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Management and site effects on carbon balances of European mountain meadows and rangelands

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We studied carbon balances and carbon stocks of mountain rangelands and meadows in a network of 8 eddy covariance sites and 14 sites with biomass data in Europe. Net ecosystem exchange of pastures and extensively managed semi-natural rangelands were usually close to zero, while meadows fixed carbon, with the exception of one meadow that was established on a drained peatland. When we accounted for off-site losses and inputs also the carbon budget of meadows approached zero. Soil carbon stocks in these ecosystems were high, comparable to those of forest ecosystems, while carbon stocks in plant biomass were smaller. Since soil carbon stocks of abandoned mountain grasslands are as high as in managed ecosystems, it is likely that the widespread abandonment of mountain rangelands used currently as pastures will not lead to an immediate carbon sink in those ecosystems.

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Introduction

Mountain pastures, heathlands and meadows are part of the classical European mountain landscape, but their extent and their management is changing rapidly. Grasslands at relatively low elevations and flat sites are being more and more intensively managed, while less fertile pastures at higher altitudes are increasingly abandoned or actively converted into forests. There has been a steady decline in the total area of grasslands in Europe and semi-natural grass and rangeland areas are disappearing at high rates (European Union 2003). For example, in England and Wales grassland and rangeland areas decreased by about 17% between 1990 and 1998 (European Union 2003). Also in the mountain areas of Austria, semi-natural grasslands decreased in area by about 21% in 30 years (Hoppilcher *et al*. 2002, Tappeiner *et al*. 2003).

The long-term carbon balance of grasslands and heathlands has received little attention in scientific research (e.g. Jones and Donelly 2004, Gilmanov *et al*. 2007, Gilmanov *et al*. 2010). Grasslands do not accumulate substantial amounts of carbon in easily measurable aboveground biomass over a rotation period of several decades like forests do in their woody biomass. However, grasslands and heathlands have substantial carbon stocks in the soil and these stocks could be affected by changes in management or climate. For example, Oechel *et al*. 2000) showed that *Carex*-dominated ecosystems in Alaska were losing carbon in response to climate warming. Furthermore, the review by Jones and Donelly (2004) suggests that carbon sequestration of grasslands could be enhanced by increased atmospheric CO_2 concentrations. Altogether, it is not clear whether grasslands should be carbon neutral and, for European mountain pastures and meadows, we are still missing a comprehensive synthesis on their carbon balances.

The objective of this paper was to integrate the findings from a number of sites where net ecosystem exchange data over a three-year period within the CARBOMONT project of the European Union's 5th framework programme were collected (Cernusca *et al*. 2008). Our goals were to determin whether (1) European pastures and meadows are generally carbon sinks, carbon sources, or carbon neutral, (2) there is a geographical pattern in net ecosystem exchange (NEE) of these systems in Europe, as it has been found for forest ecosystems (Valentini *et al*. 2000), and (3) how management affects the carbon fluxes and stocks of these semi-natural ecosystems.

Material and methods

Sites

Carbon fluxes were determined at eight European mountain-grassland sites distributed over five European mountain ranges, the Alps (three sites), the Apennines (one site), the Pyrenees (one site), the Scottish uplands (one site) and Fennoscandia (two sites) (Fig. 1, Tables 1 and 2). Four of these sites were grazed pastures (sites in Värriö, Stordalen, Auchencorth and Alinyà), two were meadows (mowed at least once a year, sites in Stubai valley and Monte Bondone) and two were grazed after mowing (Amplero and Seebodenalp). Net carbon exchange measurements were carried out at the sites for three years, except for Monte Bondone where measurements were carried out during two years. The sites were complemented with 12 sites that did not have carbon-balance measurements but did have biomass measurements (Table 1). These sites were usually located close to the sites with eddy covariance measurements. Climate of the sites varied from subarctic to warm-temperate with Mediterranean influences. The Värriö, Stordalen and Auchencorth sites were not grasslands and had less than 20% of grass coverage while at the other sites most of the ground was covered by grasses.

The Värriö site (Susiluoto *et al*. 2008) is dominated by fjell vegetation, main species being *Empetrum nigrum* and *Vaccinium vitis-idaea* and mosses (*Dicranum* sp.) and lichens (*Cladina* sp.). The vegetation grows on a thin mineral soil underlying rock and scree. One third of the area is open scree. The site is well drained. Grazing intensity is low [around 1.5 animals per km^2 in Finland (Turi 2002)], but as reindeers typically graze on fjell tops during winters, the effect of the reindeer grazing on fjell vegetation is strong and visible.



Fig. 1. Location of the sites with eddy covariance flux measurements.

