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Net ecosystem production in a Little Ice Age moraine: the role of plant functional traits

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Abstract

Current glacier retreat allows vast mountain ranges available for vegetation establishment and growth. Little is known about the effective carbon (C) budget of these new ecosystems and how the presence of different vegetation communities, characterized by their specific physiology and life forms influences C fluxes. In this study, using a comparative analysis of the C fluxes of two contrasting vegetation types, we intend to evaluate if the different physiologies of the main species have an effect on Ecosystem Respiration (R_{eco}), Gross Primary Production (GPP), annual cumulated Net Ecosystem Exchange (NEE), and long-term carbon accumulation in soil.

The NEE of two plant communities present on a Little Ice Age moraine in the Matsch glacier forefield (Alps, Italy) was measured over two growing seasons. They are a typical C3 grassland, dominated by *Festuca halleri* All. and a community dominated by CAM rosettes *Sempervivum montanum* L. on rocky soils. Using transparent and opaque chambers, we extrapolated the ecophysiological responses to the main environmental drivers and performed the partition of NEE into R_{eco} and GPP. Soil samples were collected from the same site to measure long-term C accumulation in the ecosystem.

The two communities showed contrasting GPP but similar R_{eco} patterns and as a result significantly different in NEE. The grassland acted mainly as a carbon sink with a total cumulated value of $-46.4 \pm 35.5\,\mathrm{g\,C\,m^{-2}}$ NEE while the plots dominated by the CAM rosettes acted as a source with $31.9 \pm 22.4\,\mathrm{g\,C\,m^{-2}}$. In spite of the NEE being different in the two plant communities, soil analysis did not reveal significant differences in carbon accumulation. Grasslands showed $1.76 \pm 0.12\,\mathrm{kg\,C\,m^{-2}}$, while CAM rosettes showed $2.06 \pm 0.23\,\mathrm{kg\,C\,m^{-2}}$.

This study demonstrates that carbon dynamics of two vegetation communities can be distinct even though the growing environment is similar. The physiological traits of the dominant species determine large differences in the carbon cycle. Therefore, to analyze NEE of any glacier forefield ecosystem, different functional traits of the vegetation

communities must be taken into consideration. Moreover, to assess the net ecosystem carbon balance it is necessary to consider the lateral fluxes of carbon via animal consumption, winter respiration, and in a broader temporal perspective, the different stages characterizing the primary succession.

1 Introduction

Increasing global temperatures are causing glaciers to retreat worldwide (Oerlemans, 2005). The Alps are particularly vulnerable to climate change and it has been estimated that since 1850, glaciers in the Alps have lost half of their total extent (Zemp et al., 2006). Shortly after ice melt, these large areas are colonized by vegetation in the course of primary succession and a new ecosystem begins to develop (Marcante et al., 2009). After the establishment of a scattered pioneer flora, the vegetation of the glacier forefield develops, in combination with the formation of soil, progressing towards different stages of the primary succession. Vegetation communities of old succession stages are stable and are typically present with increasing biodiversity and biomass (Matthews, 1992). However, the primary succession often does not show a single pathway mechanism. On the same stage of the succession, local site conditions can be very different, even within short distances, therefore, favouring the establishment of patchy vegetation (Burga et al., 2010).

To date there have been few studies that analysed the carbon budget in the glacier foreland (Bekku et al., 2004; Nakatsubo et al., 2005) and there is a large uncertainty about the role of the different plant communities growing on the glacier forefield in the dynamics of carbon (C) accumulation in the ecosystem. The carbon budget of an ecosystem is quantified by the Net Ecosystem Production (NEP) (Baldocchi, 2003), defined as the difference between Gross Primary Production (GPP) and Ecosystem Respiration (R_{eco}). NEP is the same as Net Ecosystem Exchange (NEE) but they have opposite signs. If we consider non-respiratory CO_2 losses, the non CO_2 losses, and the imports and exports from bordering ecosystems (Luyssaert et al., 2007), the final amount of C accumulated by any ecosystem is expressed as Net Ecosystem Carbon Balance (NECB) (Chapin et al., 2006).

Studies on the carbon budget of ecosystems that are close to glacier forefields, such as alpine grasslands (Schmitt et al., 2010), or ecosystems with the presence of similar vegetation, like the arctic tundra (Belshe et al., 2013), indicate that they can act either as a sink or a source of carbon (Oechel et al., 1993). In grassland ecosystems, climatic drivers have a strong influence in the assimilation and emission processes, leading to a large inter-annual variability (Polley et al., 2008). Moreover, plant species interact in different ways with the other components of the ecosystem (Chapin, 2003) but it is still unknown to what extent this affects the final NECB. In fact, plants belonging to different growth form and characterized by different photosynthetic pathways can differ for seasonal productivity, carbon allocation in their tissues, and therefore quality and quantity of the litter (Laine et al., 2012) that affects the heterotrophic respiration (Laganière et al., 2012). Additionally, the C allocation strategy in plant organs influences the consumption of plants by animals (Adler et al., 2005). Moreover, the interaction mechanisms, like the capacity to form symbiotic relationships (with N_2-fixing organisms or with mycorrhizal fungi) (De Deyn et al., 2008) influence the microbial community in soils. All these factors determine the variability of import/export of C from the ecosystem due to lateral fluxes.

The capacity of an ecosystem to sequester carbon (NECB) is mainly determined by the physical characteristics of the soil and by the biota of the area (De Deyn et al., 2008). By analysing the NECB of different vegetation communities on the same stage of the primary succession we can exclude differences in soil properties, instead we can focus on how the physiology of the single species affects GPP and R_{eco} (Bubier et al., 2006; Otieno et al., 2009). Functional traits of plants are expected to influence the interaction between the physical environment and the carbon sink capacity with scale dependent effects. Small-scale differences are often larger than broader-scale differences (Reichstein et al., 2014).

Few studies have investigated the differences in fluxes of CO_2 and final NECB measured from various plant communities in the same ecosystem (Hirota et al., 2010). Studies have analysed the seasonal carbon budget in relation to different plant physiologies in peatlands (Bubier et al., 2003, 2006; Glenn et al., 2006) and suggested the determinant role of plant functional traits in the NECB. Christensen et al. (2000) studied the assimilation and emission processes in different tundra vegetation communities, through the combined use of opaque and transparent chambers. Their study found that the differences in NEE rates between the communities are related to biological characteristics of the communities. In alpine ecosystems, Wohlfahrt et al. (2003) considered the influence of species physiology by modelling the carbon budget of three meadows differing in land use.

In the present study, we investigated the carbon fluxes of two well-differentiated plants communities living on the same stage of a primary succession, on the LIA moraine. One was a typical C3 grassland of glacier forefields (*Festucetum halleri* association after Braun-Blanquet and Jenny, 1926) and the second was a community mainly composed by *Sempervivum montanum* L., a succulent species exhibiting the Crassulacean Acid Metabolism (CAM) (Wagner and Larcher, 1981), commonly found on rocky and dry soils.

A comparative analysis of the ecophysiological responses to the environmental drivers of these two contrasting plants communities was carried out. This is the first time ever a trial has been conducted on CAM species for a whole vegetation season. Data collected were used to answer the following scientific questions:

i. can a reliable method be established to partition the net ecosystem exchange of CAM plants into respiration and photosynthesis, in a way similar to what is usually performed for C3 and C4 plants, in order to separate their responses to environmental drivers?

ii. Are assimilation (GPP) and respiration (R_{eco}) processes in the two vegetation types similarly influenced by the environmental factors?

iii. Is the yearly cumulated NEE similar for the two communities?

iv. Can we explain the NECB of the young ecosystem with the analysis of the NEE of these two vegetation communities?

