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Abstract
Changes in snow cover depth and duration predicted by climate change scenarios are expected to strongly affect high-altitude ecosystem processes. This study investigates the effect of an exceptionally short snow season on the phenology and carbon dioxide source/sink strength of a subalpine grassland. An earlier snowmelt of more than one month caused a considerable advancement (40 days) of the beginning of the carbon uptake period (CUP) and, together with a delayed establishment of the snow season in autumn, contributed to a two-month longer CUP. The combined effect of the shorter snow season and the extended CUP led to an increase of about 100% in annual carbon net uptake. Nevertheless, the unusual environmental conditions imposed by the early snowmelt led to changes in canopy structure and functioning, with a reduction of the carbon sequestration rate during the snow-free period.

Keywords: carbon uptake period, snowmelt, eddy covariance, net ecosystem exchange, extreme events

S Online supplementary data available from stacks.iop.org/ERL/8/025008/mmedia

1. Introduction

Understanding the processes affecting the carbon dioxide (CO_2) exchange between the ecosystems and the atmosphere is crucial to evaluate the future impacts of climate change on the biosphere and the consequent feedbacks on climate system (Cao and Woodward 1998, Denman *et al* 2007, Heimann and Reichstein 2008).

Mountain ecosystems in the European Alps are expected to be particularly impacted by future rising temperatures, changes in precipitation patterns, duration of the snow-pack

(Beniston 2005a, Solomon *et al* 2007), and by the increase in extreme events (e.g. summer and winter heat spells, summer droughts. . .) (e.g. Beniston 2005b, Alcamo *et al* 2007). In seasonally snow-covered ecosystems, such as high-altitude grasslands, the snow lying on the ground fully limits the length of the growing season and overshadows the relative influence of other environmental factors (photoperiod and temperature). Future warming of the Alpine region (Foppa and Seiz 2012) will likely result in earlier snowmelt dates, thus reducing the period in which grasslands act as a net carbon source. Although several studies have investigated the effect of snow manipulation on the phenology and growth of alpine plants (Wipf and Rixen 2010), little is known about the effects of shortened snow seasons on the annual carbon budget of high-altitude ecosystems, due to the high variability of species responses. Various studies have used the eddy covariance method, which has been proven to be an effective tool for (i) measuring CO_2 exchanges at the ecosystem level and across a spectrum of time scales (Baldocchi 2003), and (ii) evaluating the impacts of extreme events on water and carbon cycle of different ecosystems (e.g. Yi *et al* 2012, Ciais *et al* 2005). Nevertheless, only a few studies (e.g. Humphreys and Lafleur 2011) have focused on the effects of changes in snow season duration on the ecosystem carbon budget.

In this study we analysed three years of continuous measurements of CO_2 exchange across the biosphere/atmosphere interface collected in a subalpine grassland by means of the eddy covariance technique. The hypothesis was tested that smaller CO_2 losses during a shorter snow cover period and more net CO_2 uptake during the subsequent longer growing period may cause an overall larger net CO_2 uptake during years with a shorter snow season. For this purpose we took advantage of a 'natural experiment' in which phenology and ecosystem CO_2 fluxes observed during a year (2011) marked by one of the shortest snow seasons on record (83 years) were compared to those observed during average years (2009, 2010).

The following main questions were addressed: did the extremely short snow season increase the length of the carbon uptake period in the investigated ecosystem? If so, what is the effect on the ecosystem carbon uptake?

To answer these questions, (i) phenological indicators were extracted from the CO_2 flux time-series, (ii) the relationships between timing and length of the phenophases and the carbon balance of the ecosystem were investigated, and (iii) a modelling approach was used to disentangle the influence of functional changes from the direct effect of weather on the ecosystem carbon uptake.

2. Materials and methods

2.1. Site description

The study was carried out in a subalpine unmanaged grassland, in the northwestern Italian Alps, from January 2009 to December 2011. The site is an abandoned pasture located a few kilometres from the village of Torgnon in the Aosta Valley region at an elevation of 2160 m asl (45°50′40″N, 7°34′41″E).

Dominant vegetation consists of *Nardus stricta* L., *Festuca nigrescens* All., *Arnica montana* L., *Carex sempervirens* Vill., *Geum montanum* L., *Anthoxanthum alpinum* L., *Potentilla aurea* L., *Trifolium alpinum* L.. The terrain slopes gently (4°) and the soil is classified as Cambisol (FAO/ISRIC/ISS). The site is characterized by an intra-alpine semi-continental climate, with mean annual temperature of 3.1 °C and mean annual precipitation of about 880 mm. On average, from the end of October to late May, the site is covered by a thick snow cover (90–120 cm) which limits the growing period to an average of five months.

2.2. Eddy covariance data

The eddy covariance technique was used to measure the fluxes of CO_2 and H_2O between the ecosystem and the atmosphere. Measurement of wind speed in the three components (u, v, w) was performed by a CSAT3 three-dimensional sonic anemometer (Campbell Scientific, Inc.), while CO_2 and H_2O vapour air densities were measured by a LI-7500 open-path infrared gas analyzer (LI-COR, Inc.). Instruments were placed 2.5 m above the ground and measurements were performed at a frequency of 10 Hz.

