Natural variations in snow cover do not affect the annual soil CO_2 efflux from a mid-elevation temperate forest

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Abstract

Climate change might alter annual snowfall patterns and modify the duration and magnitude of snow cover in temperate regions with resultant impacts on soil microclimate and soil CO_2 efflux (F_{soil}). We used a 5-year time series of F_{soil} measurements from a mid-elevation forest to assess the effects of naturally changing snow cover. Snow cover varied considerably in duration (105–154 days) and depth (mean snow depth 19–59 cm). Periodically shallow snow cover (<10 cm) caused soil freezing or increased variation in soil temperature. This was mostly not reflected in F_{soil} which tended to decrease gradually throughout winter. Progressively decreasing C substrate availability (identified by substrate induced respiration) likely over-rid the effects of slowly changing soil temperatures and determined the overall course of F_{soil}. Cumulative CO_2 efflux from beneath snow cover varied between 0.46 and 0.95 t C ha^{-1} yr^{-1} and amounted to between 6 and 12% of the annual efflux. When compared over a fixed interval (the longest period of snow cover during the 5 years), the cumulative CO_2 efflux ranged between 0.77 and 1.18 t C ha^{-1} or between 11 and 15% of the annual soil CO_2 efflux. The relative contribution (15%) was highest during the year with the shortest winter. Variations in snow cover were not reflected in the annual CO_2 efflux (7.44–8.41 t C ha^{-1}) which did not differ significantly between years and did not correlate with any snow parameter. Regional climate at our site was characterized by relatively high amounts of precipitation. Therefore, snow did not play a role in terms of water supply during the warm season and primarily affected cold season processes. The role of changing snow cover therefore seems rather marginal when compared to potential climate change effects on F_{soil} during the warm season.

Keywords: soil CO_2 efflux, snow, winter, substrate availability, temperature sensitivity, C cycling

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Introduction

Climate change may alter annual snowfall patterns and modify the duration and magnitude of snow cover in temperate regions of the Northern Hemisphere (Laternser & Schneebeli, 2003; IPCC, 2007; Liu *et al.*, 2012). Changing snow cover can affect ecosystem processes, such as carbon (C) cycling (Sommerfeld *et al.*, 1993). The insulating snow cover decouples soil from air temperatures and generates a specific microclimate in the top-soil (Sommerfeld *et al.*, 1993; Winston *et al.*, 1995). The beneath-snow microclimate determines the activity of decomposing soil organisms and thereby largely controls the rate of the CO_2 efflux from soil (F_{soil}) (Monson *et al.*, 2006b). Wintertime F_{soil} is an important component of the annual C cycle in cold ecosystems as a substantial part of the C assimilated during the growing season can be lost during the following winter (Monson *et al.*, 2002; Suni *et al.*, 2003). Earlier research focused on high-latitude and high-altitude sites, whereas information on wintertime F_{soil} from low to

mid-elevation temperate forests remained relatively scarce (e.g., Hirano, 2005; Mo *et al.*, 2005; Groffman *et al.*, 2006; Schindlbacher *et al.*, 2007; Muhr *et al.*, 2009; Aanderud *et al.*, 2013). Mid-elevation temperate sites experience less harsh winters and wintertime air temperatures more often fluctuate around freezing. Climate warming could therefore reduce the amount of precipitation fallen as snow, increase the frequency of mild (>0 °C) periods and/or prepone snowmelt during spring (Laternser & Schneebeli, 2003). In reverse, harsher winters could produce deeper snow cover and delay snow melt during spring (Liu *et al.*, 2012). These factors could directly affect wintertime F_{soil}, but the duration and magnitude of snow cover may as well have implications on spring and summer processes such as net ecosystem exchange (NEE) (Monson *et al.*, 2002; Hu *et al.*, 2009), water table depth (Dunn *et al.*, 2007), or soil CO_2 efflux (Muhr *et al.*, 2009). Therefore, effects of changing snow cover could be diverse and the assessment of their influence on F_{soil} is challenging. Aside from artificial manipulation (removal or addition of snow), time series of annual and wintertime F_{soil} measurements under naturally changing snow cover can provide information about the potential effects of

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future changing climate. However, with the exception of the high elevation, subalpine Niwot Ridge Ameri-Flux site, where eddy flux measurements were accompanied by extensive wintertime F_{soil} measurements and microbial studies (e.g., Monson *et al.*, 2002, 2006a,b; Schmidt *et al.*, 2009), most studies focusing on CO$_2$ efflux from beneath snow cover were confined to short periods (one or two winters). Here, we present F_{soil} data from a mid-elevation (ca. 900 m a.s.l.) temperate mountain forest which were gathered from November 2007 until December 2012. The five consecutive winters varied in their duration as well as in snow properties. As snow cover insulates soil from low wintertime air temperatures, we hypothesized that (I) duration, thickness, and persistency of snow cover determined soil temperatures and thereby controlled F_{soil} rates which were considered to be over-proportionally temperature sensitive during the cold season. Regarding the annual variations in the durations of winter (= cold season) and snow cover we hypothesized that (II) the annual soil CO$_2$ efflux was lower during years with longer winters and longer lasting snow cover than during years with shorter winters and shorter snow cover. To assess other potential drivers of wintertime F_{soil} than soil temperature, the role of substrate availability was investigated. Aside from our periodical F_{soil} survey, the actual temperature sensitivity of F_{soil} around freezing was assessed by a high-frequency measurement campaign while soil temperatures fluctuated around 0 °C.