The Stordalen site is a subarctic mire with underlying non-continuous permafrost. The soil type is a histosol. The vegetation consists mostly of mosses (*Sphagnum fuscum*), dwarf shrubs (such as *Empetrum hermaphroditum* and *Vaccinium vitis-idaea*) and cotton-sedge (*Eriophorum angustifolium*). The area is grazed by reindeer. The site has not been drained. Grazing intensity is low as in Värriö.

The Auchencorth site is a blanket bog with an average peat depth of 60 cm. The vegetation is dominated by *Deschampsia flexuosa*, *Molinia caerulea*, *Eriophorum vaginatum* and *Eriophorum angustifolium* and the moss layer is formed by *Polytrichum commune*, *Rhytidiadelphus squarrosus* and *Sphagnum papillosum*. The site is not drained and is grazed by sheep (< 1 sheep per ha). The site is quite representative for northern Scottish heath and moorlands.

The Stubai valley (Schmitt *et al*. 2010) site is located on a valley bottom. The soil type is a fluvisol. The vegetation is dominated by *Dactylis glomerata*, *Festuca pratensis*, *Phleum pratensis*, *Trisetum flavescens*, *Ranunculus acris*, *Taraxacum officinale*, *Trifolium repens*, *Trifolium pratense* and *Carum carvi*. The site is mown three times a year.

The Seebodenalp site (.Rogiers *et al*. 2005, Rogiers *et al*. 2008, Merbold *et al*. 2011) is used as a pasture and meadow. Much of the area is a former lake that was drained long ago for agriculture. The soil is a stagnic Cambisol. The dominant plant species are *Trifolium repens*, *Trifolium pratense*, *Dactylis glomerata*, *Plantago lanceolata*, *Plantago major*, *Taraxacum officinalis*, *Ranunculus repens*, *Stellaria media*, *Polygonum bistorta* and *Lamium purpureum*.

The Monte Bondone site is a meadow on a mountaintop plateau. The soil is a typic Hapludalf. The plant community at the site is a *Nardetum strictum* (Ellenberg 1985). Dominant species are *Festuca rubra*, *Alchemilla vulgaris*, *Nardus stricta*, *Trifolium alpinum* and *Trollius europaeus*. The area is managed as an extensive meadow with low mineral fertilization and is cut annually in mid-July (Marcolla *et al*. 2011).

The Alinyà site is a pasture located on a plain at 1770 m a.s.l. Vegetation is dominated by herbaceous species and sparse shrubs of *Juniperus communis*. The herbaceous layer is dominated by *Festuca ovina*, *Festuca rubra* ssp. *commutata*, *Phleum pratense*, *Globularia cordifolia,* and *Taraxacum dissectum*. The site is a Lithic cryrendoll with a clay-rich soil developed on calcareous bedrock. The site was a grassland 35 years ago. After that it has always been used for summer pasture (grazed by cattle from middle to end June up to October).

The Amplero site is a meadow with a thin rendzina-type soil on calcareous bedrock. The area is dominated by *Sesleria apennina*, *Carex kitailbeliana*, *Edraianthus graminifolius*, *Anthyllis pulchella*, *Pedicularis elegans*, *Globularia meridionalis* and *Festuca ovina*. The vegetation in the area is cut once a year and is also grazed.

Carbon imports and exports

Exports and imports of carbon are here defined as losses and inputs, respectively. These include inputs and outputs from management but exclude natural losses through the hydrological cycle (i.e. through dissolved organic or inorganic carbon). Off-site losses were estimated for meadows from harvest data and were estimated from the dry weight of harvested grass. One site (Stubai valley) had large carbon inputs from manure. The other sites did not have carbon inputs during the study period.

Carbon stocks

Above-ground carbon and nitrogen stock data

Table 1. Site characteristics of the measurement places. Management types describe the different managements that were used in biomass and LAI measurements (G = grazed, M = meadow, A = abandoned, PB = peat bog). Biomass was measured at all sites; sites where LAI was measured are marked with 'yes'.

Site	Coordinates	Altitude (m a.s.l.)	Mean temperature (°C)	Mean precipitation (mm)	Management	LAI
Amplero, Abruzzi, Italy	41°52´N, 13°38´E	1500	6.3	1560	G/G,M/A	yes
Alinyà, Spain	42°09´N, 1°26´E	1770	6.1	1030	G/A	no
Auchencorth, UK	57°14´N, 3°30´W	270	5.6	1100	G/A	yes
Berchtesgaden, Germany	47°37´N, 12°35´E	620	4.7	1950	G/A	yes
Berchtesgaden, Germany	47°37´N, 12°35´E	1020	4.7	1950	G/M/A	no
Berchtesgaden, Germany	47°37´N, 12°35´E	1420	4.7	1950	G	yes
Bilý Kriz, Czech Republic	47°37´N, 12°35´E	900	4.9	1100	M/A	yes
Brenna, Poland	49°40´N, 11°17´E	667	5.5	1000	M /A	yes
Juribello, Italy	46°02´N, 11°46´E	1850	2.6	1100	G	yes
Nuorttitunturi, Finland	67°48´N, 29°40´E	480	–3.5	550	G/A	no
Polana, Slovakia	48°63´N, 19°28´E	1250	4.5	950	G/M	no
Seebodenalp, Switzerland	47°04´N, 8°28´E	1023	5.8	1320	G/M	no
Stordalen, Abisko, Sweden	68°22'N 19°03´E	360	–1.0	300	G/PB	no
Stubai Valley, Austria	47°07´N, 11°17´E	1960	3.0	1097	G/A	no
Stubai Valley, Austria	47°07´N, 11°17´E	1750	3.0	1097	M	no
Stubai Valley, Austria	47°07´N, 11°17´E	950	6.3	850	M	no
Monte Bondone, Italy	46°01´N, 11°02 E	1550	5.5	1189	M/A /GP/PB	yes
Värriö, Finland	67°46´N, 29°35´E	450	–0.5	500	P	no