Eddy fluxes were obtained by computing the mean covariance between vertical wind velocity and CO_2 and H_2O densities with a half-hour time step (Baldocchi 2003). The stored raw 10 Hz records were processed according to the Euroflux methodology (Aubinet *et al* 2000). The effect of temperature and humidity fluctuations on fluxes was corrected using the methodology described in Webb *et al* (1980) and Kramm *et al* (1995). Moreover, in order to correct CO_2 and H_2O fluxes for the effect of instrument surface heating on flux measurements, the method described in Burba *et al* (2008) (model 4) was applied.

The storage term was estimated from the time rate of change of the CO_2 mixing ratio at the measurement height (2.5 m) and CO_2 net ecosystem exchange (NEE) was calculated as:

$$NEE = Fc + Sc \qquad (2.1)$$

where Fc represents the corrected flux of CO_2 and Sc is the storage term. By convention, negative fluxes represent a net mass movement from the atmosphere to the biosphere and positive values the reverse.

Results from integral turbulence and stationarity tests (Foken and Wichura 1996) were combined to obtain an overall quality flag (Qc classes from 0, high quality, to 2, low quality) for each half-hour period using the standard procedure followed in Carboeurope-IP project (Mauder and Foken 2004). The eddy covariance flux footprint was determined through the analytical model of Schuepp *et al* (1990) and the main results of this analysis for the site were presented in Migliavacca *et al* (2011).

The filtering procedure applied to half-hourly CO_2 fluxes to remove data measured during unfavourable micrometeorological conditions, the evaluation of energy balance closure

and the uncertainty associated with flux calculations are described in the supplementary data (available at stacks. iop.org/ERL/8/025008/mmedia). The gap-filling method (www.bgc-jena.mpg.de/~ MDIwork/eddyproc/) described in Reichstein *et al* (2005) was used to produce daily, seasonal and annual sums of CO_2 exchange.

2.3. Meteorological, radiometric and ancillary measurements

Air (Tair) and soil (Tsoil) temperature were measured respectively by a HMP45 (Vaisala Inc.) and with temperature probes type therm107 (Campbell Scientific, Inc.) at different depths (2, 10, 25, and 35 cm). Soil water content (SWC) was assessed with soil water reflectometers, model CS616 (Campbell Scientific, Inc.), and soil heat flux (G) was measured by HFP01 plates (Hukseflux). Net radiation was measured with a CNR4 (Kipp and Zonen Corp.) net radiometer. Photosynthetically active radiation (PAR) was assessed by a LI-190 (LI-COR, Inc.) sensor. Snow height (HS) was measured with a sonic snow depth sensor (SR50A, Campbell Scientific, Inc.), which was used to determine snowmelt and snow season onset dates for years 2009–2011. Long-term snowmelt, snow season onset and Tair averages were computed on the basis of data collected since 1928 at a site (Cignana, 45°52′31″N, 7°35′19″E) located nearby the Torgnon site, and at the same altitude.

An automatic spectrometric system (HyperSpectral Irradiometer, Meroni *et al* 2011) was installed to collect high temporal resolution spectral signatures of canopy-reflected radiation. The instrument hosts a spectrometer (HR4000, OceanOptics) operating in the visible and near-infrared region of the solar spectrum (range 400–1000 nm) with a spectral resolution of 1 nm, which allows the computation of different vegetation indices. In this study the meris terrestrial chlorophyll index (MTCI) (Dash and Curran 2004) was used to infer the variation of chlorophyll content (Chl) during the growing season. MTCI values were converted to Chl concentrations using a linear regression model calibrated using Chl concentrations extracted from leaf samples collected every ten days at 12 plots during 2010 (Rossini *et al* 2012). The relationship ($R^2 = 0.83$) between MTCI and total Chl, used to estimate chlorophyll content for the three years, was:

$$\text{Chl}(\mu\text{g g}^{-1}) = 1.16\text{MTCI} - 1.17. \qquad (2.2)$$

Finally, leaf area index (LAI) was determined as described in Migliavacca *et al* (2011).

2.4. Extraction of grassland phenophases

Information about the phenology of net CO_2 uptake was extracted from the seasonal time-series of NEE (Richardson *et al* 2010). We focused on different phases of the vegetative period: the beginning of the carbon uptake period (BGS_{cup}), the peak season, the end of the carbon uptake period (EGS_{cup}) and the derived length of carbon uptake period (CUP).

BGS_{cup} and EGS_{cup} represent the dates in which the ecosystem switched from a source to a sink in spring and

vice versa in autumn. Three different approaches were used to identify these dates: in the first approach we identified BGS_{cup} and EGS_{cup} as the first zero-crossing date after which NEE turned from daily positive values to negative ones in spring and from negative to positive values in autumn; in the second approach, zero-crossing dates were defined as above but using a moving average with a 5-day window (Richardson *et al* 2009); in the last approach a regression line was fitted between NEE and DOYs (day of the year) using a subset of spring and autumn data (15 days for each period). The BGS_{cup} or EGS_{cup} date was identified by the DOY at which the fitted line passed through 0 (Baldocchi *et al* 2005). The average of the BGS_{cup} and EGS_{cup} extracted applying the three methods was used in the analysis.