Materials and methods

Site description

The study site was located at 910 m a.s.l. on a north-north-east slope of a mountain in the Northern Limestone Alps, Achenkirch, Austria (47° 34′ 50″ N; 11° 38′ 21″ E). The 125-year-old forest was dominated by Norway spruce (*Picea abies*), with interspersed European beech (*Fagus sylvatica*) and silver fir (*Abies alba*). The understory mainly consisted of naturally regenerating beech. The bedrock was formed of dolomite. The soils were a mosaic of shallow Chromic Cambisols and Rendzic Leptosols. Soils showed high small scale variability in soil types as well as horizon depths. Mull was the dominant humus form and the depths of the litter and O-layer reached from 0 to 5 cm. A-horizons thickness varied from 10 up to 40 cm. Organic C stocks were estimated to be ca. 10 t ha^{-1} in the organic layer and ca. 120 t ha^{-1} in the mineral soil (Schindlbacher *et al.*, 2010).

The site was characterized by a cool humid climate. Local mean annual air temperature and precipitation were 6.9 °C and 1506 mm (1992–2012), respectively (Achenkirch village; ca. 7 km away at similar altitude; ZAMG data). Precipitation was evenly distributed throughout the seasons with 20–40% falling as snow. The duration of snow-cover recorded at Achenkirch village was on average 122 days yr^{-1} (1992–2012), ranging from a minimum of 73 days in 1994 to a maximum of 163 days in 1999. Permanent snow cover built up during November/December and lasted until March/April.

Measurement of climate parameters and soil CO$_2$ efflux

The field site hosted a long-term climate change manipulation experiment (Schindlbacher *et al.*, 2009, 2012). For this study, the untreated control plot data from November 2007 until December 2012 were used. The untreated control plots had a size of 2 × 2 m and were replicated three times. At each of the three plots, soil temperature and soil moisture were measured at 5 cm and 15 cm soil depth. Soil temperature (PT$_{100}$ temperature sensors; EMS, Brno) and soil moisture (ECH$_2$O-10 soil moisture probes; Decagon, Washington) records were stored on different data loggers (Campbell CR 10×, Campbell Scientific, Inc., North Logan; Delta-T DL2, Delta-T Devices Ltd, Cambridge; MiniCube, EMS, Brno) as half hourly averages. Air temperature (ST1 sensor, Delta-T Devices Ltd, Cambridge) and relative air humidity (OTM-592 C sensor, Sommer, Koblach) were measured in close vicinity to the plots at 2 m height and stored as half hourly averages. Precipitation was measured with an ombrometer (NIWA/MED-K505, Sommer, Koblach) at 1-min resolution at a meteorological station ca. 100 m away from the site in an open area. Snow depth was measured manually during each wintertime CO$_2$ measurement campaign. The measured snow depth onsite showed good fit with the snow depth measured at Achenkirch village (Fig S1). We therefore used the daily snow depth record from Achenkirch village to fill the gaps in the on-site record.

Soil CO$_2$ efflux was measured fortnightly during the snow free seasons and every third week during snow cover. During the snowfree season F_{soil} was measured from permanently installed chambers (20 cm diameter, 10 cm height). Three chambers were randomly distributed at each plot and inserted 1 cm into the mineral soil to establish an airtight seal. Chambers were closed with a stainless steel lid for 300 sec. CO$_2$ concentrations were measured every 30 sec using an EGM4 infrared gas analyzer (PP-Systems, Amesbury). The CO$_2$ concentration increase in the chamber headspace during the last 120 sec was used to calculate the flux (linear fit). A detailed description of the system and measurement procedure can be found in (Schindlbacher *et al.*, 2009). During snow cover F_{soil} was estimated according to Schindlbacher *et al.* (2007). On each plot, three CO$_2$ concentration profiles were determined. CO$_2$ concentration profiles in the snow cover were measured with a 2 m long aluminum probe (outer diameter 6 mm, inner diameter 3 mm) which was directly connected to the CO$_2$ analyzer (EGM 4; PP-Systems, Amesbury) by a flexible 1.5 m long tube. Prior to inserting the probe into the snow, CO$_2$ was measured ca. 1 cm above the snow surface to assess the atmospheric CO$_2$ concentration. Then, the CO$_2$ concentration in the snow profile was measured every 20 cm until the soil surface was reached. During periods with <20 cm snow depth, CO$_2$ concentration was measured at ca. 1 cm above the snow surface and at the soil surface. Soil surface CO$_2$ efflux through the snow was estimated using

Fick's law of diffusion, following Musselman *et al.* (2005) and Hubbard *et al.* (2005):

$$F_{Soil} = f\tau D \frac{P_0}{RT_0} \left(\frac{T}{T_0}\right)^{0.81} \frac{dg}{dz}, \quad (1)$$

where F_{soil} is the gas flux ($\mu mol\ m^{-2}\ s^{-1}$), D is the diffusion coefficient for CO_2 in air ($0.1381(10^{-4})\ m^2\ s^{-1}$) (Massman, 1998), P_0/RT_0 is the molecular density of CO_2 at STP (44.613), f is snow pack porosity (unitless), τ is tortuosity (unitless), T is the average snow pack temperature (K). The gradient function dg/dz was derived from fitting a linear regression through the measured CO_2 concentration profile. Probe measurements were only performed at windless conditions to avoid disturbance by pressure pumping effects. Snow pack parameters were estimated from three snow pits, which were dug at each sampling date. The snow pits were dug at a distance of about 3 m to the plots to avoid any interference with the measured snow profile. At each pit, we measured snow density and temperature in 10 cm increments for the entire depth of the snow profile. The mean density of the snow pack ($kg\ m^{-3}$) was estimated from a weighted average of the 10 cm layers. Porosity was calculated from the mean density (ρ) as $f = 1 - \rho/973$ where 973 is the density of ice ($kg\ m^{-3}$). Tortuosity was estimated as a function of porosity (Millington, 1959; Millington & Shearer, 1971) as $\tau = f^{1/3}$. The gradient method did not yield reliable CO_2 fluxes at snow depth <7 cm. Therefore, chamber measurements were performed during periods of <7 cm snow depth. Snow was removed from and around the chambers 30 min prior to CO_2 flux measurements which were performed as described above. After measurements, snow was redistributed into and around the chambers. A comparison of CO_2 flux estimates by snow probe and chamber measurements showed that the two methods were comparable when snow depths were shallow (Fig S2). In general, the gradient method gives rather conservative estimates of F_{soil}. It was recently shown that the gradient method produced lower soil respiration estimates as eddy covariance measurements under certain winter conditions (Sullivan *et al.*, 2012; Merbold *et al.*, 2013).