were collected using destructive sampling, mostly by clipping the vegetation. At all sites clipping was done as near the ground as possible. Sampling methods varied among sites. However, at all sites a systematic sampling approach was used. More detailed descriptions of biomass inventory methods are in Wohlfahrt *et al*. (2001, Monte Bondone), Rogiers *et al*. (2005, Seebodenalp), Wohlfahrt *et al*. (2005, Stubai), Ström and Christensen (2007, Stordalen), and Susiluoto *et al*. (2008, Värriö and Nuorttitunturi).

Soil carbon stocks were measured by coring with at least 9 cores per site. Only at the Värriö site carbon stocks were estimated via the excavation of large soil monoliths (since coring was not feasible in the stony soil). Soil carbon stocks were given for the upper 20 cm of soil. Samples were sieved and roots were removed from the samples. Carbon and nitrogen content of the soil samples were estimated using elemental analysers.

Leaf area was measured for herbaceous plants and grasses from cut biomass using scanners or leaf area meters and the results were used to estimate the one-sided planar leaf area index (LAI) of each site. At most sites sampling was carried out at a certain interval and was repeated several times a year, but at some sites samples were taken from a few, large sampling plots (e.g. 1 m^2). Clipping the vegetation for leaf area estimation was always done as close to the soil surface as possible. Mosses and lichens were not included in the leaf area index calculations. The number of samples for vegetation analysis varied so from 5 to 30.

At most sites, annual plants and perennial grasses formed the largest part of the vegetation. The above-ground biomass of these plants dies during winter and their peak biomass can be used as lower bounds for net primary production (NPP) estimates. Notable exception to that were the Scottish (Auchencorth), Swedish (Stordalen), Finnish (Värriö) and Spanish (Alinyà) sites, where a large proportion of the vegetation was formed by mosses and dwarf shrubs.

Carbon fluxes

Net ecosystem exchange (NEE) was calculated from eddy covariance measurements (as described by Wohlfahrt *et al*. 2008b). Descriptions of the measurement systems, instrumentation and data processing are given in Wohlfahrt *et al*. (2008b: table 1). All eddy covariance measurements were processed in a similar way as described by Aubinet *et al*. (2000), which includes coordinate rotation and frequency response correction after Moore (1986) or Eugster and Senn (1995). Data from open-path instruments were additionally corrected for concurrent density fluctuations using the algorithm by Webb *et al*. (1980). Fluxes were based on 30 min sampling intervals and gapfilling was done by regression methods (Wohlfahrt *et al*. 2008b) separately by the individual research groups. More detailed descriptions of the eddy covariance methods used can be found in Wohlfahrt *et al*. (2008b).

Soil respiration was measured at three sites using portable gas exchange systems. Three sites allowed the partioning of the carbon balance into plant and soil respiration. Measurements were done regularly at all three sites and were converted to yearly values using the regression

Table 2. Off-site inputs and losses and NEE of the eddy covariance measurements sites.

Site name	Management	NEE (Mg C ha^{-1} yr^{-1})	Off-site inputs (Mg C ha^{-1} yr^{-1})	Off-site losses (Mg C ha^{-1} yr^{-1})
Amplero, Abruzzi, Italy	Meadow/Pasture	–1.24	Negligible	0.78
Alinyà, Spain	Pasture	–1.09	Negligible	Negligible
Monte Bondone, Italy	Meadow	–0.75	Negligible	0.62
Värriö, Finland	Rangeland	0.01	Negligible	Negligible
Seebodenalp, Switzerland	Meadow/Pasture	1.55	Negligible	3.9
Stubai Valley, Austria	Meadow	–0.13	2.86	3.17
Auchencorth, UK	Peatland, rangeland	0.55	Negligible	0.23
Stordalen, Sweden	Peatland, rangeland	–0.33	Negligible	Negligible

on temperature and soil moisture as described by Bahn *et al*. (2008). At the Stubai and Seebodenlp sites, the LICOR system with the LI6400-09 soil respiration system was used; while at the Värriö site, a home made system using a EGM gas analyser and a closed chamber was used. The number of measurements was 138 for Seebodenalp and 26 for Värriö. More details for Värriö can be found in Susiluoto *et al*. (2008).