2 Material and methods

2.1 Study area

The study was conducted in the upper catchment area of the Matsch valley, which has a drainage area of approximatively 11 km^2. The Matsch valley is enclosed within the upper Vinschgau valley in the Province of Bozen/Bolzano situated among the Italian Alps (Fig. 1). From a geological point of view, the Matsch valley belongs to the Ötztal-Stubai complex and consists mainly of Orthogneis (Habler et al., 2009). The bottom of the valley has a relatively dry climate with an annual average rainfall of 550 mm (1970–2000). Rainfall increases with altitude and reaches even 1000 mm in the upper catchment part. The annual average temperature at 1570 m a.s.l. is 6.6 °C (Penna et al., 2014).

The Matsch glacier is a part of the Palla Bianca-Weisskugel Glacier complex and is located between 2700 and 3700 m a.s.l. In 1850, at the end of the Little Ice Age (LIA), the maximal extent of the Matsch Glacier was 4.88 km^2, and it decreased to 2.78 km^2 in 2006 (Knoll and Kerschner, 2010). The study site lies at 2400 m a.s.l., and has been free from ice for about 160 years. The primary succession on the Matsch glacier forefield is similar to that of nearby localities as described by Raffl and Erschbamer (2004). The colonization process can be observed from a few meters from the glacier tongue with mosses and single vascular plants (*Leuchantemopsis alpina* L. and *Arenaria biflora* L). On the moraine ridges of 1940, the total vegetation cover amounts for 35 % of the soil and in the area is present a pioneer grassland community dominated by *Poa laxa* Haenke and *Gnaphalium supinum* L., *Cerastium cerastoides* (L.) Britton, and *Arenaria biflora* L. On the LIA moraine, the vegetation cover amounts for 70 %

of the soil and is made up of different vegetation communities. These patchy vegetation groups have a lower rate of habitat disturbance, for example *Festucetum halleri* after Braun-Blanquet and Jenny (1926), a community composed mainly by the succulent species *Sempervivum montanum* L., the *Cetrario-Loiseleurenion* alliance (Braun-Blanquet et al., 1939), and single plants of Rhododendron (*Rhododendron ferrugineum* L). Beyond the moraine ridges, the vegetation for the upper Match valley is represented by the grass meadow *Nardion strictae* (Braun-Blanquet and Jenny, 1926) on the valley bottom, and along the sides of the valley with the shrub community *Rhododendro-Vaccinion* (Braun-Blanquet and Jenny, 1926).

2.2 Meteorological data

Air temperature and relative humidity were measured at 0.1 and 2 m above ground (RHT Plus, Skye Instruments, UK) along with global radiation (pyranometer model CM6b, Kipp and Zonen, Delft, Holland), and wind speed (anemometer A100r, Vector Instruments, UK). Measurements were taken every 10 s and collected at 10 min intervals by a DL2 datalogger. Soil temperature and soil relative humidity at 5 cm below soil surface were measured by PT100 and 10HS, Decagon, USA, respectively, and collected by the Li 8100 system (LiCor Biosciences, Lincoln, NE, USA, LiCor hereafter). All the data were then averaged at 30 min time steps.

2.3 NEE measurements

NEE, under light and dark conditions, was measured using the chamber technique in 2012 and 2013 in two typical plant communities situated on the LIA moraine. The two vegetation communities were chosen purposely because of the different photosynthetic pathways and plant traits of the two dominant species, which were *Festuca halleri* All. (hereafter, termed *Festuca* plots) and *Sempervivum montanum* L. (hereafter, termed *Sempervivum* plots). An infrared gas analyser (Li 8100, LiCor) connected to a multiplexed system was used (Li 8100-105, LiCor). It was made of eight automated closeddynamic chambers: four transparent (Li 8100-104C LiCor) and four opaque ones (Li 8100-104 LiCor). The transparent chambers were used to measure the gas exchange of the selected ecosystems during ambient light conditions while the opaque ones were used to measure the gas exchange under dark conditions. This combined technique on the same collars enables the partitioning of photosynthetic and respiratory fluxes and provides an accurate C-balance measurement (Heinemeyer et al., 2013).

In 2012, measurements were aimed to assess spatial variability of C fluxes of two representative vegetation communities with different photosynthetic pathways. For the purpose, five plots with a dominant presence of *S. montanum* (S1–S5) and five plots with *F. halleri* (F1–F5) were chosen for the study. Each plot was monitored for three days with transparent chambers and then for the next three days with opaque chambers. Measurements were carried out during the peak vegetative growing season for 18 days (28 July–14 August 2012).

In 2013, measurements were taken from 06 June, just after snowmelt, until 17 September after the first relevant snow fall, totalling 103 days, covering most of the carbon-uptake period as we were interested in the seasonal trend of the fluxes. During this year, measurements in the five plots for each vegetation community were set as follows: one plot was monitored for the entire vegetative season with the transparent chambers ($\mathrm{Ft}_{\mathrm{LT}}$ = *Festuca* transparent long term; $\mathrm{St}_{\mathrm{LT}}$ = *Sempervivum* transparent long term), and another with the opaque chambers ($\mathrm{Fo}_{\mathrm{LT}}$ = *Festuca* opaque long term; $\mathrm{So}_{\mathrm{LT}}$ = *Sempervivum* opaque long term). In the remaining three plots, an opaque and a transparent chamber were rotated every week. These were called short-term plots ($\mathrm{Ft}_{\mathrm{ST}}$, $\mathrm{St}_{\mathrm{ST}}$, $\mathrm{Fo}_{\mathrm{ST}}$ and $\mathrm{So}_{\mathrm{ST}}$). In this way, data were collected from two opaque and two transparent chambers for each vegetation type for the entire measurement period, and at the same time we also considered the spatial variability of the fluxes.

Iron collars (20 cm diameter, 8 cm depth) were placed in soil and after two weeks data collection began. This was to minimize the disturbance effect of installing the collars (Swanson and Flanagan, 2001). Gas exchange data was collected at half hour time steps. For both opaque and transparent chambers, after the chamber closed on

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the collar, 20 s were considered as a mixing period and excluded from the calculation of the soil CO_2 efflux. The CO_2 concentration was then logged during the next 40 s. The CO_2 flux was measured as a change in CO_2 dry molar density during these 40 s ($\delta[CO_2]/\delta t$), using a linear regression. The exact chamber volume was computed every time when the chambers were moved on new collars, by measuring the distance from the top of the collar to the ground surface at three regularly spaced points on the collar.

2.4 Carbon content analysis

After the flux measurements were concluded in 2013, total above-ground biomass was collected from each collar. The above-ground biomass was divided into green biomass and necromass. A known volume of the soil at an average depth of 10 cm was also taken from each collar. The soil samples were separated from the roots (diameter > 2 mm). Samples of above-ground biomass and roots were oven-dried at 60 °C until the sample reached a stable weight. In addition, ten samples of the top 10 cm of mineral soil were collected few meters away from the glacier tongue to determine the carbon concentration in the soil at the beginning of the colonization process (t_0). Soil was oven-dried at 105 °C until the sample reached a stable weight and then weighed and acidified with Hydrochloric acid to eliminate the carbonate present (Brodie et al., 2011). The biomass and soil samples were analysed for total carbon and nitrogen content and for the carbon isotopic ratio ($\delta^{13}C$) by a FlashEA™ 1112 Elemental Analyzer (Thermo Fisher Scientific, Germany). The analysis $\delta^{13}C$ was used to distinguish between photosynthetic pathways. During photosynthesis, the different enzymes involved in C assimilation discriminate against 13C resulting in a different ratio of 13C/12C. Therefore, $\delta^{13}C$ in C3 plants are known to range between −25 and −29 ‰, while C4 plants have a $\delta^{13}C$ between −12 and −16 ‰. CAM plants have $\delta^{13}C$ between −10 to −20 ‰ (Black and Osmond, 2003).