2.5. Analysis of light–response curve of photosynthesis

In order to evaluate the impact of the anomalous 2011 snowmelt on NEE, we used a modelling approach to disentangle the effect of biotic response to early spring environmental conditions from the direct effect of the growing season weather (e.g. Richardson *et al* 2007, Marcolla *et al* 2011, Wu *et al* 2012). The light–response curve of photosynthesis was analysed to describe the relationship between NEE and PAR in the different years. The rectangular hyperbolic light–response function (Falge *et al* 2001) was used:

$$\text{NEE} = \frac{A_{\max}\alpha\text{PAR}}{\alpha\text{PAR} + A_{\max}} + R_{\text{eco}} \qquad (2.3)$$

where PAR ($\mu\text{mol}_{\text{photons}}$ m^{-2} s^{-1}) is the incident photosynthetically active radiation, $A_{\max}$ ($\mu\text{mol}_{\text{CO2}}$ m^{-2} s^{-1}) is the light-saturated rate of CO_2 uptake, α ($\mu\text{mol}_{\text{CO2}}/\mu\text{mol}_{\text{photons}}$) is the apparent quantum yield, and R_{eco} ($\mu\text{mol}_{\text{CO2}}$ m^{-2} s^{-1}) is the ecosystem respiration. $A_{\max}$, α, and R_{eco} were estimated by fitting equation (2.3) to non gap-filled, half-hourly NEE with a 15-days moving window shifted each 5 days. The model parameters estimated for each year were compared and used to model NEE. In detail, by running the model with one year's PAR and the model parameters of the other years, and vice versa, using fixed model parameters and varying PAR datasets, we evaluated the biotic response (embedded in the values of the parameters) against direct effects of weather (i.e. PAR). In particular, NEE simulated during a summer period representing for all the three years a portion of the BGS_{cup}–peak phase (DOY 176–190) was analysed.

3. Results

3.1. Long-term climatic conditions and weather during the study period

Figure 1 shows the mean annual course of HS and Tair averaged over the period 1928–2010, and the annual courses of HS, Tair, Tsoil, PAR, and SWC observed during the study period 2009–2011.

The snow season lasted on average 7 months during the 1928–2010 period and less than 5 months in 2011 (figure 1(a)). In detail, in spring 2011 snowmelt (14 April,
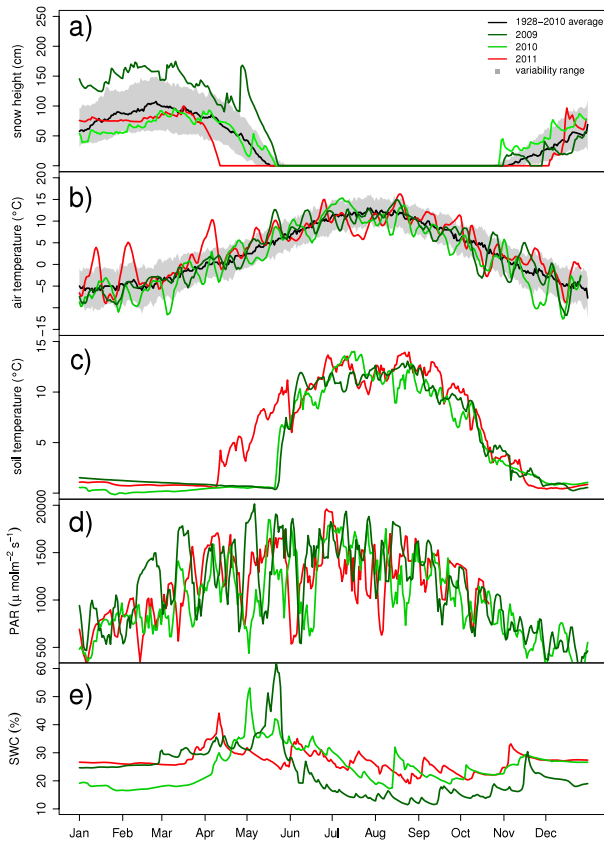
Figure 1. Annual course of the major meteorological variables. The following colour codes are used: black line for long-term data (average of the period 1928–2010) and grey area for the variability range; green line, light-green line and red line for the study years 2009, 2010 and 2011 respectively. (a) Snow height (cm) long-term data are presented as the daily median and the variability range is computed as 25th and 75th percentiles; (b) daily air temperature (°C) variability range is computed as standard deviation and data for the 3 study years are presented as 5 day running mean; (c) daily mean soil temperature (°C); (d) midday PAR (μmol m^{-2} s^{-1}) presented as 5 day running mean; (e) daily SWC (%).

DOY 104) occurred 33 days earlier than the long-term mean (17 May, DOY 137) and was the earliest snowmelt since 1945. Instead, the 2009 and 2010 snowmelt dates (26–24 May, DOY 146–144, in 2009 and 2010 respectively) fell well within the variability range of the long-term period, and therefore are considered as average years. In autumn 2011 the snow season onset (establishment of continuous winter snow cover) occurred 29 days later compared to the long-term average and 32–35 days later compared to 2009 and 2010, leading to the longest snow-free period on record (83 years). Specifically, the snow-free period lasted on average 170 days during the 1928–2010 period, 160 days in 2009, 159 days in 2010 and 234 days in 2011. Maximum HS differed across study years: maximum height measured in 2009 was 1.74 m, while in both 2010 and 2011 was similar ranging around 0.90 m. Winter 2009 was particularly snowy compared to the long-term average (1.07 m for the period 1928–2010).