A high-frequency measurement campaign was conducted from February 13 to February 15 2008 to assess the temperature sensitivity of soil CO_2 efflux at soil temperatures around freezing. On February 12, snow (ca. 15 cm) was removed from three adjacent plots, releasing six chambers for CO_2 flux measurements. Flux measurements started the next day 10:30 and were repeated every fourth hour until February 15 07:00 (from 22:00 until 06:30, no measurements were undertaken). The timing of the campaign was chosen because air and top-soil temperature showed strong diurnal fluctuation during these days. During each CO_2 flux measurement, soil temperature was measured with a handheld probe at 1 cm, 5 cm, and 10 cm soil depth. CO_2 efflux was measured as described above for the snow free season.

Substrate induced respiration (SIR)

To assess the effect of potential substrate limitation on wintertime soil CO_2 efflux, a modified SIR experiment was carried out in the field (Göttlicher *et al.*, 2006). The aim of the method was to test how decomposers responded to an artificial increase in labile substrate at the beginning and toward the end of winter. A C_4 sucrose solution (100 g m^{-2}) was added to three adjacent plots in November 2007 and February 2008. Before adding the solution, snow was removed from the plots. All 2×2 m plots were used in a preliminary experiment and were already equipped with plastic chambers (20 cm diameter, 10 cm height) for CO_2 measurements, as described above for the snow free season. Each plot was equipped with three chambers. One chamber was used for sucrose amendment in November and another in February. The distance between two chambers was always larger than 1 m to avoid a contamination from the previous sucrose amendment. On squares of 0.5×0.5 m around the chambers, sucrose solution was added. One hundred and fifty grams of cane sugar (VERIVAL, EP Naturprodukte AG, Austria) was dissolved in 3-L snow water. With a syringe, 0.5 L of sucrose solution was added per chamber (63 ml directly into the camber). On three adjacent control plots, the same amount of untreated melted snow was suspended in the same way as the sugar treatment to quantify potential side-effects of the procedure. CO_2 efflux was measured prior to sucrose amendment (1 h after snow removal). After the initial CO_2 efflux measurements and the sucrose amendment, the snow pit was refilled and opened again after 24 h, allowing for measurements of the substrate induced soil respiration. After the SIR measurements, CO_2 efflux from the plots was measured periodically until the end of winter (ca. every 20 days).

To assess the source of SIR (indigenous C_3-C or C_4-C from the added sugar), the isotopic signature of the soil CO_2 efflux was determined. After SIR-efflux measurements, all chambers were closed with lids and air samples (12 ml) for mass spectrometry were taken at 0, 15, 30, 45, and 60 min from the chambers. Samples were taken with a glass syringe and injected into previously evacuated 12-ml glass vials (Exetainer, Labco Ltd, High Wycombe, UK). The stable carbon isotopic ratio of soil-respired CO_2 was then analyzed by continuous-flow isotope-ratio mass spectrometry on a Thermo Finnigan Delta V Advantage Mass Spectrometer (Thermo Fisher Scientific, Waltham, MA, USA) coupled to a Finnigan GasBench. Sample CO_2 concentrations were measured with the same system after calibration with reference gases with 400 and 1000 ppm CO_2 (Air Liquide, Vienna, Austria). To assess the isotopic composition of soil respired CO_2, the Keeling plot approach was used (Keeling, 1958). The intercept of a linear regression of $\delta^{13}C$ of sampled CO_2 vs. $1/[CO2]$ provided an estimate of $\delta^{13}C$ of soil-respired CO_2 (where [CO2] was the CO_2 concentration in%). Although the CO_2 efflux during the two winter sampling dates was low, the fit of the linear regression was overall sufficient for keeling plot analysis (November 2007 r^2 from 0.97 to 0.99; February 2008 treated plots r^2 from 0.92 to 0.99; control plots r^2 from 0.90 to 0.99).

The fraction (f) of C_4-C-derived CO_2 in F_{soil} was calculated as follows:

$$fC_4 = \frac{\delta^{13}C_{SIR} - \delta^{13}C_{control}}{\delta^{13}C_{4suc} - \delta^{13}C_{control}}, \quad (2)$$

where fC_4 is the proportion that can be attributed to the respiration of C_4-substrate, $\delta^{13}C_{SIR}$ is the C isotope composition

(‰) of soil respired CO_2 in sucrose-amended plots, $\delta^{13}C_{control}$ is the C isotope composition in CO_2 from control plots and, $\delta^{13}C_{4suc}$ is the C isotope composition (-10.97 ± 0.06‰) of the C_4 sucrose solution applied.

Data analysis

The duration of snow cover was defined as the period during which a permanent, closed, snow-layer covered the soil surface. In addition, the duration of the most persistent snow cover throughout the study (7th November to 8th April) was defined as 'maximal snow cover'. This fixed time frame allowed for a direct quantitative comparison of F_{soil} during the period. Winter (= freezing period) was defined as the period during which the smoothed 5-day mean air temperature remained below 0 °C for at least five consecutive days. The year, as the basis for annual values, was defined from 7th of November (the earliest beginning of snow cover during the study) to 6th of November the following year. Using the calendar year (January 01 to December 31) would have split winters in two parts and precluded a reasonable analysis. The warm season was defined as the period of the year during which the smoothed 5-day mean air temperature remained above 0 °C for at least five consecutive days.