NECB is the organic carbon accumulation rate, described as the change in the organic carbon pool per unit time, and is usually expressed as mass of carbon per unit area for a specific time interval (Lovett et al., 2006). As our ecosystem appeared after glacier retreat at the end of the Little Ice Age, approximately 160 years ago, the NECB represents the organic C accumulated by the ecosystem over 160 years. To calculate NECB, the sum of carbon content found in soil, above- and below-ground biomass, was measured from each collar. Results in this study are given for each vegetation community as an average of the five collars used. NECB is expressed as $\mathrm{kg\,C\,m^{-2}}$.

2.5 Data analysis

The data obtained in 2012 with both transparent and opaque chambers were used to compare the daily courses of NEE in *Festuca* and *Sempervivum* plots. Daily cumulated NEE ($\mathrm{g\,C\,m^{-2}\,d^{-1}}$) was measured for each plot with dark and clear chambers in 2012 to assess the spatial variation of the fluxes. To assess the temporal variation of the fluxes in the three days of measurement in each plot, we calculated the mean range of the fluxes as the average variation of the flux measured at a given half hour in the 3 days. Differences between plots were determined by conducting the one-way ANOVA test.

As described by Osmond (1978), the photosynthetic daily pattern of CAM plants can be divided in four phases:

Phase 1 at night; carboxylation of atmospheric CO_2 occurs through phosphoenol pyruvate (PEP) carboxylase and storage of C through the production of malic acid;

Phase 2 in the morning; carboxylation of atmospheric CO_2 occurs through both PEP and ribulose bisphosphate carboxylase oxygenase (Rubisco);

Phase 3 during the central hours of the day; the decarboxylation of malic acid and the consequently fixation of C through Rubisco carboxylase occurs;

Phase 4 during the afternoon; fixation of atmospheric CO_2 occurs through Rubisco carboxylase.

To verify the response to light of the two vegetation communities, we applied a logistic sigmoid model (Moffat et al., 2010; Eugster et al., 2010) to NEE data measured with the transparent chambers:

$$\mathrm{NEE} = 2\cdot F_\infty \left(0.5 - \frac{1}{1+\exp\left(\frac{-2\cdot\alpha\cdot\mathrm{PPFD}}{F_\infty}\right)}\right) + R_\mathrm{d} \quad (1)$$

where PPFD (photosynthetic photon flux density) is the driving variable, while α (initial quantum yield), F_∞ (maximum NEE at full light) and R_d (daytime ecosystem respiration) are the three model parameters.

Due to photosynthesis performed at night by CAM species, we could not approximate R_eco of the two vegetation communities using night values of NEE measured with the transparent chambers. Instead, by analysing CO_2 exchange data of the opaque chambers, we recognized that phase 3 corresponded to both vegetation types for maximum CO_2 efflux over the entire measured season. Therefore, we considered NEE measured with opaque chambers during phase 3 being equal to R_eco, where temperature is the main controlling factor. An Arrhenius type model (Lloyd and Taylor, 1994) was used to quantitatively assess the R_eco response function to air temperature of each measured plot by applying the following equation:

$$R_\mathrm{eco} = R_\mathrm{ref}\cdot e^{\left[E_0\left(0.0178507-\frac{1}{T+46.02}\right)\right]} \quad (2)$$

where R_ref is the respiration flux at the constant reference temperature $T_0 = 10\,^\circ\mathrm{C}$, E_0 is an empirical parameter which indicates the temperature sensitivity of R_eco and T is the air temperature in °C. A two-sample Wilcoxon test was applied to check for statistically significant differences between the two plant communities with respect to the two parameters R_ref and E_0. We analysed the data using a non-parametric statistical test because of the intrinsic uncertainty of normality tests (e.g. two sample t test) when applied to a limited sample size ($n = 4$ per plant community type). Modelling efficiency (MEF) and residual standard error (RSE) were used to evaluate the goodness of the curve fitting. MEF was calculated as following:

$$\mathrm{MEF} = 1 - \frac{\sum_{i=1}^{N}(\mathrm{OBS}_i - \mathrm{SIM}_i)^2}{\sum_{i=1}^{N}(\mathrm{OBS}_i - \overline{\mathrm{OBS}})^2} \tag{3}$$

where OBS_i and SIM_i are the observed and simulated values respectively (Janssen and Heuberger, 1995). In contrast to the R^2 value, the modelling efficiency not only measures the correlation between modelled and observed data but also their coincidence, and it is sensitive to systematic deviations between model and observation (Reichstein et al., 2005). RSE is the square root of the error variance from the ANOVA table and is commonly given among the outputs when fitting a non-linear regression curve with the statistical software R (version 3.1.3, R Foundation for Statistical Computing, Vienna, AT), by which all statistical analyses were conducted.

3 Results

3.1 Photosynthetic pathways and daily patterns of NEE

To verify the CAM behaviour in *S. montanum*, we investigated the carbon isotopic ratio (δ^{13}C) in the biomass and in the soil of each sampled plots of the two vegetation communities (Table 1). The isotopic ratio in the above-ground biomass was significantly different ($P \leq 0.001$) highlighting the different photosynthetic pathway of the two main species (Table 1). The average δ^{13}C of the five plots of *Festuca* was -26.90 ± 0.47 ‰ compared to the average δ^{13}C of the five plots of *Sempervivum* with -21.18 ± 0.41 ‰. The difference between the δ^{13}C in the soil was less significant ($P = 0.02$).

The spatial variability of the C fluxes measured with the transparent chambers in 2012 (Table 2) was similar for all plots belonging to the same vegetation communities, but was significantly different ($P = 0.020$) between the two communities. The average NEE for the five *Festuca* plots was $0.05 \pm 0.32\,\mathrm{g\,C\,m^2\,d^{-1}}$, and $0.57 \pm 0.23\,\mathrm{g\,C\,m^2\,d^{-1}}$ for the *Sempervivum* plots. The average daily patterns of the measurements performed with the transparent chambers in 2012 were also distinct for the two plant communities (Fig. 2a). The *Festuca* plots presented the typical day and night cycle of photosynthesis pattern in C3 plants where the net assimilation of CO_2 occurs under light conditions with an assimilatory peak in the central hours of the day and CO_2 emission during the dark period. The daily NEE trend of *S. montanum* (Fig. 2a) clearly followed the four phases as described by Osmond (1978) for CAM plants. The measurements in this study showed that during phase 1, under dark conditions, *Sempervivum* plots emitted CO_2, and only few records showed negative NEE values around 3 a.m. During phase 2, a peak of negative NEE was recorded that signifies assimilation, and the CO_2 balance reached values around zero a few hours before midday. In the central part of the day, the *Sempervivum* plots emitted CO_2 (phase 3) and reverted to CO_2 assimilation in the final part of the light period (phase 4).

The two vegetation communities showed similar trends in NEE fluxes when measured with the opaque chambers (Fig. 2b) and the cumulated value of NEE was similar (Table 2). The average value of daily NEE for the five *Festuca* plots was $2.53 \pm 0.46\,\mathrm{g\,C\,m^2\,d^{-1}}$ and $2.23 \pm 0.29\,\mathrm{g\,C\,m^2\,d^{-1}}$ for the *Sempervivum* plots. During the day, both vegetation communities showed an increase of emission fluxes with maximum respiration around midday. Between night and day emissions, the two plant communities showed different patterns. *Sempervivum* plots showed lower emissions during the night and higher emissions in the central part of the day than *Festuca* plots.

The daily trends of opaque and transparent chambers in the two communities were different. *Festuca* plots reached at noon the maximum assimilation value measured with the transparent chambers and the maximum CO_2 emission measured with the opaque chambers. Instead, in *Sempervivum* plots, the maximum assimilation measured with the transparent chambers occurred during phases 2 and 4 of the day, which did not correspond to the maximum of respiration.