As expected for an alpine ecosystem, Tair (figure 1(b)) showed large fluctuations from winter to summer and varied from a minimum of $-10 \pm 4.0\,°C$ (1928–2010 average $\pm$ sd)
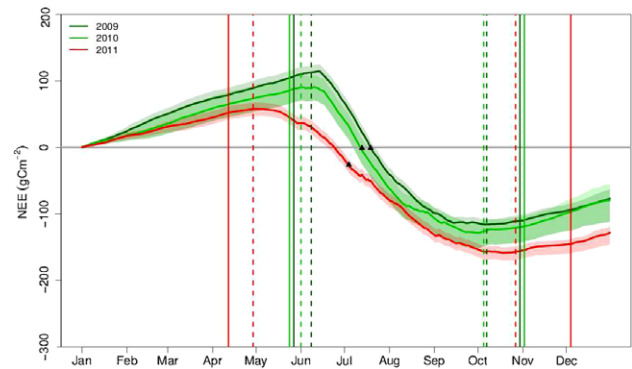

Figure 2. Cumulative NEE during the 3 study years. Coloured areas represent uncertainty on the flux computation. Vertical solid lines represent the snowmelt (left side) and snow onset (right side) dates in each year (green, light-green and red for 2009, 2010 and 2011 respectively), vertical dashed lines represent the BGS$_{cup}$ and EGS$_{cup}$, the black triangles indicate the peak dates.

in January to a maximum of $17 \pm 3.9\,°C$ in July (1928–2010 average $\pm$ sd). Regarding 2011, the main discrepancies compared to previous years were observed in the period March–April, characterized by a mean temperature $2.2\,°C$ warmer than the 1928–2010 average and $2.7–3.0\,°C$ warmer than the mean temperature of previous study years—a difference that was very likely responsible for the early snowmelt.

Soil temperature (figure 1(c)) under snow cover showed constant values above $0\,°C$. Immediately after snowmelt Tsoil exhibited a characteristic rise. In spring 2009 and 2010 this rise was fast and in a few days Tsoil reached temperature values similar to those of Tair. In 2011, the increase in Tsoil after snowmelt was slower.

The seasonal pattern of midday (11:00–13:00) mean values of incident PAR (figure 1(d)) was similar among the different years.

The snow-free period SWC (figure 1(e)) showed mean values of 26.3 and 25.1% in 2011 and 2010 respectively, and a lower mean of 16.4% in 2009. SWC in all years exhibited a typical peak around the day of snowmelt, when the highest seasonal value was reached.

3.2. Phenology and CO$_2$ source/sink strength

Figure 2 shows the time course of cumulative NEE in the three years analysed in this study. The seasonal variation of CO$_2$ fluxes (see also figure 1 in supplementary data available at stacks.iop.org/ERL/8/025008/mmedia) exhibited different dynamics in 2009 and 2010 as compared to 2011: NEE in 2009 and 2010 sharply increased in spring, just after snowmelt, rapidly reaching peak values in early July (18–13, DOY 199 and 194, respectively). In contrast, the NEE increase in 2011 occurred earlier but at lower rate. The grassland turned to a sink on 8 June in 2009 (DOY 159), 1 June in 2010 (DOY 152) and 29 April in 2011 (DOY 119). In 2011 BGS$_{cup}$ occurred 33–40 days in advance compared to the previous two years and the time lag between snowmelt and BGS$_{cup}$ was slightly larger than in 2009 and 2010 (13, 8 and 16 days in

Table 1. NEE sums (gC m^{-2} ± uncertainty range, see supplementary data available at stacks.iop.org/ERL/8/025008/mmedia) and average rates (i.e. NEE sum in each phenophase divided by number of days) partitioned by phenophase and associated with the corresponding averages of the meteorological variables (Tair °C, SWC%, PAR μmol m^{-2} s^{-1}, Tsoil °C).