Net ecosystem exchange (NEE) is defined from an atmospheric point of view (carbon sinks are denoted by negative NEE values). Net biome productivity (NBP) was estimated as carbon imports minus carbon exports minus NEE, i.e. assuming that carbon that is removed from the site is lost to the atmosphere off-site and that all carbon put into the system is decomposed.

Results

Net ecosystem exchange

Net ecosystem exchange differed between the ecosystems. Especially one site (Seebodenalp) behaved quite differently than the other ones. We know that this depended largely on the land use history of the site, as the site is drained, old peatland where still after more than 100 years soil organic matter of the ancient peat layers is decomposed and makes the Seebodenalp site a permanent C source (*see* Rogiers *et al*. 2008). This is different from the other sites, but is not really exceptional for the European Alpine region. Due to this the results on the fluxes are given with and without the values for Seebodenalp. Our yearly NEE values ranged from –109 g C m^{-2} yr^{-1} to 55 g C m^{-2} yr^{-1} (or +240 g C m^{-2} yr^{-1} with Seebodenalp). The mean NEE was –42 g m^{-2} (–17 g m^{-2} with the site Seebodenalp included). The standard deviations of mean fluxes were high (67 g m^{-2} which increases to 91 g m^{-2} if Seebodenalp is included). Subsequent analysis did not show any relation between NEE and temperature, precipitation or standing biomass of the sites (Fig. 2). We also tested if grasslands are generally source or sinks of CO_2. A *t*-test showed that NEE was not statistically different from 0 g m^{-2} irrespective of whether Seebodenalp was included or not. For NEE, there was more variation and perhaps slightly more negative NEE values at the southern latitudes but this change along the latitude gradient was, however, not significant ($r^2 = 0.42$, $p = 0.12$, $n = 7$ if Seebodenalp is omitted). Correcting NEE for off-site losses and C inputs further blurred any potential correlation with latitude ($r^2 = 0.13$, $p = 0.33$, $n = 8$, Fig. 2).

In general, NEE as measured by the eddy covariance method was close to 0 for natural ecosystems and pastures, while meadows had usually a negative NEE. The NBP values (NEE corrected for off site inputs and off site losses) were usually closer to 0 g C m^{-2} yr^{-1} than the NEE values (Fig. 3). The average NBP for all sites was –14 ± 58 (SD) g C m^{-2} yr^{-1} and 29 ± 135 g C m^{-2} yr^{-1} when Seebodenalp was included. According to the *t*-test, also NBP was not statistically different from 0.

There were notable exceptions to this carbon neutrality. Seebodenalp acted as a large carbon source of more than 100 g C m^{-2} yr^{-1}. We investigated this further by breaking down the carbon balance for three sites with different management types in gross primary production, above and below ground respiration and ecosystem respiration (*see* Fig. 4). Fluxes at all sites were dominated by photosynthetic and respiration fluxes. Off-site losses and inputs of carbon for the two meadows (Stubai valley and Seebodenalp) were substantial. In the Stubai valley, the carbon inputs (manure) had the same magnitude as the carbon losses (harvested grass). For the pastures, off-site carbon losses (by harvesting of lifestock) were negligible.

Carbon stocks

Above-ground biomass estimates varied between 1.0 and 14 Mg DM ha^{-1} with an average of 4.4 ± 2.6 (SD) Mg DM ha^{-1}. This variation was not explained by the differences in climate among sites used in the CARBOMONT project. There was also no correlation between biomass and annual average temperature (Fig. 5).

Management was another determinant of plant standing biomass. Abandoned sites had a higher above-ground biomass than the managed ecosystems (Fig. 6). We used two approaches to