3.2 Light response curve

The most evident difference in response to PPFD of *Festuca* and *Sempervivum* plots was related to the daytime fluxes (phase 3). As a result higher net carbon uptake was observed in *Festuca* plots than in *Sempervivum* plots (Fig. 3). The latter showed photosynthesis saturation at low light levels. By modelling the photosynthetic light response according to Eq. (1), we found that the three parameters α, F_∞ and R_d were 0.013 ± 0.001, -10.100 ± 0.297 and 2.620 ± 0.13 for *Festuca* plots, and 0.010 ± 0.002, 1.280 ± 0.077 and 0.450 ± 0.055 for *Sempervivum* plots. It should be noted that during dark conditions the assimilation in *Sempervivum* plots continued, so the computed value represents a balance between respiration and assimilation, while in *Festuca* plots only respiration occurred.

3.3 Ecosystem respiration and GPP modelling

The relationship between NEE measured in 2012 with the opaque chambers and air temperature for the two vegetation communities was calculated. It revealed that both our communities responded to temperatures in dark conditions, but eventually adapted to light until the closure of the opaque chambers (Fig. 4). Plants in the C3 *Festuca* plots responded to temperature changes during all daily phases, while the CAM *Sempervivum* plots correlated with this driver only during the Osmond's phase III, the deacidification. During the other phases the relation between NEE measured with the opaque chambers and air temperature was weak, and in some occurrences during phase II, acidification, the CO_2 assimilation prevailed over the emission.

Therefore, we decided to consider the NEE data measured with the opaque chambers during phase 3 only as R_eco for both communities. The relationship between R_eco and air temperature was calculated by applying Eq. (2) to all the data of phase 3. Results of respiration flux at the constant reference temperature $T_0 = 10\,^\circ\mathrm{C}$ (R_ref), and the temperature sensitivity (E_0) for each replicates of *Festuca* and *Sempervivum* plots measured in 2013, are presented in Table 3. The values of MEF and RSE of every fitted curve indicate an overall good fitting of the selected model (Table 3). The average reference respiration at 10 °C resulted slightly higher for *Sempervivum* than *Festuca.* The average R_{ref} was 2.17 in *Sempervivum* and 1.83 µmol $\text{CO}_2\,\text{m}^{-2}\,\text{s}^{-1}$ in *Festuca* plots, while the response to temperature was more pronounced for *Festuca* than for *Sempervivum* (average of E_0 was 206.53 and 179.80, respectively). However, the result of the two-sample Wilcoxon test showed no significant differences between the parameters indicating that the two vegetation types are characterized by similar respiration patterns. The average R_{ref} and E_0 parameters calculated for each vegetation type, combined to the half-hourly temperature dataset, were used to develop a vegetation-specific half-hourly R_{eco} estimate for the entire measured period.

The daily patterns of measured NEE, and the values of R_{eco} and GPP obtained after flux partitioning in the month of August 2013 is shown in Fig. 5. The maximum value of GPP (-6.6 ± 1.15 µmol $\text{CO}_2\,\text{m}^{-2}\,\text{s}^{-1}$) for the *Festuca* plots in August was obtained at 12:00 LT, the maximum value of GPP for *Sempervivum* plots (-3.35 ± 0.53 µmol $\text{CO}_2\,\text{m}^{-2}\,\text{s}^{-1}$) was obtained around 11:00 LT. Both vegetation types shared very similar value of R_{eco}, with the maximum value obtained around 12:30 LT (maximal R_{eco} for *Festuca* $= 2.16 \pm 0.43$ µmol $\text{CO}_2\,\text{m}^{-2}\,\text{s}^{-1}$; maximal R_{eco} for *Sempervivum* $= 2.51 \pm 0.43$ µmol $\text{CO}_2\,\text{m}^{-2}\,\text{s}^{-1}$).

3.4 Seasonal pattern of NEE

The data collected in the permanent plots over 2013 vegetative period was used to analyse the NEE temporal trend of the two vegetation communities. The daily trend measured in the *Festuca* plots with the transparent chamber remained almost the same all along the measured period (Fig. 6a). The intensity of assimilation fluxes increased during summer (maximal negative average value of NEE for the entire period registered in August -4.47 ± 1.23 µmol $\text{CO}_2\,\text{m}^{-2}\,\text{s}^{-1}$) and the assimilation peak underwent a shift from midmorning in June and July, to noon in August and even later in September. The *Sempervivum* community showed a typical CAM daily pattern in June, July, and August, with very similar values of NEE during the same period of the day, in different months. The maximal negative average values of NEE measured during phase 2 was −1.18 ± 0.62 µmol CO_2 m^{-2} s^{-1} in June; −0.69 ± 0.53 µmol CO_2 m^{-2} s^{-1} in July and −0.98 ± 0.66 µmol CO_2 m^{-2} s^{-1} in August. When the average temperature and PPFD decreased in September (Fig. 6c and d), the morning peak of assimilation and the emission period around noon were no longer recognizable. Measurements conducted with the opaque chambers (Fig. 6b) showed that the two communities shared similar daily trends along the growing season, with a peak of respiration during the central hours of the day. The maximal positive average value of NEE for *Festuca* plots registered in July was 2.66 ± 0.73 µmol CO_2 m^{-2} s^{-1}; the maximal positive average value of NEE for *Sempervivum* plots registered in June was 3.04 ± 1.45 µmol CO_2 m^{-2} s^{-1}. The intensity of the fluxes in the two plant communities remained almost constant during the entire summer. *Festuca* plots always registered a higher intensity of emission during the night and *Sempervivum* plots showed a sharper peak during the day (Fig. 6a and b). In September, the patterns of the two vegetation types largely overlapped.

3.5 Seasonally cumulated NEE and NECB

The cumulated value of NEE along the four months of study (Fig. 7) in the permanent plots was −45.8 and 11.9 g C m^{-2} for *Festuca* and *Sempervivum*, respectively. The cumulated values of GPP and R_{eco} resulting from NEE flux partitioning were 239.3 and 193.5 g C m^{-2} for the *Festuca* plot and 232.7 and 244.6 g C m^{-2} for the *Sempervivum* plot. By averaging the measured values of the permanent plots with the filled time series of the non-permanent plots of both the plant communities, the cumulated value of NEE (mean ± SD) resulted −46.4 ± 35.5 and 31.9 ± 22.4 g C m^{-2} highlighting an opposite sink-source pattern of the two plant communities with respect to atmospheric CO_2. GPP was 230.4 ± 50.3 and 186.5 ± 35.3 g C m^{-2} and R_{eco} was 184.0 ± 16.4 and 218.4 ± 38.9 g C m^{-2} for *Festuca* and *Sempervivum*, respectively.

Soil analysis of samples collected few meters from the glacier tongue showed that total organic carbon in the upper 10 cm soil layer was $< 0.15\,\mathrm{kg\,C\,m^{-2}}$; therefore, we considered the total amount of C found in the soil-vegetation system in our plots on the LIA moraine as representative of the C accumulated by the ecosystem in 160 years. The soil C in the upper 10 cm soil layer was not different in plots dominated either by *Festuca* or by *Sempervivum* (Table 4).

The total carbon content (NECB) was measured as the average of the C content in soil and biomass of the five plots for each vegetation type, which was slightly higher in the *Sempervivum* community than in *Festuca* (2.08 ± 0.52 and $1.77 \pm 0.3\,\mathrm{kg\,C\,m^{-2}}$, respectively). The ANOVA test applied to the different categories, in which the soil-plant system was divided, showed statistically significant differences only for the quantity of carbon stored in the green above-ground biomass with higher content in *Sempervivum* than in *Festuca* plots (Table 4).

4 Discussion

Robust differences in CO_2 fluxes between the two vegetation types was achieved by capturing measurements every half hour over the vegetative period.