Preceding studies indicated a strong positive relationship between soil temperature and F_{soil} at the study site. Accordingly, a temperature function was fitted to the F_{soil} data of the five seasons to obtain seasonal and annual flux estimates. A Gaussian function was fitted to the F_{soil} data of each plot (Fig. 1) by means of a least square fitter (SigmaPlot 10.0) and the daily CO_2 efflux from each plot was modeled according to the function parameters. Compared to simple exponential functions, the Gaussian function has the opportunity of vary-
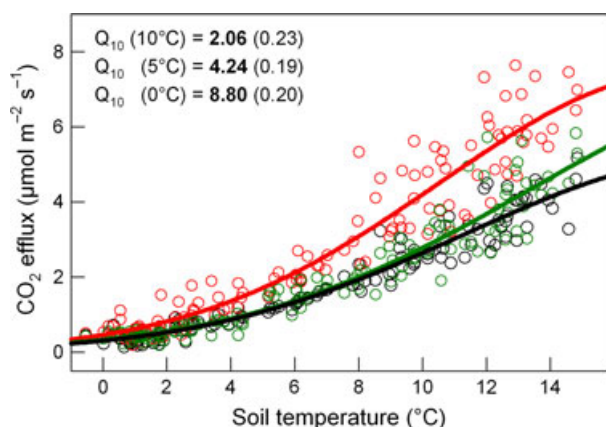
ing temperature sensitivity (Q_{10}) over the temperature range. The modeled daily average CO_2 efflux of the three individual plots was summed for and a corresponding mean cumulative CO_2 efflux was calculated by averaging the periodical plot estimates. Alternatively to the modeled efflux, the cumulative CO_2 efflux during seasons and years was estimated by linear interpolation between the measurement dates (below the CO_2 data points in Fig. 2). Although this method misses temporal variations in F_{soil} between measurements, it efficiently reflects the efflux during periods when soil temperature does not primarily drive F_{soil}. Due to the low number of replicates ($n = 3$ plots) the spatial variability in F_{soil} at the site was not fully covered. For a temporal analysis such as the comparison of seasons and years, the replication was sufficient because F_{soil} was always measured at the same locations. Potential variations of cumulative seasonal CO_2 efflux, as well as the relative contribution of wintertime efflux during the five periods (2007/08 until 2011/12) were statistically tested by means of one-way ANOVA. ANOVA was only applied for the linear interpolation estimates. Testing the modeled estimates would actually have meant testing for differences in soil temperature. Correlation analysis was used to test for potential correlation of cumulative soil CO_2 efflux with duration, amount, and average depth of snow cover as well as with the duration of winter and mean air and soil temperature during snow cover.

Temperature sensitivity of the overall soil CO_2 efflux was calculated for each plot from the 5 years data record by deriving Q_{10} from the Gaussian function (Tuomi et al., 2008)

$$R(T) = Re^{(aT+bT^2)} \qquad (3)$$

describing the soil CO_2 efflux rates $R(T)$ as function of soil temperature T. R, a, and b are constants ($R > 0$, $a > 0$, $b < 0$). The function was found to best describe the temperature dependence of heterotrophic soil respiration during the annual course of soil temperature (Tuomi et al., 2008). Q_{10}, the relative growth of soil CO_2 efflux as the temperature increases by 10 °C from the initial temperature T, was derived as

$$Q_{10} = e^{(10a+100b+20bT)} \qquad (4)$$

For wintertime, during which soil temperature varied in a narrow range, a simple exponential function

$$R(T) = R_{10}Q_{10}^{\frac{(T-10)}{10}} \qquad (5)$$

was fitted. Q_{10} represents the relative growth of soil CO_2 efflux as the temperature increases by 10 °C while R_{10} is the soil CO_2 efflux at 10 °C soil temperature. Eq. 5 was applied for all CO_2 efflux measurements beneath snow (Fig. 3) and for the higher frequency measurement campaign (Fig. 4).

The effect of sucrose addition on the soil CO_2 efflux (SIR) was tested by repeated measures ANOVA. Early winter treatment and late winter treatment were tested interpedently because measurements were made at different chambers. All CO_2 efflux rates were temperature corrected prior to statistical analysis because soil temperature varied (2.6–0.5 °C) between measurement dates. All flux values were adjusted to a soil temperature of 2.6 °C using the parameters of the temperature