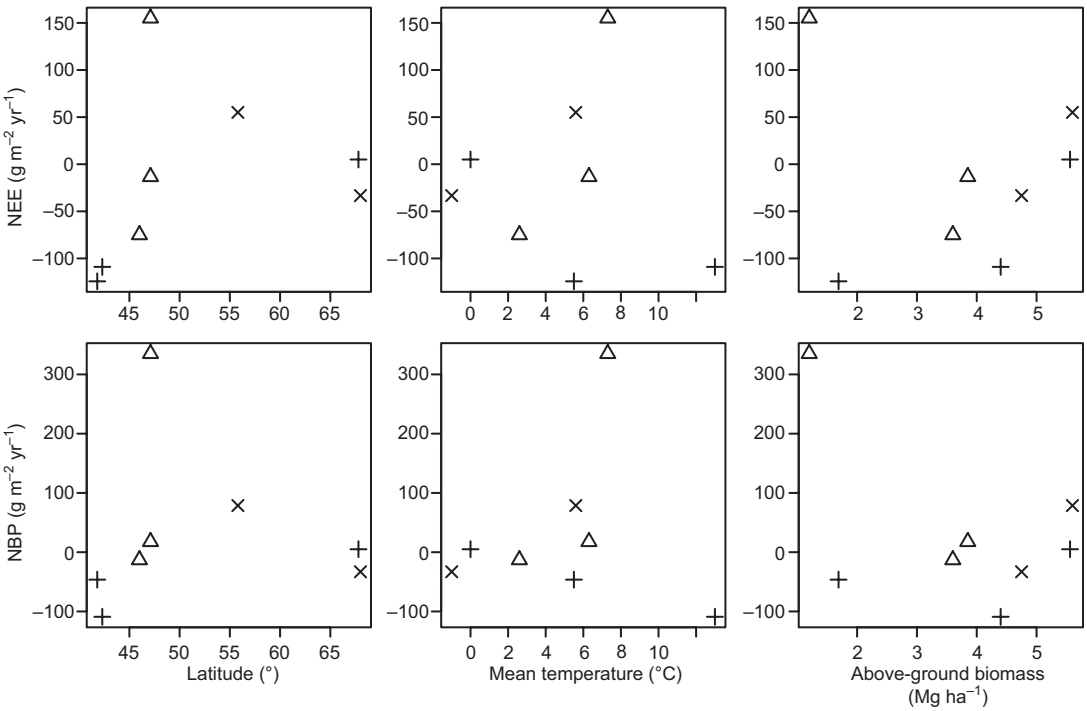


Fig. 2. Net ecosystem exchange (NEE) and NEE corrected for off-site losses (NBP) as a function of latitude, the mean temperature at the sites and maximum standing above-ground biomass. Symbols are Δ for meadows, + for pastures and × for peatlands.

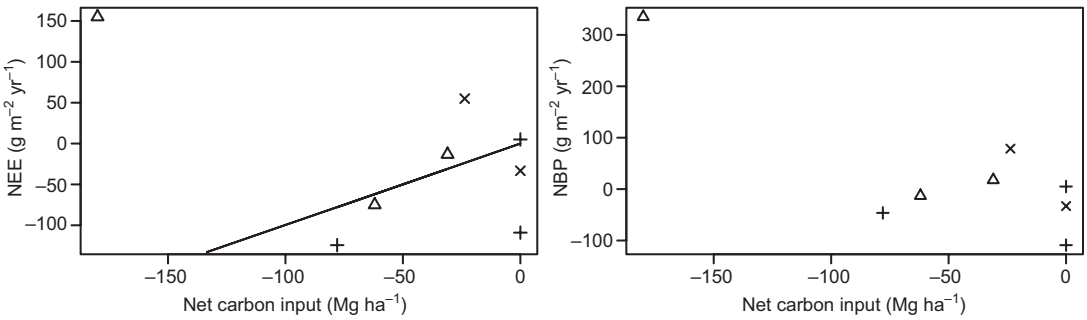


Fig. 3. Net ecosystem exchange (NEE) and net ecosystem exchange corrected for off-site losses (NBP) of the ecosystems calculated as a function of the net carbon inputs of these ecosystems. The line in the left panel is the one-to-one line that assumes that NEE is fully compensated by off-site carbon losses. Symbols are Δ for meadows, + for pastures and × for peatlands.

test for differences in standing biomass of differently-managed ecosystems. Firstly, we compared differently managed ecosystems using a paired *t*-test, with location as grouping variable. Abandoned sites had significantly higher values (difference 1.4 Mg DM ha^{-1}; $t_{11} = 3.11, p < 0.05$). Differences between meadows and rangelands were not statistically significant. Secondly we used an ANOVA ($df_1 = 3$, $df_2 = 64$) to test for differences between abandoned and managed ecosystems. There were statistically significant differences between abandoned and managed ecosystems (Tukey's HSD: $p < 0.01$ for meadows and $p < 0.02$ for pastures), while pastures and meadows were not significantly different from each other (Tukey's HSD: $p = 0.79$). Peat

