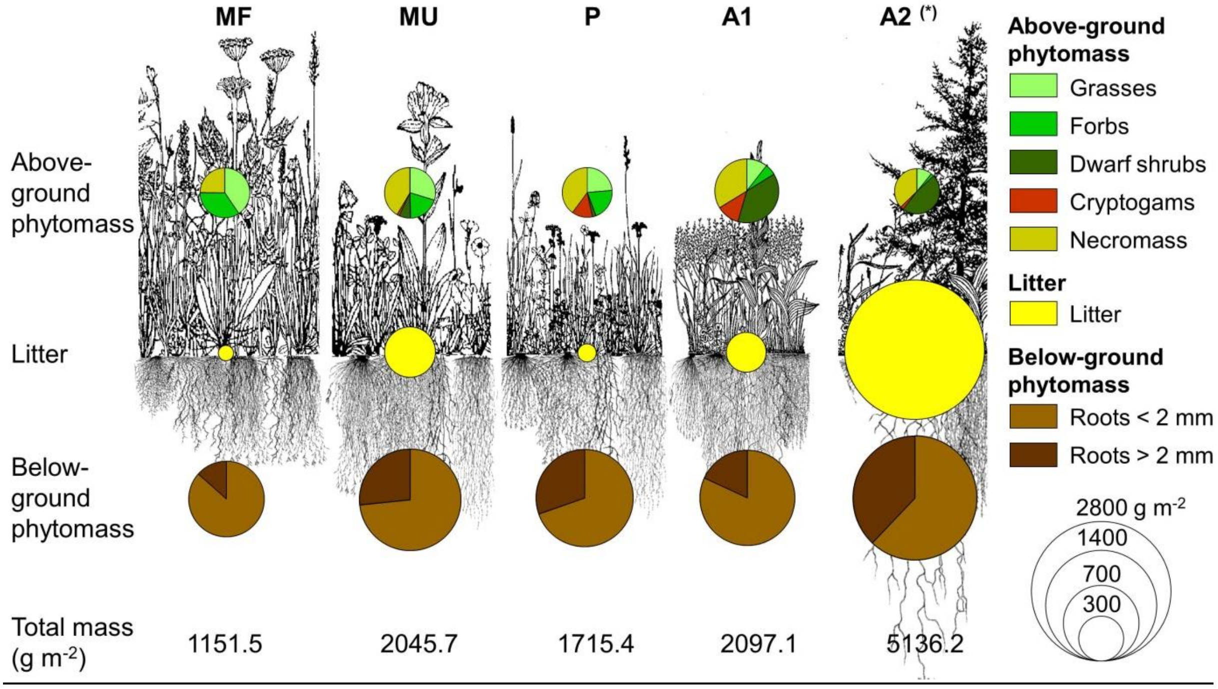

Figure 2: Above-ground and below-ground components of phytomass across the different types of grasslands studied (*). MF … intensively used fertilized meadows, MU … lightly used unfertilized meadows, P … pastures, A1 … grasslands abandoned for less than 30 years, A2… grasslands abandoned for more than 30 years.