Fig. 1 Relationship between soil temperature at 5 cm soil depth and the manually measured soil CO_2 efflux during the 5 years observation. The three plots are shown in different colors. Curves show the fit of a Gaussian function (Eqn 3). Temperature sensitivities of soil CO_2 efflux are shown as Q_{10} values. According the Gaussian function, the temperature sensitivity varies with soil temperature. Mean Q_{10} values ($\pm$ SE, $n = 3$) are shown for 10, 5, and 0 °C soil temperature.
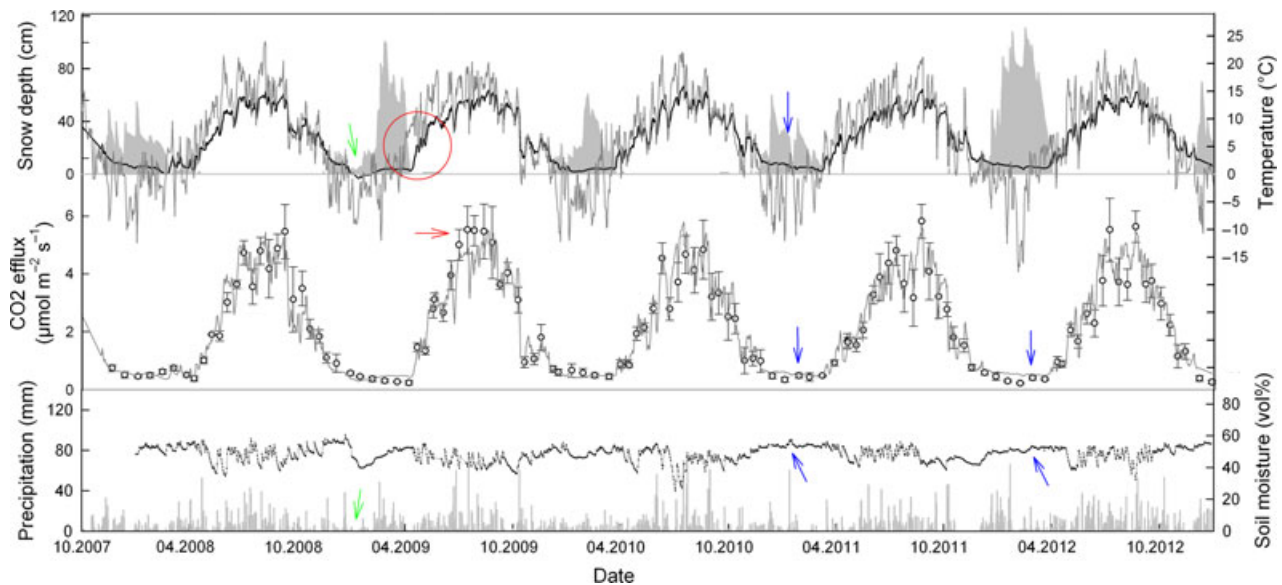
Fig. 2 Course of daily air temperature (gray line, upper panel), soil temperature (black line, upper panel), and soil moisture (black line, lower panel). Gray areas in the upper panel show the depth of the snow cover. Manually measured soil CO_2 efflux (open circles; means ± SE, $n = 3$) and the mean daily CO_2 efflux modeled with a simple temperature function (gray line) are shown in the medium panel. Gray bars in the lower panels are precipitation in mm. The red circle indicates a period during which snow cover delayed the increase of soil temperature during spring; the red arrow indicates underestimated CO_2 efflux by the temperature model; blue arrows indicate rising soil CO_2 efflux after periods of snow-melt; green arrows indicate periods with less precipitation. The exact meaning of arrows and cycles is explained in the results and discussion.

function of Plot B in Fig. 1. Differences in $\delta^{13}C$ values were tested using a *t*-test. All statistics were carried out with SAS 9.2 (SAS Institute, Cary, NC, USA, www.sas.com) at a significance level of 95%.

Results

Annual snow cover showed considerable variations in duration and thickness (Table 1, Fig. 2). The average depth of the snow cover ranged from 19 cm in the first, to 59 cm in the last year. Snow cover lasted longest in the first year (154 days), whereas the shortest snow cover was 105 days in 2010/11. The build-up of snow cover fell well within the beginning of winter during most years, except for the last year 2011/12 where build-up of snow cover was delayed due to lack in precipitation during early winter. The duration of winter and the duration of snow cover were strongly correlated ($r = 0.926$, $P = 0.02$) but snow cover always lasted into the following spring; particularly when late winter snow packs were thick (Table 1, Fig. 2). Mean air temperature during snow cover varied between −0.3 °C and −2.7 °C and was positively correlated with the duration of snow cover (Table 2). Mean soil temperatures beneath snow cover ranged from 0.8 °C to 1.6 °C, but did not correlate with any snow parameter (duration, mean depth, and amount). Variations in annual air and soil temperatures were comparatively small (Table 1).

Soil CO_2 efflux was closely related to soil temperature at 5 cm soil depth (Fig. 1). The Gaussian function (Eqn. 3) showed a good fit (Fig. 1 and 2) and the modeled data explained 95% of the variance in F_{soil} throughout the 5 years. The temperature sensitivity (Q_{10}) of F_{soil} obtained from all F_{soil} measurements ranged from 2.06 (± 0.23) at 10 °C soil temperature to 8.80 (± 0.20) at 0 °C soil temperature (Fig. 1). The Q_{10} of F_{soil} during the high-frequency measurement campaign in winter (February) 2008 ranged from 9.70 to 47.50 and strongly depended on soil temperature measurement depth (Fig. 4). The Q_{10} of 47.50 is unrealistically high for a physiological process and indicates that most of the measured variation in F_{soil} occurred from above the corresponding temperature sensor depth (5 cm). Overall, the low F_{soil} rates during winter were well reproduced by the Gaussian model. However, the temporal course of F_{soil} beneath snow did not always match with the model output (Fig. 2). Fig. 3a shows that the relationship between F_{soil} and soil temperature beneath the snow cover was rather weak. During three out of 5 winters, there even was no relationship between soil temperature and F_{soil} at all. During winter 2008/2009, a period of minor precipitation led to shallow (2–5 cm) snow cover, causing a mild freezing down to 5 cm soil depth (Fig. 2, green arrows). The freezing did however not affect F_{soil} rates. During all other winters, soil
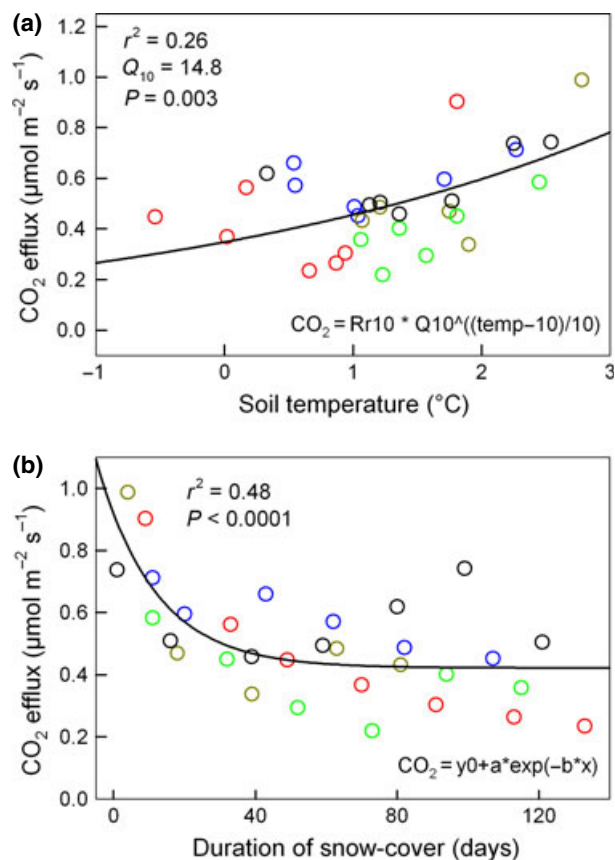
Fig. 3 (a) Relationship between soil temperature at 5 cm soil depth and mean soil CO_2 efflux during snow cover (efflux measurements with snow probe). The different colors represent different seasons (2007/2008 black, 2008/2009 red, 2009/2010 blue, 2010/2011 yellow, 2011/2012 green). (b) Relationship between soil CO_2 efflux and duration of snow cover (same colors as for a). The functions of the fitted curves are shown in the right lower corners.