The two communities are significantly different in their daily NEE pattern. *Festuca* plots showed a daily NEE pattern similar to that registered for other alpine grasslands (Li et al., 2008; Schmitt et al., 2010), although with a slightly lower intensity of fluxes. The daily pattern of *Sempervivum* plots measured with the transparent chambers in the field reproduces the phases described and tested by Osmond (1978) under controlled conditions, but with interesting differences. In general, *S. montanum* performed like a weak CAM, with a greater CO_2 uptake occurring in the light period than in the dark period. The weak CAM behavior can be confirmed by looking at the carbon isotopic ratio found in the biomass of *Sempervivum* plots. It represents the typical behavior that CAM plants display in condition of middle range temperature and under no particular water stress (Wagner and Larcher, 1981). In general, CAM plants are considered plastic organisms, as they finely regulate the amplitude of malic acid change and the amount of day vs. night CO_2 fixation in relation to the peculiar combination of environmental factors (Black and Osmond, 2003). The pattern of NEE in *Sempervivum* plots, compared to the chart proposed by Osmond (1978), shows an upper shift to a higher emission rate of CO_2. During phase 1, when CAM plants are supposed to show dark photosynthesis (Nobel, 1991), we almost registered some CO_2 emissions. As described by Wagner and Larcher (1981), *S. montanum* shows a clear nightly CO_2 uptake when large differences in air temperature between day and night occur. In our study area, the diurnal air temperature fluctuation never exceeded 15 °C, although real temperature measured in the rosettes of the plant can reach higher values (Körner, 2003). However, looking at the measurements conducted with the opaque chambers, we observed that night values of NEE of the *Sempervivum* plots are always lower than those of the *Festuca* plots, presumably because dark photosynthesis is also occurring. Past studies conducted in laboratory under controlled conditions suggested that it is almost impossible to find a temperature threshold that allows the switch from the emission to the assimilation process in the CAM cycle. The regulation of the CAM cycle does not directly depend on the current environmental condition, but on the internal reserve of malic acid generated in previous days (Wagner and Larcher, 1981). Interestingly, in September, when the average temperature is usually around 10 °C, the CAM metabolism is no longer evident and the plant behaves as a C3 plant. As a result the daily pattern of *Sempervivum* plots, measured with opaque and transparent chambers becomes almost the same as those of *Festuca* plots.

The combined use of transparent and opaque chambers was effective in providing reliable data of NEE and to model assimilatory and respiratory fluxes (Heinemeyer et al., 2013). Night time NEE data are generally used to extrapolate ecosystem respiration during the day by adopting a temperature response function, although it has been suggested that this method can lead to an overestimation of R_{eco} (Sun et al., 2014). We could not apply the customary methodology to *Sempervivum* plots, as NEE night data describe the assimilation processes, too. The results of flux partitioning performed well for both vegetation types and for all the periods of the trial. The two vegetation types have different assimilation processes, confirming that species physiology strongly affects CO_2 uptake, but they are characterized by similar emission patterns. A similar result was found by Wohlfahrt et al. (2003), who considered the influence of species physiology by modelling the carbon budget of three meadows differing in land use. Similar results have also been shown in comparing different tundra vegetation communities, where variations in NEE are more largely driven by differences in photosynthesis than in respiration rates (Christensen et al., 2000).

The NEP observed during the growing season indicates that the vegetation characterized by *F. halleri* acted as a sink of carbon in the emergent ecosystem, while the scattered plant community mainly characterized by the presence of *S. montanum* was a source of CO_2 during the measured period. A similar CO_2 source was also found for arctic vegetation in harsh habitats (Lloyd, 2001; Oechel et al., 1993). Relatively dry tundra, which is similar to our ecosystem with regard to climatic conditions, was proved to be mostly a carbon source (McGuire et al., 2012). Peatland ecosystems in mountain environments are also subject to a yearly switch from source to sink of carbon depending on soil moisture (Bubier et al., 2003; Otieno et al., 2009). Also, alpine grasslands can act as both a sink and a source due to changes in land management (Wohlfahrt et al., 2008). Inter-annual variability in the C balance, very typical of grassland communities with low productivity, is mainly linked to yearly fluctuations of soil respiration due to temperature and water availability (Flanagan and Johnson, 2005). In fact, below-ground respiration of plant communities in glacier forelands can significantly contribute to soil CO_2 efflux due to high allocation rates of carbon in the below-ground organs (Nakatsubo et al., 1998, 2005).

The values of NECB reached in both communities after 160 years are in the same range of those found for other glacier forefields (Smittenberg et al., 2012; Egli et al., 2010). In spite of a different NEP, the NECB results are similar for the two investigated vegetation types. The reasons for this inconsistency can be attributed to the fact that current vegetation is representative only for the current stage of plant succession.

In the past 160 years, there were different stages of vegetation succession growing on the same area, limiting the relevance of the current stage in the whole carbon accumulation process after the glacier retreat. The observed carbon isotopic ratio in the soil which was almost the same for the two communities in spite of the different assimilation pathways, is consistent with this interpretation. Another consideration to the similarity between NECB in the two plant communities is that lateral fluxes can influence the annual carbon budget of the small vegetation patches, thus further confusing the influence of current vegetation types in the overall process. Above all, the different palatability of the two species strongly affects a different consumption of the two vegetation types by the animals. In addition, the composition and quantity of the organic matter originated by the two communities and their associated compounds, like lignin and secondary metabolites, possibly influencing the rate of decomposition and soil winter respiration (Laganière et al., 2012; Merbold et al., 2011) can contribute to the similarity in NECB. It has been shown that high GPP values are not always coupled with high rates of C accumulation in the ecosystem. Annual grasses like *F. halleri* provide a consistent quantity of fresh material as substrate for heterotrophic respiration diminishing the C retention capacity of the ecosystem (Fontaine et al., 2004). Therefore, despite different NEE fluxes, the two vegetation communities reach similar values of NECB indicating that species physiology and the life form play an important role in the long-term carbon accumulation of the ecosystems.

In conclusion, this study reports the comparative ecophysiological analysis of two alpine plant communities presenting different pathways of assimilation, a typical C3 grassland and succulent CAM rosettes. We demonstrated the feasibility of the combined use of opaque and transparent chambers to assess the Net Ecosystem Exchange, the Ecosystem Respiration and the Gross Primary Productivity of CAM plants. We showed that data collected with opaque chambers during the Osmond's phase III, the central part of the day when the stomata are closed can be used to model the relation with temperature, and the data collected during phase II (morning, acidification) using transparent chambers, can be used to model the assimilation response to PPFD availability.

The comparative analysis demonstrates that the carbon dynamics of the two vegetation communities are quite distinct. The physiology of the dominant species determines large differences in the carbon cycle. The two investigated plant communities showed similar respiratory patterns (R_{eco}) but had different assimilation pattern (GPP), because of their response to the climatic constrains, in particular light intensity. The different photosynthetic pathway determines contrasting NEE, which was found to be positive for the CAM rosettes and negative for the C3 plants.

The overall NECB obtained from soil and vegetation analyses was not explained by the NEE observed during a whole vegetation season. To fully understand the process of soil formation and carbon accumulation on a glacier forefield it is recommended to monitor the dormant season, all the stages occurring during the primary succession characterized by different vegetation communities with different functional traits, and the lateral flows due to animal consumption.

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Table 1. Comparison of isotopic ratio of carbon in the vegetation communities. Values are reported as averages of five samples ± standard error. *P* value of the ANOVA test with 12 (δ^{13} C in soil) and 8 (δ^{13} C in biomass) degrees of freedom, significance codes: $< 0.001\ ^{c} = 99.9\,\%$; $< 0.01\ ^{b} = 99\,\%$; $< 0.05\ ^{a} = 95\,\%$.