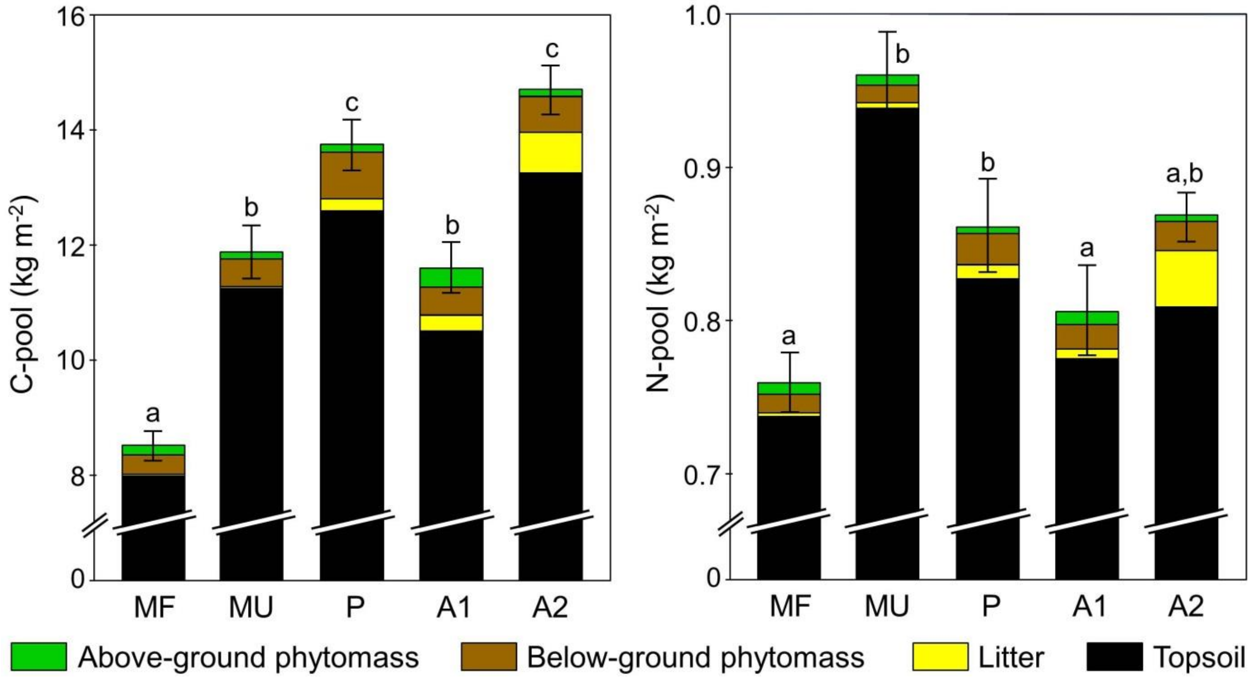

Figure 3: Total carbon (C) and nitrogen (N) pools and their partitioning to above- and below-ground phytomass, litter and topsoil across European mountain grasslands differing in management intensity and land use. Different letters indicate significant differences (based on Tuckey post-hoc test, $p<0.05$) in the individual fractions between land-use types. MF… intensively used fertilized meadows, MU…lightly used unfertilized meadows, P… pastures, A1… grasslands abandoned for less than 30 years, A2… grasslands abandoned for more than 30 years.

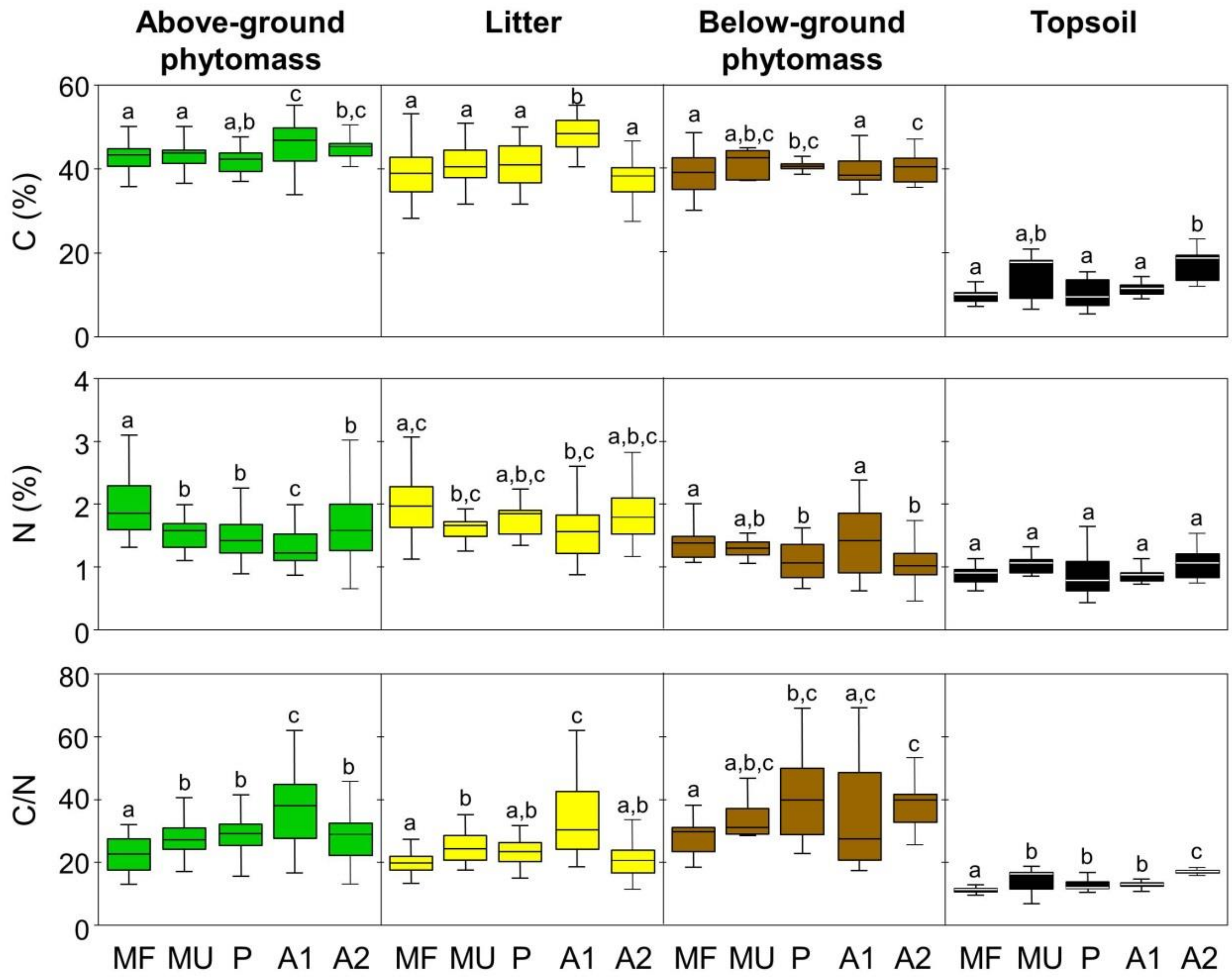

Fig. 4: Carbon (C) and nitrogen (N) concentrations, as well as C/N ratios of the different ecosystem compartments in mountain grasslands differing in management intensity and land use. Different letters indicate significant differences (based on Tukey post-hoc test, $p<0.05$) between land-use types. MF… intensively used fertilized meadows, MU… lightly used unfertilized meadows, P… pastures, A1…grasslands abandoned for less than 30 years, A2… grasslands abandoned for more than 30 years.