Fig. 4 Temperature sensitivity of soil CO_2 efflux during a three days measurements campaign in February 2008. Black triangles show CO_2 efflux vs. soil temperature measured at 1 cm soil depth. Open and full circles show CO_2 efflux vs. soil temperatures measured at 5 cm and 10cm soil depth, respectively. An exponential function (Eqn. 5) was fitted. Q_{10} values as a measure of temperature sensitivity are shown for 1 cm and 5 cm depth. At 10 cm soil depth, the relationship was not significant. The inner panel shows the course of air and soil temperature during CO_2 efflux measurements (same symbols plus open squares for air temperature).

temperature at 5 cm depth remained above freezing. During late winter 2007/08 a warm period caused a short gap in snow cover and increased soil temperatures as well as F_{soil} rates (Fig. 2). Deep snow cover during spring 2008/09 delayed the increase in soil temperature, compared to that of air temperature (Fig. 2, red circle). No such effect was observed in 2011/12 where spring air temperatures were lower. Generally, beneath snow F_{soil} gradually declined throughout winters (Fig. 3b). The decline was periodically interrupted by short-term increases in F_{soil}; mostly after mild periods and snow-melt triggered increases in soil moisture (Fig. 2, blue arrows). The addition of sucrose significantly affected the CO_2 efflux during early and late winter (repeated measures ANOVA, $P < 0.05$). F_{soil} rates increased significantly the day after sucrose was added (Fig. 5). The increase was more pronounced in late winter (absolute increase in F_{soil} early winter = 80%, late
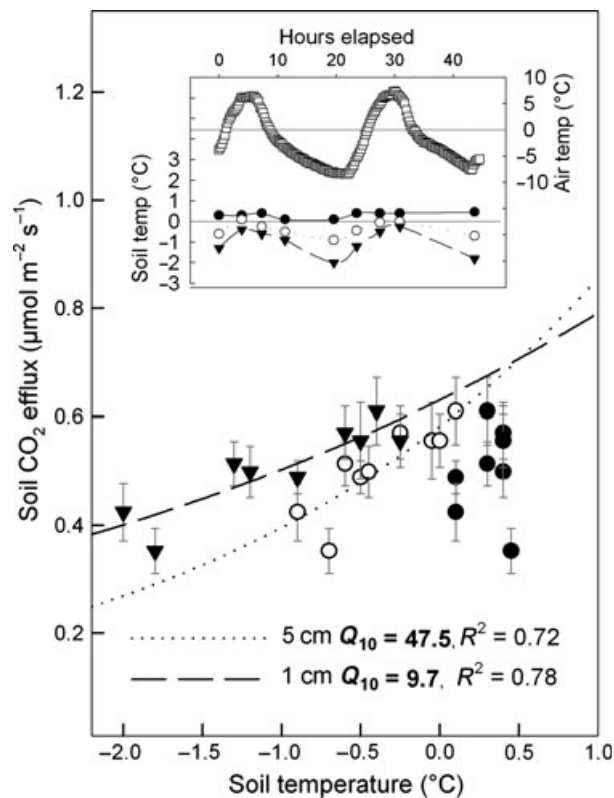
winter = 135%) but absolute flux rates after sucrose addition were nearly equal during early and late winter (Fig. 5). After sucrose addition, the $\delta^{13}C$ value was slightly (not significantly) less negative in early winter (Fig. 5a). The difference in $\delta^{13}C$ corresponded to a roughly 25% contribution of CO_2 from sucrose to the observed increase in F_{soil} (SIR) in early winter. The $\delta^{13}C$ value significantly changed from −22.24 ‰ to −18.70 ‰ in late winter (Fig. 5b) corresponding to a roughly 50% contribution of the added source to the SIR in late winter. Both, the more pronounced response of F_{soil} as well as the higher contribution of the added C source to F_{soil} during late winter indicate a temporal decrease in substrate availability throughout snow cover.