	Festuca	*Sempervivum*	*P* value
δ^{13}C soil	−26.18 ± 0.30	−25.74 ± 0.58	0.020^{a}
δ^{13}C biomass	−26.90 ± 0.47	−21.18 ± 0.41	$< 0.001^{c}$

Table 2. Daily cumulated NEE ($\mathrm{g\,C\,m^{-2}\,d^{-1}}$) measured for each plot with dark and clear chambers in 2012. This value was obtained as the sum of the grams of C exchanged every 30 min (average of three days of measurements for each plot). The day-to-day variability in the fluxes, reported in brackets, was addressed by calculating the mean range (average of max-min value at a given half-hour). *P* value of the ANOVA test with 8° of freedom.

Vegetation community	Plots	NEE ($\mathrm{g\,C\,m^{-2}\,d^{-1}}$) opaque chamber	NEE ($\mathrm{g\,C\,m^{-2}\,d^{-1}}$) transparent chamber
Festuca	F1	2.644 (0.006)	0.044 (0.011)
	F2	2.530 (0.010)	0.390 (0.020)
	F3	2.260 (0.012)	0.294 (0.016)
	F4	2.000 (0.008)	−0.132 (0.028)
	F5	3.215 (0.006)	−0.369 (0.015)
Sempervivum	S1	1.977 (0.010)	0.160 (0.012)
	S2	1.873 (0.007)	0.661 (0.010)
	S3	2.454 (0.020)	0.648 (0.014)
	S4	2.510 (0.014)	0.687 (0.010)
	S5	2.360 (0.009)	0.737 (0.007)
P value		0.260	0.020[a]

Table 3. Respiration flux at the constant reference temperature $T_0 = 10\,^{\circ}\mathrm{C}$ (R_{ref}), and the temperature sensitivity (E_0) calculated using Eq. (2) for each replicates of *Festuca* and *Sempervivum* plots measured in 2013, with standard error and P value. For each replicates, the modelling efficiency (MEF) and relative standard error (RSE) of the model is also given.

	Plot	Parameters	Estimate	St. error	P value	MEF	RSE μmol CO_2 m^{-2} s^{-1}
Festuca plots	$Fo_{ST}1$	R_{ref}	1.95	0.04	< 0.001	0.38	0.60
		E_0	156.64	12.89	< 0.001		
	$Fo_{ST}2$	R_{ref}	1.84	0.08	< 0.001	.72	0.71
		E_0	352.70	24.00	< 0.001		
	$Fo_{ST}3$	R_{ref}	1.60	0.03	< 0.001	.52	0.37
		E_0	182.32	14.95	< 0.001		
	Fo_{LT}	R_{ref}	1.92	0.04	< 0.001	.22	0.79
		E_0	134.45	11.89	< 0.001		
		$R_{\mathrm{ref\ average}}$	1.83	0.08			
		$E_{0\ \mathrm{average}}$	206.53	49.70			
Sempervivum plots	$So_{ST}1$	R_{ref}	1.78	0.05	< 0.001	0.05	0.71
		E_0	64.05	17.59	< 0.001		
	$So_{ST}2$	R_{ref}	1.86	0.11	< 0.001	0.47	0.97
		E_0	282.26	32.25	< 0.001		
	$So_{ST}3$	R_{ref}	2.59	0.07	< 0.001	0.38	0.91
		E_0	206.45	22.96	< 0.001		
	So_{LT}	R_{ref}	2.44	0.06	< 0.001	0.24	1.19
		E_0	166.41	13.99	< 0.001		
		$R_{\mathrm{ref\ average}}$	2.17	0.40			
		$E_{0\ \mathrm{average}}$	179.80	90.89			

Table 4. Comparison of C content in the plots of the two vegetation communities. Soil (0–0.1 m) and vegetation inside the plots are considered (total *n* of samples = 40). Values are reported as averages of five samples ± standard error for each categories in which the soil-plant system was divided. P values given are the result of the ANOVA test with 8 Degrees of Freedom, significance codes < 0.001 *= 99.9 %.

C content	*Festuca* (g m^{-2})	*Sempervivum* (g m^{-2})	*P* value
Soil	1073.87 ± 117.22	1360.20 ± 205.57	0.26
Above-ground biomass	53.02 ± 5.88	189.18 ± 19.58	< 0.001*
Necromass	66.58 ± 5.81	62.59 ± 11.19	0.76
Below-ground biomass	431.71 ± 63.05	375.37 ± 25.86	0.43

Table A1. Abbreviations.

C	carbon
CAM	crassulacean acid metabolism
Fo_{LT}	*Festuca halleri* plots measured with opaque chamber for a long term period
Fo_{ST}	*Festuca halleri* plots measured with opaque chamber for a short term period
Ft_{LT}	*Festuca halleri* plots measured with transparent chamber for a long term period
Ft_{ST}	*Festuca halleri* plots measured with transparent chamber for a short term period
GPP	gross primary production
NECB	net ecosystem carbon balance
NEE	net ecosystem exchange
NEP	net ecosystem production
R_{eco}	ecosystem respiration
So_{LT}	*Sempervivum montanum* plots measured with opaque chamber for a long term period
So_{ST}	*Sempervivum montanum* plots measured with opaque chamber for a short term period
St_{LT}	*Sempervivum montanum* plots measured with transparent chamber for a long term period
St_{ST}	*Sempervivum montanum* plots measured with transparent chamber for a short term period

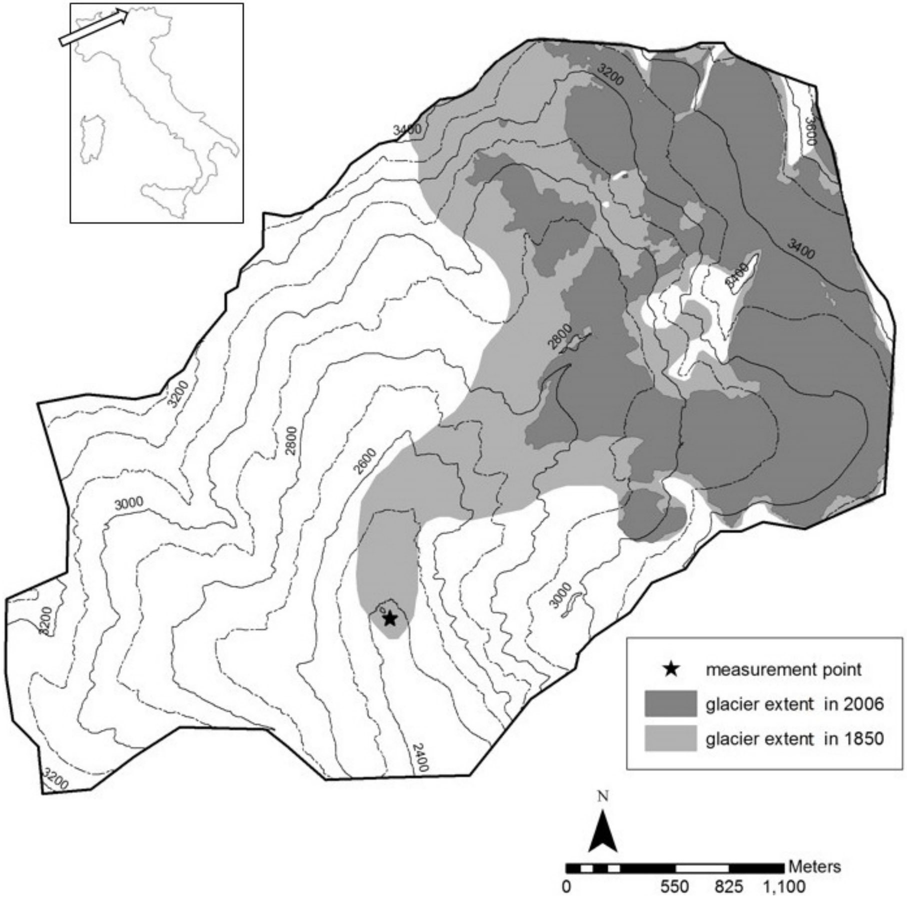

Figure 1. Study area in the upper Matsch valley (Northern Italy) where the glacier extent in 2006 and 1850 is shown. The star indicates the measurements location.