	1 Jan-snowmelt		Snowmelt-BGS$_{cup}$		BGS$_{cup}$–peak		Peak–EGS$_{cup}$		EGS$_{cup}$-snow onset		Snow onset-31 Dec	
	Days		Days		Days		Days		Days		Days	
2009	146		13		41		83		26		60	
2010	144		9		43		85		26		63	
2011	104		16		67		116		39		28	
NEE	Sum	Rate	Sum	Rate	Sum	Rate	Sum	Rate	Sum	Rate	Sum	Rate
2009	116.2 ± 30.9	0.8	7.1 ± 0.4	0.54	−108.7 ± 0.6	−2.65	−127.0 ± 5.3	−1.53	7.0 ± 2.1	0.27	38.3 ± 11.8	0.63
2010	103.7 ± 40.2	0.72	5.01 ± 0.1	0.55	−94.9 ± 1.8	−2.3	−127.8 ± 6.3	−1.51	6.3 ± 0.9	0.24	49.8 ± 20.2	0.79
2011	62.6 ± 20.6	0.60	4.5 ± 0.4	0.28	−85.2 ± 0.9	−1.27	−133.5 ± 2.9	−1.15	10.5 ± 3.4	0.26	19.8 ± 6.0	0.70
Tair	Mean		Mean		Mean		Mean		Mean		Mean	
2009	−1.73		7.60		10.25		9.99		2.81		−2.72	
2010	−2.96		7.13		10.42		9.00		2.13		−3.89	
2011	−1.13		1.60		7.65		8.92		1.75		−2.83	
SWC												
2009	—		27.8		18.0		14.0		15.7		—	
2010	—		34.5		30.5		22.0		22.8		—	
2011	—		30.4		28.7		23.9		27.9		—	
PAR												
2009	—		1428.8		1547.0		1361.7		897.1		608.5	
2010	—		1325.9		1393.5		1307.0		921.7		550.7	
2011	—		1237.0		1370		1251.5		697.7		488.3	
Tsoil												
2009	0.69		8.15		12.0		11.24		3.9		0.25	
2010	−0.08		8.1		11.9		11.16		4.3		0.59	
2011	0.44		4.95		10.24		10.9		0.76		−0.12	

2009, 2010 and 2011 respectively). NEE peaked 40 days after BGS$_{cup}$ in 2009 and 2010 and 65 days in 2011. The ecosystem turned to a net source on 7 October (DOY 281), 4 October (DOY 278) and 26 October (DOY 300) in 2009, 2010 and 2011 respectively. In 2011 the CUP lasted 55 and 59 days longer than the two previous years.

Annual cumulative NEE in 2011 (−118 ± 31 gC m^{-2} yr^{-1}) doubled 2009 (−62 ± 52 gC m^{-2} yr^{-1}) and 2010 (−55 ± 60 gC m^{-2} yr^{-1}) values. In contrast, despite the two-month longer CUP observed in 2011, seasonal cumulative NEE between BGS$_{cup}$ and EGS$_{cup}$ (i.e. the CUP cumulative) were similar among years: −230 ± 6 gC m^{-2} in 2009, −218 ± 8 gC m^{-2} in 2010 and −215 ± 4 gC m^{-2} in 2011. Moreover, in 2011 NEE did not reach the peak daily values of previous years (−5.0 gC m^{-2} d^{-1}, −4.7 gC m^{-2} d^{-1}, −3.4 gC m^{-2} d^{-1} in 2009, 2010 and 2011 respectively).

Table 1 shows the differential contributions of the considered phenophases to the annual cumulative NEE in terms of sums and average rates (i.e. NEE sum in each phenophase divided by the number of days). The averages of the environmental variables measured in each period are also reported. The peculiarities of 2011 were: the overall shorter snow season, lower respiration during the January-snowmelt and snowmelt-BGS$_{cup}$ periods, a longer time for net CO$_2$

uptake (i.e. longer CUP), but the latter was associated with reduced rates during the developing phases (i.e. BGS$_{cup}$ to peak).

The lower cumulative NEE from January to snowmelt in 2011 was mainly a result of the shorter duration of that period and of the slightly lower (16%) respiration rate (figure 2, table 1) compared to the same period in 2009 and 2010. Lower rates of CO$_2$ losses in 2011, together with lower mean Tsoil, Tair and midday PAR, were also observed in the period between snowmelt and BGS$_{cup}$ (in figure 2 the maximum cumulative NEE after snowmelt reached lower positive values in 2011). Less CO$_2$ was taken up in 2011 compared to 2009/2010 during the longer period between the BGS$_{cup}$ and the peak value because of a lower NEE rate (∼50%), as highlighted by the less steep slope in 2011 (figure 2). This period was again associated with lower mean Tair, Tsoil and PAR compared to previous years. This pattern is also evident in figure 3(a), showing the mean diurnal patterns of NEE from the BGS$_{cup}$ to peak period. Maximum diurnal NEE in this period reached −9.4, and −8.1 μmol$_{CO2}$ m^{-2} s^{-1} in 2009 and 2010, while it was −5.2 μmol$_{CO2}$ m^{-2} s^{-1} in 2011. Moreover, figures 4(a) and (b), showing seasonal courses of LAI and Chl, revealed that also biophysical parameters related to canopy development were lower in 2011 compared to 2009/2010. LAI showed maximum values of 2.7 m^2 m^{-2}
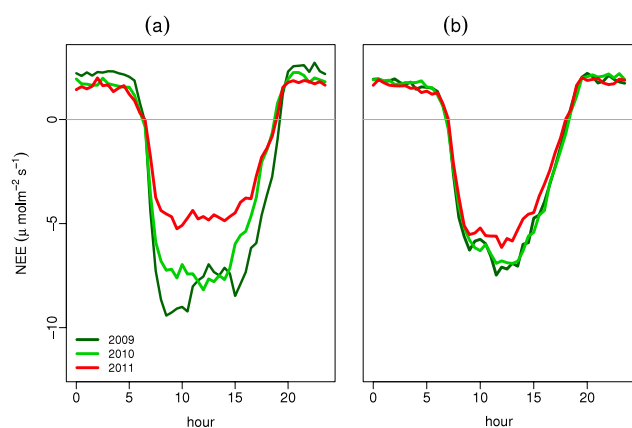
Figure 3. (a) Mean diurnal variation of NEE during the BGS$_{cup}$–peak, and (b) peak–EGS$_{cup}$ phases. Different colours represent the different years (green, light-green and red for 2009, 2010 and 2011 respectively).
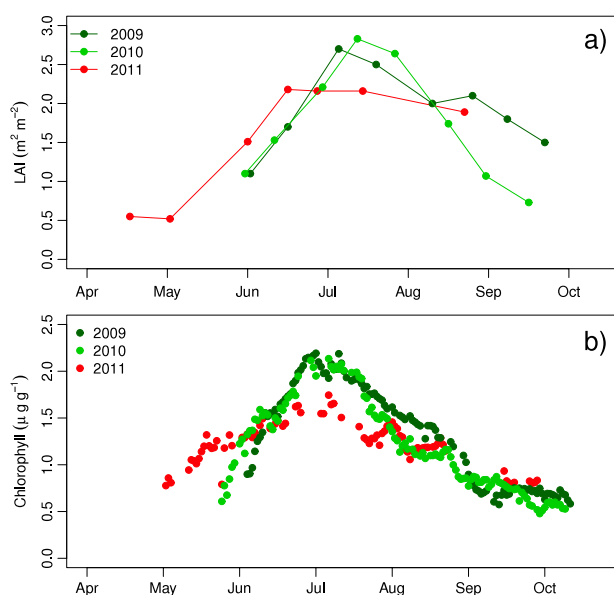