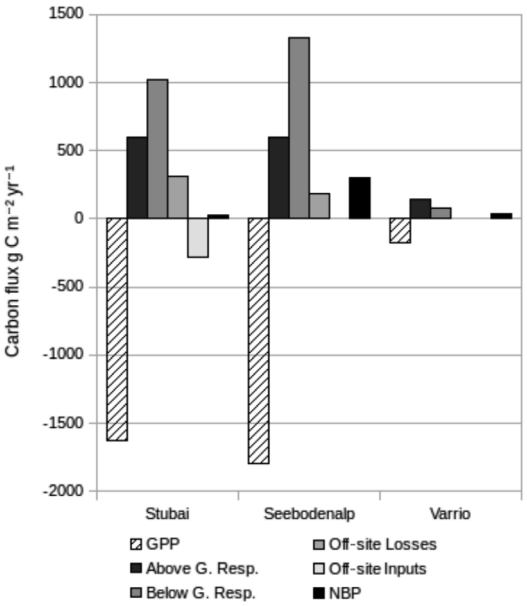


Fig. 4. Carbon flux (Mg C ha^{-1} yr^{-1}) for three selected ecosystems [Stubai valley (meadow), Seebodenalp (meadow/pasture) and Värriö (pasture)] broken down into different components. Note the large positive NBP for Seebodenalp that is a result of decomposition of a drained peat soil as was detailed by Rogiers *et al.* (2008).

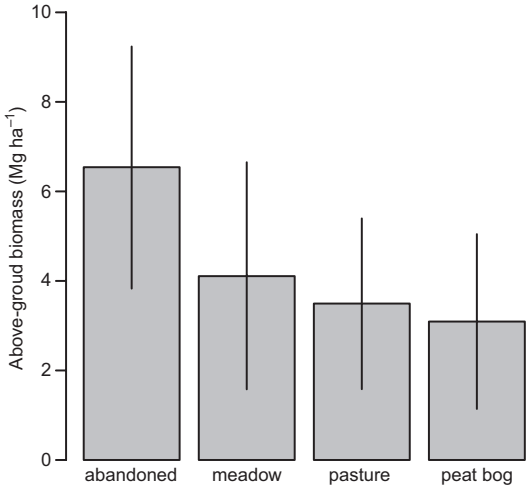


Fig. 6. Above-ground biomass ± SD of abandoned ecosystems, meadows, pastures and peatlands. The values for abandoned ecosystems were significantly higher (Tukey's HSD, $p < 0.05$) than those of meadows or pastures and bogs.

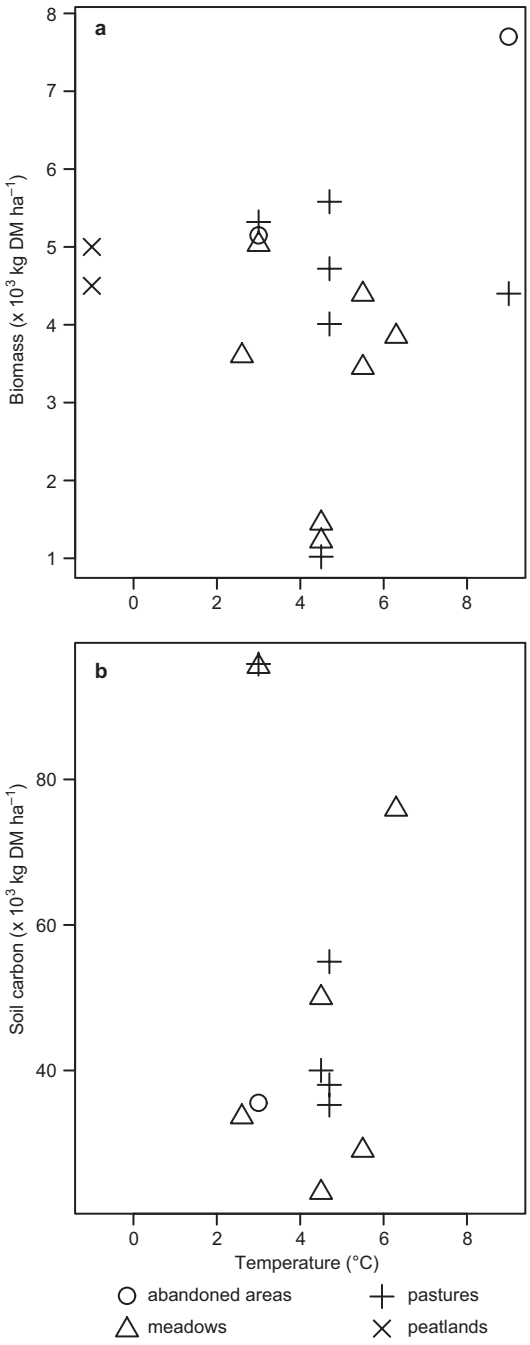


Fig. 5. (**a**) Standing biomass at the end of the season as a function of the annual mean temperature at each site. (**b**) Soil carbon in the top 5 cm as a function of the annual mean temperature. Peatlands were excluded from the analysis

bogs did not differ from managed ecosystems. The standing biomass values for abandoned ecosystems, peatlands, rangelands and meadows were 6.5 ± 2.7 (SD) Mg ha^{-1}, 3.1 ± 2.0 Mg ha^{-1},

4.1 ± 2.5 Mg ha^{-1} and 3.5 ± 1.9 Mg ha^{-1}, respectively. The root biomass values were generally about three times the above-ground biomass [mean ratio of root/above-ground biomass was 3.2 ± 0.91 (SE)]. The average root biomass was 11.04 Mg DM ha^{-1}.