Cumulative C efflux during snow cover was between 0.46 and 0.95 t ha^{-1}, but did not differ significantly between years (Table 3). Cumulative C efflux during

Table 1 Snow and climate parameters

Period	2007–2008	2008–2009	2009–2010	2010–2011	2011–2012
Snow cover	Nov 07–Apr 08	Nov 22–Apr 08	Dec 04–Mar 23	Nov 23–Mar 07	Dec 06–Apr 01
Duration (days)	154	138	110	105	118
Average snow depth (cm)	19	30	23	22	59
Amount (average depth × days)	2967	4117	2516	2322	6568
Mean air temp (°C)	−0.3	−1.1	−2.7	−1.8	−1.6
Mean soil temp (°C)	1.6	0.8	1.0	1.6	1.6
Precipitation (mm)	529	362	345	386	548
Max. snow cover (Nov 07–Apr 08)					
Mean air temp (°C)	−0.3	−0.6	−0.7	−0.3	−0.8
Mean soil temp (°C)	1.6	1.2	1.9	2.2	2.0
Winter (5 days mean air temp <0 °C)	Nov 12–Mar 25	Nov 21–Mar 23	Dec 12–Mar 15	Nov 23–Mar 3	Nov 15–Mar 11
Duration (days)	135	124	95	102	118
Mean air temp (°C)	−1.0	−1.8	−3.5	−2.7	−2.4
Mean soil temp (°C)	1.5	0.8	0.9	1.5	1.8
Annual (Nov 08–Nov 07)					
Mean air temp (°C)	6.9	6.8	6.2	6.6	6.5
Mean soil temp (°C)	6.3	6.2	6.4	6.6	6.5
Precipitation (mm)	1602	1665	1636	1439	2001
Annual (Jan 01–Dec 31)	2008	2009	2010	2011	2012
Mean air temp (°C)	7.1	6.9	5.8	6.9	6.5
Mean soil temp (°C)	6.3	6.3	6.3	6.6	6.6
Precipitation (mm)	1554	1763	1661	1478	2037

The duration of snow cover was defined as the period during which a permanent, closed, snow-layer covered the soil surface. Winter was defined as the period during which the smoothed 5-days mean air temperature was below 0 °C for at least 5 consecutive days. The year was defined from November 07 to November 06 of the next calendar year to avoid splitting apart the winter seasons. For periodical comparison, climate parameters during the period of most persistent snow cover (November 07–April 08) during the 5 years are shown (= max. snow cover). The lower panel shows annual values based on calendar years 2008–2012 for comparison.

snow cover was positively correlated with the duration of snow cover, but did not correlate with average snow depth, average winter air temperature, or average beneath snow soil temperature (Table 2). The C efflux during snow cover amounted between 6.4% and 11.9% of the annual C efflux. The relative contribution during the year with the longest lasting winter and snow cover (11.9%) was statistically significantly higher than all others (Table 3). During the period of maximal snow cover (November 07–April 08) cumulative C efflux was between 0.77 t ha^{-1} and 1.18 t ha^{-1} but differences between years were not statistically significant either (Table 3). When set into relation to the corresponding annual soil C efflux, C efflux during maximal snow cover ranged from 10.5% to 15.1%. The contribution during the year with the shortest winter (15.1%) was statistically significantly higher than in years with longer snow cover (Table 3). Annual C efflux ranged between 8.02 t ha^{-1} and 7.44 t ha^{-1} when estimated by linear interpolation and between 8.14 t ha^{-1} and 7.91 t ha^{-1} when estimated by the model output (Table 3). Annual soil C efflux did not differ significantly between years and was not correlated with the duration of snow cover, average snow depth, or air and soil temperature during snow cover (Table 2).

Discussion

Serving as a temporary insulation layer, snow cover largely regulated wintertime soil temperatures. According to our hypothesis (I), snowpack parameters affected wintertime soil temperatures. It turned out that the onset of snow cover was a decisive factor because it determined the starting point of soil insulation. If the first freezing coincided with snowfall, snow cover built up early and the beneath snow soil temperatures remained relatively high when compared to years with delayed snowfall. Snow depth did not affect soil temperatures as long as a minimal insulation layer was present. A shallow (~ 10 cm) snow layer was enough to keep wintertime soil temperatures above freezing at our site. At high-elevation sites, below zero soil temperatures were measured even beneath deep snowpacks (Mast *et al.*, 1998; Monson *et al.*, 2006a,b). Snow depth therefore might have considerable more impact on wintertime F_{soil} at high-elevation or at other colder sites

Table 2 Correlation coefficients between different snow and climate parameters and the soil CO_2 efflux (F_{soil}) during snow cover (F_{soil} snow), without snow cover (F_{soil} no snow) and annually (F_{soil} annual) from 2007/08 until 2011/12

	Snow duration	Snow depth	Snow amount	Air temp. (snow)	Soil temp. (snow)	F_{soil} snow	F_{soil} no snow	F_{soil} annual
Snow duration	1.000							
Snow depth	−0.191	1.000						
Snow amount	0.068	0.964*	1.000					
Air temp. (snow)	0.899*	−0.082	0.150	1.000				
Soil temp. (snow)	−0.071	0.177	0.103	0.239	1.000			
F_{soil} snow	0.628*	−0.459	−0.313	0.503	−0.026	1.000		
F_{soil} no snow	0.023	−0.051	−0.033	0.024	−0.115	0.586*	1.000	
F_{soil} annual	0.104	−0.107	−0.072	0.089	−0.109	–	–	1.000

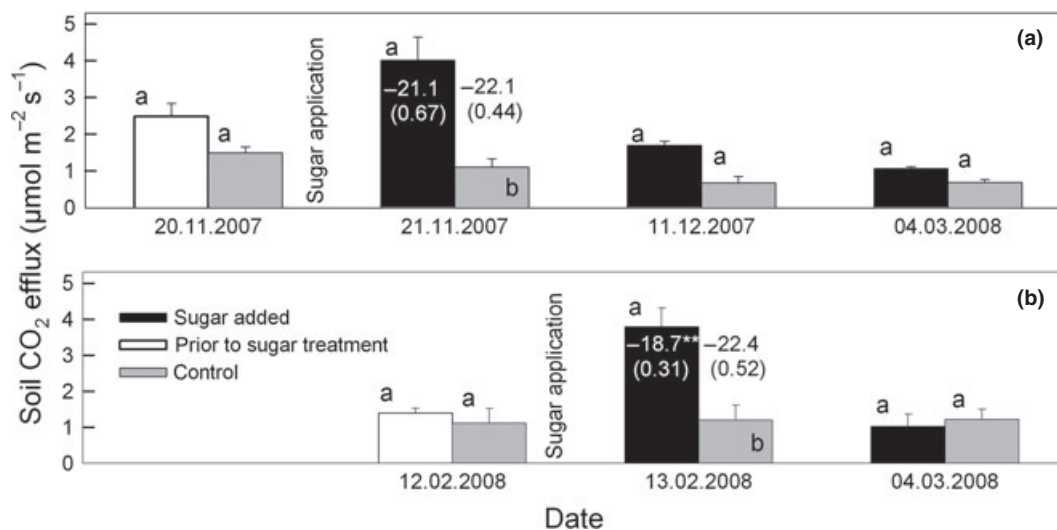*Correlation is significant. Pearson ($n = 9$ chambers).