Figure 4. Seasonal course of (a) leaf area index, LAI (m^2 m^{-2}), and (b) chlorophyll content (μg g^{-1}) during the three years of study (green, light-green and red for 2009, 2010 and 2011 respectively). Chlorophyll content was derived fitting a linear regression model to meris terrestrial chlorophyll index (MTCI) values, calibrated using Chl concentrations extracted from leaf samples at the study site.

and 2.8 m^2 m^{-2} in 2009 and 2010 respectively and only 2.18 m^2 m^{-2} in 2011. Not only leaf area but also maximum chlorophyll content attained in 2011 was lower, with a peak value of 2.2 and 2.1 μg g^{-1} in 2009 and 2010 and of 1.7 μg g^{-1} in 2011.

During the long period separating the peak value and the EGS$_{cup}$ in 2011, the ecosystem CO$_2$ uptake was higher than in previous years, even if the average rate remained slightly lower (table 1, figure 3(b)).

Finally, respiratory rates after EGS$_{cup}$ were similar among years (table 1) as highlighted in figure 2 by the similar slopes of NEE. The lower cumulative CO$_2$ loss in 2011 during this phase was therefore mainly related to the shorter period.

Table 2. Summary of light–response curve analysis results. (a) Average and standard deviation of the model parameters (absolute values are reported) estimated for each year with the light–response curve analysis. (b) Estimated NEE sums (gC m^{-2}) in the period DOY 176–190. Each column represents the cumulative NEE predicted using a fixed PAR dataset and varying physiology parameters. Each row represents the cumulative NEE predicted using the model parameters obtained for the considered year and varying PAR dataset.

(a)

	α	A_{max}	R_{eco}
2009	0.027 ± 0.01	24.28 ± 2.1	2.46 ± 0.13
2010	0.022 ± 0.01	20.56 ± 0.9	1.70 ± 0.12
2011	0.017 ± 0.01	16.30 ± 1.53	1.62 ± 0.28

(b)

	PAR 2009	PAR 2010	PAR 2011
Physiology parameters			
2009	-60.73	-61.05	-66.63
2010	-57.93	-58.54	-62.38
2011	-41.2	-41.71	-44.29

The results of the modelling analysis (table 2) clarified whether in 2011 the ecosystem was unable to reach NEE values and rates similar to previous years as a consequence of changes in canopy structural and physiological properties (e.g. lower Chl and LAI) due to the early development or as a direct effect of unfavourable summer weather conditions. The analysis showed that: (i) model parameters (i.e. α, A_{max} and R_{eco}) obtained from light–response curve in 2011 were significantly lower compared to 2009 and 2010 ($p < 0.05$ Wilcoxon–Mann–Whitney test); (ii) using fixed PAR and varying physiology parameters (i.e. using PAR data of one year for all three physiology parameter sets), predicted NEE sums using the 2011 parameters were always higher (i.e. lower uptake, ranging from -41.2 to -44.29 gC m^{-2}) than those obtained using 2009 (from -60.73 to -66.63 gC m^{-2}) or 2010 (from -57.93 to -62.38 gC m^{-2}) parameters; (iii) using fixed physiology parameters with varying PAR dataset, NEE sums simulated using the 2011 PAR dataset were always lower (i.e. higher uptake) than those obtained using 2009 or 2010 PAR dataset. This underlined that the NEE reduction observed in 2011 can be attributed to changes in grassland structural and physiological properties rather than to direct limiting weather conditions in this period.

4. Discussion

In seasonally snow-covered ecosystems, earlier snowmelt and later establishment of snow cover potentially reduce the continuous off-season CO$_2$ losses and may result in longer periods of CO$_2$ uptake and growth. In this study we took advantage of a natural experiment (i.e. an exceptionally short snow season) to test the hypothesis that shorter snow-covered periods may enhance the CUP and the annual net CO$_2$ uptake of subalpine grasslands. Results confirmed this assumption. Nevertheless, two different effects were observed: less CO$_2$

losses took place during the shorter snow season and lower CO_2 uptake rates occurred during the longer CUP.