Abandonment changed the appearance of shrubs at several sites (e.g., Alinyàsites or the abandoned Brenna site) and increased the biomass of preferentially-grazed species (like lichens at the Värriö site). Necromasses of plants ranged from being not important (not measurable as in the Värriö abandoned site) to up to 30% of the standing biomass at the Alinyà site.

The soil carbon contents were much greater than the plant carbon contents with the average soil carbon stock in the uppermost 20 cm at the sites on mineral soil being 46.9 ± 7.4 Mg C ha^{-1} (mean ± SE) in the 0–5 cm layer, and 110 ± 33.8 Mg C ha^{-1} in the 0–20 cm layer. As the standard errors indicate, the variation in these carbon stocks was huge. The average ecosystem soil nitrogen stock in the 0–20 cm layer was 8.2 ± 2.1 Mg N ha^{-1}.

There were no statistically significant differences (F-test) in the below-ground soil carbon stocks and root biomass among the different management types. Though, it is noteworthy that in one case (Alinyà) abandonment led to a slight increase in the above-ground carbon stocks and a decrease in the below ground carbon stocks.

Leaf area index was measured at most sites and it showed a very weak correlation with biomass ($r^2 = 0.28$, $p < 0.001$, $n = 8$), but not with total carbon stocks.

Off-site losses

The off-site losses varied between 0 and 3.9 Mg C ha^{-1} yr^{-1} (Table 2). These losses were negligible for all pastures, while for meadows they were usually large. The Stubai valley was the only site that had any off-site input of carbon (2.86 Mg C ha^{-1} yr^{-1}) in the form of manure.

Discussion

The present paper synthesizes the results on carbon stocks and fluxes from a large number of mountain grassland and rangeland sites. The data illustrates the diversity of these ecosystems in terms of their structure and carbon relations. Management categories (e.g., rangeland or meadow) explained only a fraction of this diversity. There was also no effect of temperature (Fig. 5). Above-ground biomass in these ecosystems was only a small part of the total biomass and an even smaller part of the ecosystem carbon stocks. Management affected the above-ground carbon pools with the abandoned ecosystems having higher biomass than the managed ones. Unfortunately, below-ground pools were much more difficult to measure than above-ground pools, and hence uncertainties in below-ground estimates were considerable. Hence, the fact that we were not able to detect any change in below ground carbon stocks due to abandonment does not prove that there is no change. We think that this failure of detection is because these changes are difficult to detect using standard inventory methods which is an argument for the use of flux-based methods to measure carbon sequestration rates of these ecosystems. Studies that successfully detect changes in ecosystem carbon stocks were restricted to ecosystems with relatively low soil carbon contents (i.e. Richter *et al*. 1999). Estimation of carbon stock changes might be especially difficult in peatland ecosystems (e.g., Auchencorth and Stordalen) or stony ecosystems (e.g., Värriö) due to the depth of the peat layer in peatlands and problems in sample collection from stony soils. These ecosystems make up a significant proportion of the European montane, subalpine and alpine ecozones. Carbon stocks in the soil of the grassland systems were relatively high and comparable to stocks in forest ecosystems. For example Liski *et al*. (2002) give an average soil carbon stock for central European forests of 54 Mg C ha^{-1}. Though, soil respiration has been shown to be lower in forests as compared with that in grasslands (Bahn *et al*. 2010a).

The carbon balance of the studied ecosystems varied considerably. While some ecosystems were considerable carbon sinks (e.g. Amplero: –1.24 Mg C ha^{-1} yr^{-1}), others were large carbon sources (Seebodenalp: +1.55 Mg C ha^{-1} yr^{-1}) (*see* also Bahn *et al*. 2008 and Wohlfahrt *et al*. 2008). Off-site losses compensated generally for nega-

tive NEE values (Fig. 3) except at the Seebodenalp site (*see* below).

Mountain farms have traditionally patterns of carbon transfer between the different parts of the farm. Grass is removed from the more extensively managed semi-natural grasslands, fed to the cattle and the resulting manure is preferentially used on the more intensively used area in the vicinity of the cattle barns. The importance of off-site losses and inputs shows that these patterns have to be taken into account when landscape-scale carbon budgets are calculated.