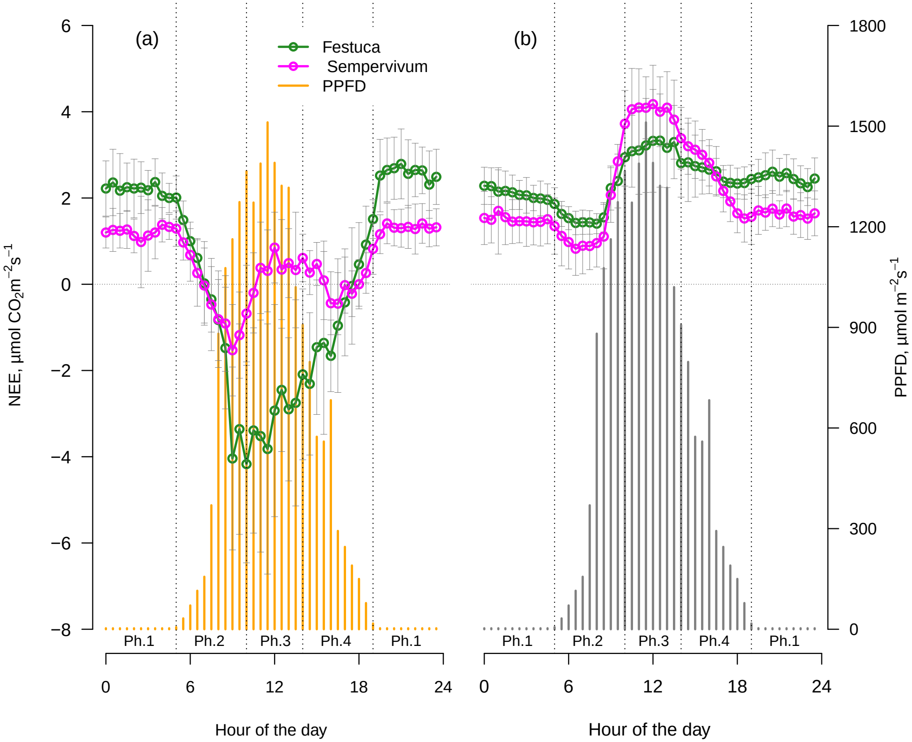

Figure 2. Average daily pattern (mean of three days of measurements ± SD) of net ecosystem exchange (NEE) measured in 2012 with **(a)** the transparent chambers and **(b)** the opaque chambers. Vertical bars indicate the average diurnal pattern of the photosynthetic active photon flux density (PPFD). Dotted lines split the day in the four CAM phases modified from Osmond (1978) as follows: phase 1: the night; the period characterized by PPFD < 2 μmol m^{-2} s^{-1}. Phase 2: the morning; PPFD > 2 μmol m^{-2} s^{-1} until phase 3 starts. Phase 3: the noon; the four central hours of the day, two hours before and two after the local midday. Phase 4: the afternoon; starting after phase 3 until PPFD < 2 μmol m^{-2} s^{-1}.

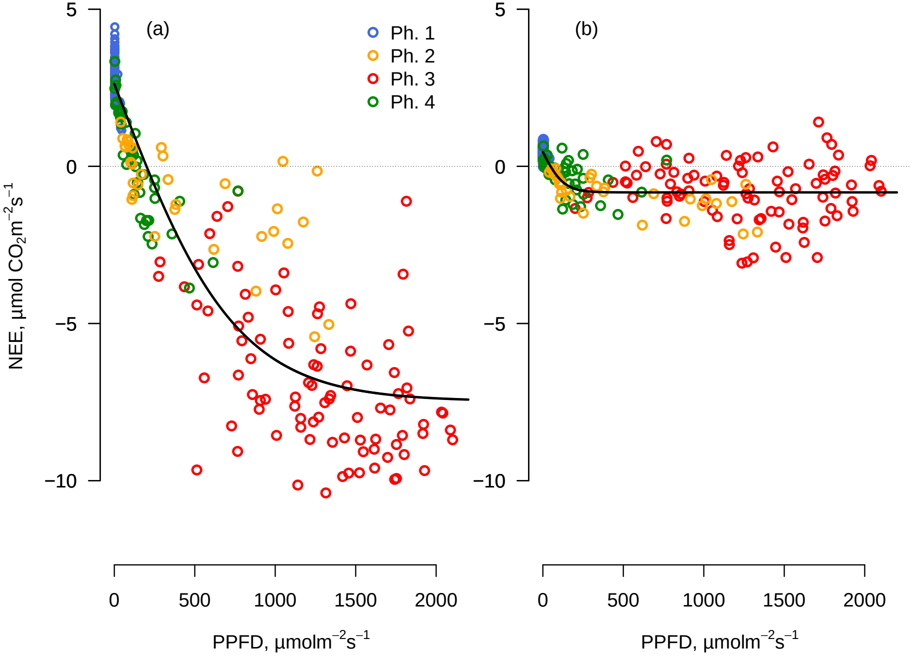

Figure 3. NEE of **(a)** *Festuca* and **(b)** *Sempervivum* measured with clear chambers as a function of photosynthetic active photon flux density (PPFD). Data reported correspond to a week of measurements in 2012 (07–14 August 2012). The solid line indicates the light response curve obtained using Eq. (1). Each color of the dots indicates one of the four "Osmond phases" in which the flux was measured, according to Fig. 2.

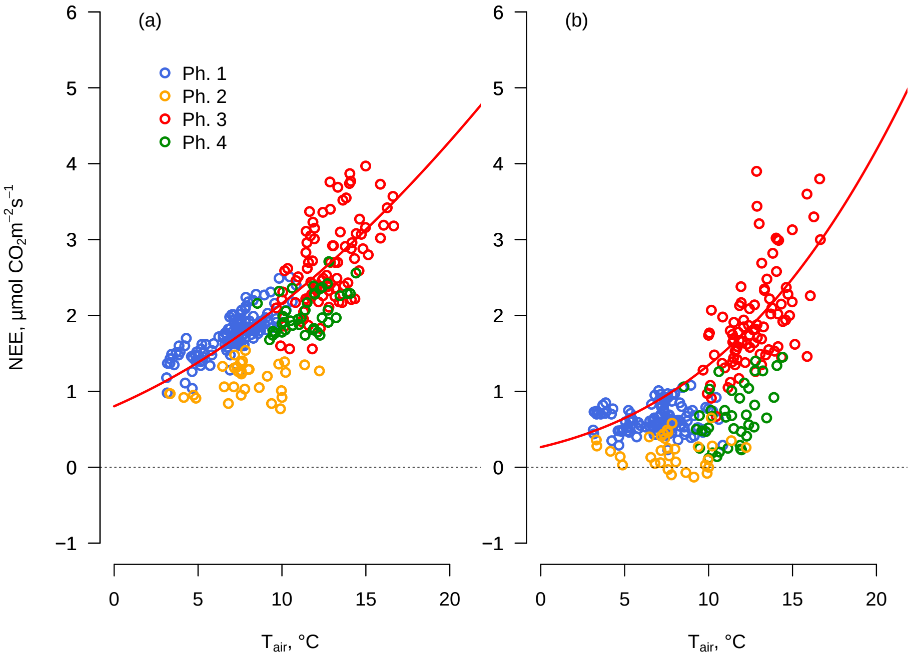

Figure 4. Net ecosystem exchange (NEE) of **(a)** *Festuca* and **(b)** *Sempervivum* measured with opaque chambers as a function of air temperature. Data reported correspond to a week of measurements in 2012 (07–14 August 2012). Each color of the dots indicates one of the four "Osmond phases" in which the flux was measured according to Fig. 2. The red solid line represents the modelled NEE response to temperature obtained by applying Eq. (2) only on data of phase 3, when we assumed that no photosynthesis was occurring in the *Sempervivum* plots.