Did the extremely short snow season increase the CUP in the investigated ecosystem?

We observed that a variation of more than one month (43 days) in the date of snowmelt caused a similar shift (35–40 days) in the beginning of the CUP. However, the earlier snowmelt was followed by a slower increase of the biological activity compared to years with average snowmelt. This observation was supported by the larger time lag between the date of snowmelt and the beginning of the subsequent phenological phases in 2011, i.e.: the ecosystem processes were slower in reaching the different thresholds considered.

The date of snowmelt imposes a clear physical limit to canopy spring development of high-altitude grasslands. When the snowpack-imposed decoupling between vegetation, ambient light and temperature finishes, biological processes quickly take advantage of favourable weather conditions optimizing the short snow-free period available for growth (Körner 2003, Monson *et al* 2005). This dynamic pattern is typical of warm-season vegetation types, for which photosynthesis in spring recovers generally faster than the senescence at the end of the season (Gu *et al* 2009). In alpine ecosystems, extreme climate events, such as particularly warm spring spells and the subsequent early snowmelt, could change this typical pattern. The result is a lengthening of the CUP but also an exposure of the vegetation to early spring unfavourable weather conditions (e.g. lower PAR and temperature colder than usual) and an increased risk of cold damage. When snowmelt occurred around the end of May in 2009 and 2010, weather conditions (Tair and Tsoil, photoperiod, PAR) at the study site were already at optimal level and, as a consequence, the up-regulation of photosynthetic activity was fast. On the contrary, the early snowmelt recorded at the beginning of April 2011 led to the advancement of each phenophase, but caused the ecosystem to face less favourable weather conditions, typical of an earlier time of the year, characterized by shorter day-length, lower PAR and colder temperatures.

While the effect of recent warming trends on the onset of plant activity in spring has been outlined in several works (Richardson *et al* 2013), uncertainties exist on how climate change may affect autumn phenology and CO_2 fluxes (e.g. Wu *et al* 2013, Piao *et al* 2008). Moreover, the end of CUP variability and its environmental drivers are poorly investigated within grassland sites. In 2011 we observed a late snow onset in autumn, due to a prolonged period of warm temperatures and absence of precipitation. As a consequence, the ecosystem turned to a source about 20 days later than in previous years, further contributing to the increase of the CUP duration.

What is the effect on the ecosystem CO_2 uptake?

The two-month longer CUP observed in 2011 (figure 5(a)) did not lead to higher, but rather similar seasonal cumulative carbon uptake compared to average years, as a result of the compensation between a longer CUP and a lower NEE rate (figure 5(c), table 1). In 2011 daily NEE rate during the CUP was generally lower compared to previous years, especially during the spring development, and reached a peak
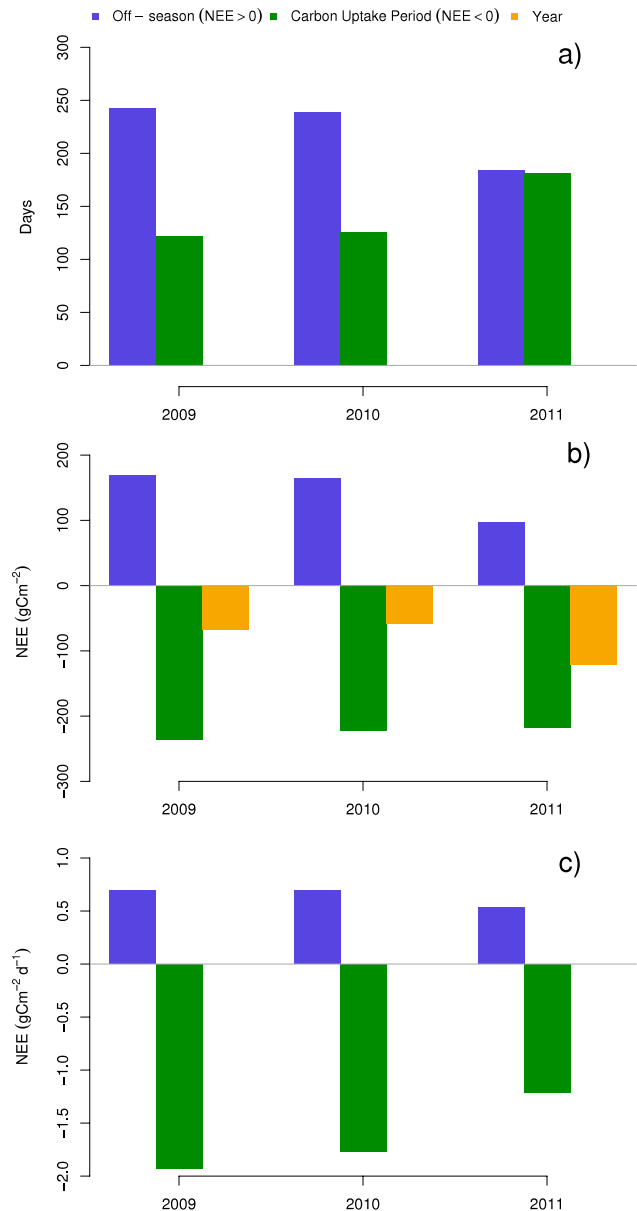