The Seebodenalp site that had the highest carbon losses, is an old peatland that has been drained. Rogiers *et al*. (2008) estimated that 5–9.1 Mg C ha^{-2} yr^{-1} is still being lost due to continued decomposition of drained peat. This is a substantial contribution to total respiration and is responsible for the high carbon losses at that site (Fig. 4). The ash content that remains in soil samples after combustion as drained peat decomposes confirmed that the role of soil respiration induced by land use changes (draining of peatland) at that site was pronounced (Rogiers *et al*. 2008). Although apparently huge, these high carbon losses agree with those reported by Lohila *et al*. (2004), who found that respiration in a drained peatland was still double that for mineral soil 100 years after drainage. Lohila *et al*. (2004) concluded that this drained peatland remained a carbon source even several decades after drainage. Waddington *et al*. (2002) concluded that the carbon balance of cutover peatlands depends mostly on the level of the water table. At low water tables, natural and cutover peatlands in Québec were similar sources of carbon. In contrast, the relative pristine blanket bog Auchencorth showed low interannual variation in carbon budgets and was carbon neutral, as was the mire of Stordalen. This can be attributed to the fact that at these sites the ground water table was not lowered and decomposition of peat was limited by anoxic conditions. Valentini *et al*. (2000) demonstrated that the net carbon sequestration of forests increases from the north to the south of Europe. We were, however, not able to find this in our study.

When grasslands are abandoned the export of biomass ceases and most semi-natural grasslands get slowly invaded by shrubs and trees. Therefore, we would expected an increase in carbon stocks and a more negative carbon balance in abandoned grasslands. When managed and unmanaged areas at the same study sites were compared, there was no indication that abandoned grassland ecosystems would accumulate carbon at the early stages of succession. This is an important difference between permanent grassland ecosystems and agricultural fields, since studies on carbon sequestration after abandonment of agricultural fields show that carbon pools tend to increase (Richter *et al*. 1999). In agreement with our findings, a comparative study by Richter and Markewitz (1996) in the southern Appalachians did not find differences in the soil carbon stocks of permanent grasslands and forests, which were established on the same old field. Furthermore, a recent study on the dynamics of soil organic matter fractions in differently managed and abandoned grasslands in the Alps suggests that abandonment does not provide a substantial net soil carbon sink (Meyer *et al*. 2012).

Mountain grassland ecosystems have high carbon stock below ground and our estimates were comparable with the estimates by Liski *et al*. (2002) for European forest soils. Therefore, we do not expect that soil carbon pools would change when pastures are converted into forests (either through abandonment or active planting). However, biomass in the trees of medium-aged and old forests is large and therefore the average total carbon stocks in Liski *et al*. (2002) are well above our values for grasslands, and due to this possible carbon pool in trees, the total biomass of forested meadows would certainly be higher than in non-forested areas.

Most mountain grassland ecosystems were close to being carbon neutral, in other words being neither a source nor a sink. Especially, the natural mountain grasslands in our study were quite close to carbon neutrality. Furthermore, we found that the soil carbon stocks in these grasslands were high, similar to those of forest ecosystems. Widespread abandonment of mountain grasslands is therefore not expected to lead to a rapid sequestration of large quantities of carbon in the near future.

The sites that are drained peatlands make an exception to the carbon neutrality of mountain

rangeland because they act as persistent sources of CO_2. While natural peatlands (like the site in Stordalen) are mainly carbon neutral, drained peatlands seem to be long-term sources of CO_2 unless water tables are raised (Waddington *et al*. 2002). The drained peatland in Seebodenalp was, therefore, a large source of CO_2. Changes in the hydrological cycles seem to have everywhere a major effect on the carbon balance of semi-natural grassland and pasture ecosystems: Novick *et al*. (2004) found that their warm-temperate grassland was limited by drought. Oechel *et al*. (2000) showed that arctic ecosystems, similar to those in Stordalen and Värriö, were losing carbon due to climate warming since the 1980s. Heikkinen *et al*. (2004) confirmed large carbon losses in the Russian tundra during a warm summer.

While the literature suggests that atmospheric CO_2 increase might, indeed, fertilise grassland ecosystems and enhance carbon sequestration (Loiseau and Soussana 1999), it seems likely that changes in management will overshadow these effects. Also, increases in temperature seem to decrease carbon sequestration in all our ecosystems. These decrease in carbon storage due to interannual fluctuations of temperature and soil moisture seems to be a general response of grassland ecosystems to climate change, since other studies show that also other natural grasslands loose carbon during dry years (Flanagan *et al*. 2002, Novick *et al*. 2004).

Several review papers have suggested methods to increase carbon sequestration of agricultural lands (Freibauer *et al*. 2004, Post *et al*. 2004). The most important measures were no tillage and shift to perennial vegetation. These management practices are past and current practice in mountain grasslands, i.e. mountain grasslands have been managed for a long time in a way that maintains high carbon stocks. Indeed, the site which was the highest net carbon sink (Amplero) was used a long time ago as an agricultural field and might be recovering its carbon stocks.

We do not know if the high carbon fixation is due to accumulation in the soil after land use change. Therefore, it seems that there are limited possibilities to increase the carbon sequestration of mountain grasslands and current management practices should focus on how to keep the high carbon pools in the soil of these ecosystems and support the other ecosystem services mountain grasslands provide.

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