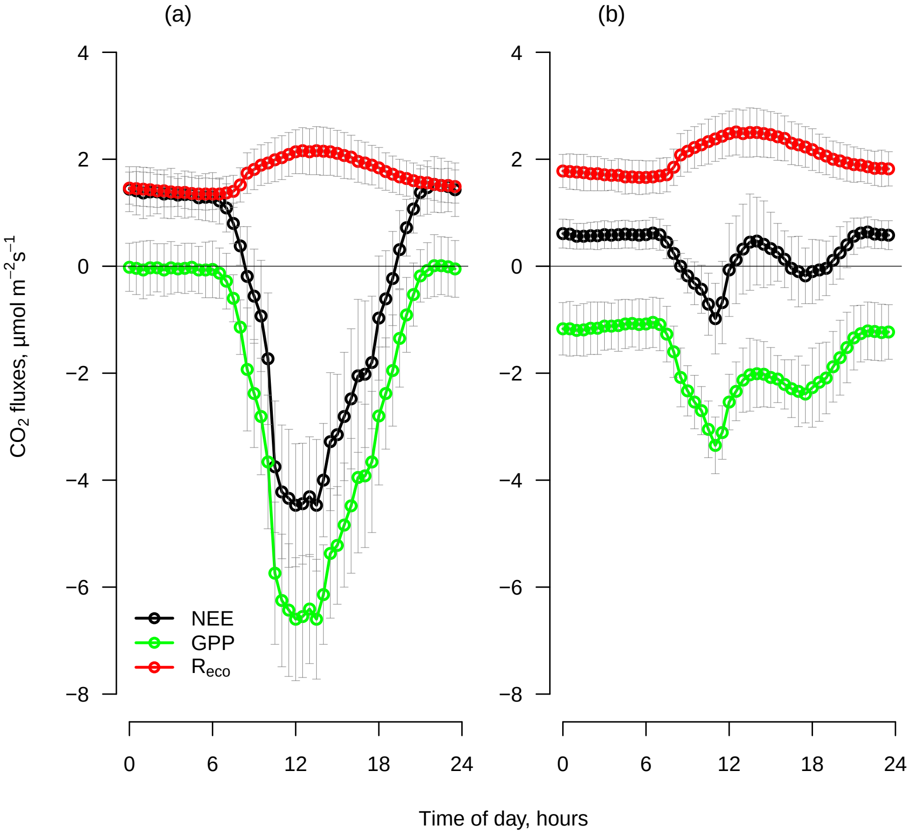

Figure 5. Daily patterns (mean ± SD) during August 2013 of the net ecosystem exchange (NEE) measured at all the plots, and the modelled ecosystem respiration (R_{eco}), and gross primary productivity (GPP) as obtained after flux partitioning for **(a)** *Festuca* and **(b)** *Sempervivum* plots. GPP is represented here as negative, for consistency with the other fluxes.

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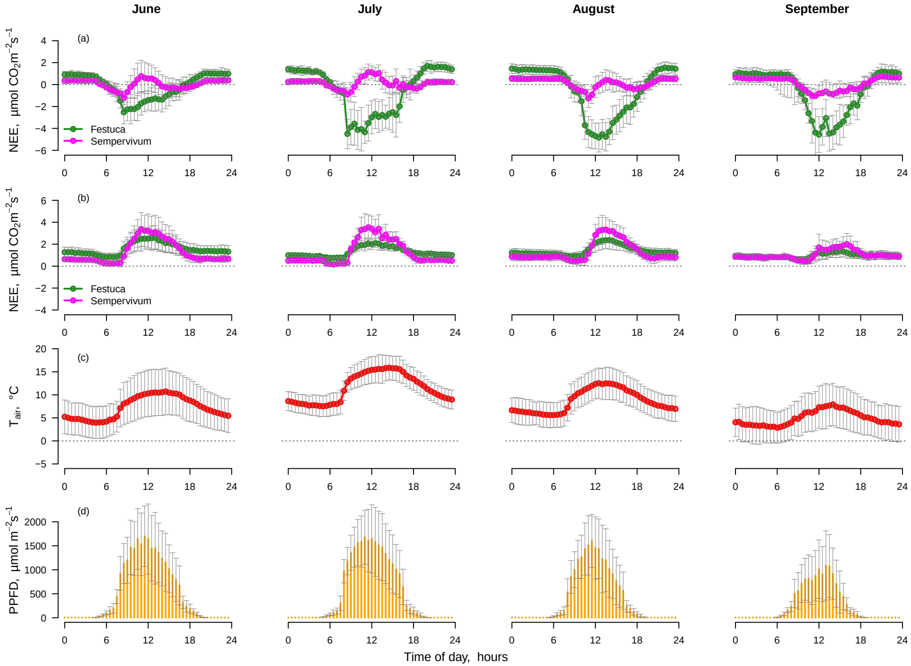

Figure 6. Daily pattern of net ecosystem exchange (NEE) measured with **(a)** transparent chambers, **(b)** opaque chambers. Panels **(c)** and **(d)** report the diurnal pattern of air temperature and photosynthetic active photon flux density (PPFD). Data are presented as monthly average ± SD in June, July, August, and September 2013.

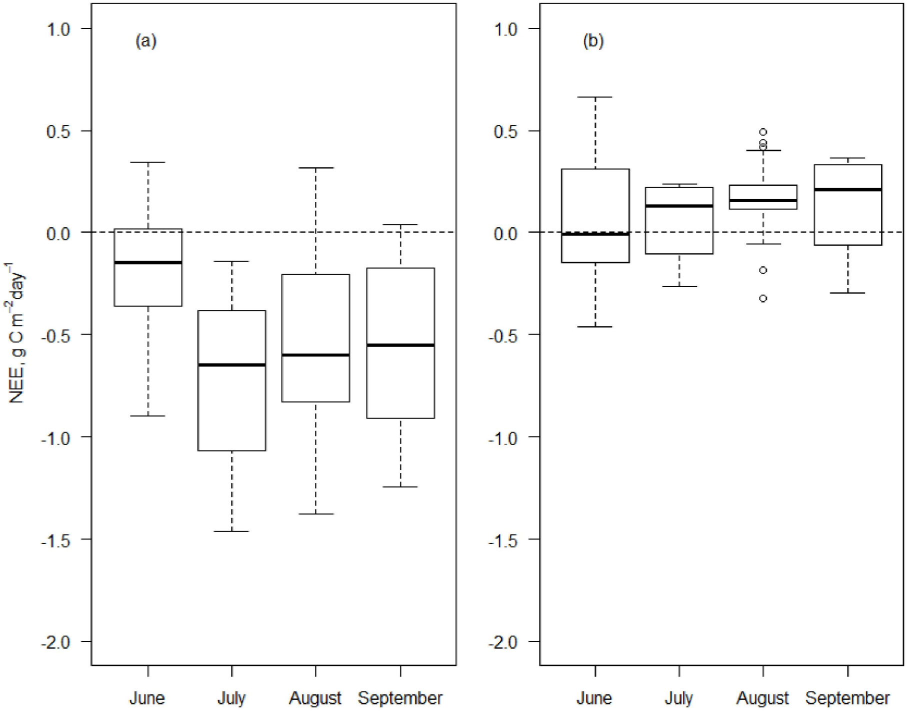

Figure 7. Box plots of cumulated daily values of net ecosystem exchange (NEE) measured with the long term transparent chambers in 2013 ($\mathrm{g\,C\,m^{-2}\,d^{-1}}$) in **(a)** *Festuca* and **(b)** *Sempervivum* plots.