Figure 5. (a) Duration of the off-season (i.e. snow-covered and non-snow-covered periods with NEE >0) (blue) and CUP periods (green); (b) cumulative NEE (gC m^{-2}) during the off-season (blue), CUP (green), and yearly periods (orange); (c) NEE average rate during the off-season (blue), and CUP periods (green).

value lower than other years. We observed that environmental conditions during the summer period were fairly similar among years and, thus, unlikely to account for the observed differences in physiology parameters and photosynthetic rates. The lower summer CO_2 uptake appears to be the result of the biotic response of the ecosystem to an exceptional climate event: the early spring weather that the ecosystem experienced as a consequence of early snowmelt, changed the typical trajectory of canopy development and physiological responses of the ecosystem to environmental conditions. Compared to previous years, plants developed in unusual spring conditions may have adjusted their physiological

responses to lower PAR, shorter day-length and lower temperature experienced during the early development and were unable to capitalize on later growing season weather conditions (Monson *et al* 2005). The snowmelt observed in 2011 is the third earliest snowmelt in 83 years and hence represents an unusual event for plants that are very likely acclimated to a narrower range of weather conditions. This observation was also supported by LAI and Chl data, since the ecosystem modifies its photosynthetic capacity through variations in LAI and chlorophyll content in relation to changes in limiting factors (Dawson *et al* 2003). To our knowledge there are few studies highlighting similar findings. Indeed, although shifts in structural or reproductive phenology as a result of variations in snow cover depth and duration have clearly been described in several experimental studies of snow manipulation (e.g. Wipf and Rixen 2010), results concerning the effects on growth and productivity are less clear and differ among species, growth forms and habitats (snowbeds, fellfields, meadows…). Moreover, most studies have focused on the effect of a delayed rather than an earlier snowmelt (Wipf and Rixen 2010). For example Wipf and Rixen (2010) found that a delayed snowmelt decreased productivity (peak season biomass). On the contrary there is evidence (Walker *et al* 1995, Wipf *et al* 2009) that the growth of some alpine species was reduced in years with advanced snowmelt as a consequence of unfavourable conditions that plants experienced in early spring. Moreover, if reproductive and vegetative phases are partially influenced by different environmental factors, an early snowmelt can determine in some species an early flowering causing differences in reproductive and vegetative resource allocation compared to standard snowmelt date (Inouye 2008, Körner and Basler 2010), resulting in a decrease in vegetative development.

Changes in snow cover amount and duration cause also a change in nutrient supply in spring (Körner 2003). Our results suggest that the timing of soluble N availability may be more likely of concern than the total amount of N in melted water (Smith *et al* 2012): 2010 and 2011 had indeed similar HS and SWC at the time of snowmelt, but different NEE rates and canopy properties (LAI and Chl) during the CUP. Since there is evidence that plants may take up N maximally after snowmelt (Jaeger *et al* 1999, Bardgett *et al* 2007), nutrient uptake in 2011 may have been limited by the low Tsoil following early snowmelt (Karlsson and Nordell 1996). Moreover, Brooks and Williams (1999) suggested that the availability of soil N is strongly regulated by the timing and duration of the snow cover, with higher N immobilization under long-lasting snowpacks and consequent higher net N conservation in the soil pool. Following this interpretation, less N may have been immobilized in soil during shorter winter 2011 and subsequently available in early spring 2011, thus contributing to suboptimal conditions for plant development.

We hypothesized that shorter snow seasons potentially enhance the annual net CO_2 uptake of seasonally snow-covered ecosystems. Since the two-month longer CUP alone cannot explain the twice as high annual uptake observed in 2011 (figure 5(b)), explanations were found in the short 2011

off-season period (i.e. snow-covered and non-snow-covered periods with continuous respiration, i.e. NEE >0) during which the ecosystem lost less CO_2 than in previous years. The off-season period lasted 245 and 242 days in 2009 and 2010 and was 58–52 days shorter in 2011 (figure 5(a)). The shortened snow season translated in a 40% reduction of the off-season cumulative CO_2 loss compared to average years. Conversely, differences in CUP cumulative NEE amounted to less than 5%, since, despite the longer CUP, the average 2011 NEE rate was lower (figure 5(c)) compared to 2009/2010. Taken together, these observations confirm that the higher annual net CO_2 uptake in 2011 was mainly caused by a shorter period of off-season respiration rather than by an enhanced CO_2 uptake during a longer CUP.

5. Conclusion

During a year characterized by an extremely short snow season, a 100% increase in the annual net CO_2 uptake was observed at a subalpine grassland. The larger carbon sink was attributable to smaller cumulative CO_2 loss during the shorter snow season, as lower CO_2 uptake rates during the longer CUP resulted in similar cumulative NEE during the vegetation period as compared to average years. If an increase of future occurrence of events such as the observed is assumed, this trade-off between reduced CO_2 losses during shorter winters and lower uptake during longer summers will be crucial in determining the annual NEE.

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