Fig. 5 Substrate induced respiration (SIR). Bars show the mean CO_2 efflux $\pm$ SE ($n = 3$) from chambers prior to sugar amendment (white bars), after sugar amendment (black bars), and from corresponding control plots (gray bars). Sugar was added to different chambers in early winter (a) and late winter (b). Different letters indicate statistically significant differences between control and sugar treatment (Student-Newman-Keuls' *Post hoc* test, repeated measures ANOVA) for each measurement date. Values in and above bars show the $\delta^{13}C$ of soil CO_2 efflux in ‰ $\pm$ SE ($n = 3$; significantly difference between treatment and control is indicated by **). All flux values were temperature corrected.

than at comparatively warmer mid-elevation sites. This may also explain why Monson *et al.* (2006b) found a clear relationship between annual amount of snow and F_{soil} in a subalpine forest at Niwot Ridge while we did not find such a relationship at our mid-elevation site. Inconsistencies in snow cover (periods of very shallow snow or temporary gaps) strongly affected soil temperature. Lack of sufficient snow cover during freezing periods caused periodic soil frost or low soil temperatures while gaps in snow cover during warmer periods increased soil temperatures. Accordingly, the temporal variability of soil temperatures was higher during winters with inconstant snow conditions. During winters with permanent snow cover soil temperatures gradually decreased throughout snow cover. Surpris-

ingly, the temporal trend of soil temperature was often not reflected in the course of F_{soil} which tended to steadily decrease throughout snow cover (Fig. 3). As F_{soil} is a temperature dependent process (Lloyd & Taylor, 1994) with even higher temperature sensitivity at low temperatures [Fig. 1, Fig. 4; (Mikan *et al.*, 2002)], other processes must have over-ridden the effects of slowly changing soil temperature. Changes in microbial biomass or community structure can affect F_{soil} (Schmidt *et al.*, 2009) but such changes are rather unlikely according to previous studies conducted at the same plots. Microbial biomass was at least as high during winter as during the warm season (Schindlbacher *et al.*, 2011). In contrary to high latitude and altitude sites where substantial shifts in the microbial community structure

Table 3 Soil CO_2 efflux (cumulative; tons C ha^{-1} $\pm$ SE (n = 3) in parenthesis)

Period	2007–2008	2008–2009	2009–2010	2010–2011	2011–2012
Snow cover (model)	0.91 (0.13)	0.67 (0.09)	0.56 (0.08)	0.71 (0.13)	0.69 (0.17)
Snow cover (linear)	0.95 (0.11) ns	0.68 (0.11) ns	0.63 (0.15) ns	0.53 (0.10) ns	0.46 (0.04) ns
Max. snow cover (model)	0.91 (0.13)	0.87 (0.12)	1.04 (0.15)	1.13 (0.18)	1.05 (0.15)
Max. snow cover (linear)	0.95 (0.11) ns	0.90 (0.14) ns	1.18 (0.25) ns	0.97 (0.18) ns	0.77 (0.06) ns
Winter (model)	0.79 (0.11)	0.59 (0.08)	0.52 (0.07)	0.61 (0.09)	0.74 (0.11)
Winter (linear)	0.83 (0.10) ns	0.65 (0.10) ns	0.54 (0.12) ns	0.51 (0.10) ns	0.52 (0.03) ns
Annual (model)	7.97 (1.17)	8.04 (1.18)	7.91 (1.17)	8.06 (1.22)	8.14 (1.20)
Annual (linear)	8.02 (1.06) ns	8.41 (0.98) ns	7.74 (1.38) ns	7.87 (1.36) ns	7.44 (1.16) ns
% snow cover (model)	11.4 (0.1)	8.4 (0.1)	7.0 (0.7)	8.9 (0.1)	8.6 (0.1)
% snow cover (linear)	11.9 (0.5) a	8.0 (0.3) b	8.0 (1.0) b	6.7 (0.1) b	6.4 (0.6) b
% max snow cover (model)	11.4 (0.1)	10.8 (0.1)	13.0 (0.1)	14.1 (0.5)	13.1 (0.1)
% max snow cover (linear)	11.9 (0.5) a	10.6 (0.5) a	15.1 (0.7) b	12.3 (0.3) a	10.5 (0.7) a
% winter (model)	9.8 (0.1)	7.4 (0.1)	5.8 (0.1)	7.6 (0.6)	9.3 (0.1)
% winter (linear)	10.4 (0.5) a	7.6 (0.3) b	6.9 (0.7) b	6.5 (0.1) b	7.2 (0.7) b
Annual (Jan 01 – Dec 31)	2008	2009	2010	2011	2012
Annual (model)	7.97 (1.17)	8.11 (1.19)	7.91 (1.17)	8.06 (1.20)	8.14 (1.20)
Annual (linear)	8.20 (1.13) ns	8.43 (0.99) ns	7.58 (1.36) ns	7.84 (1.27) ns	7.42 (1.22) to

Cumulative values were calculated from daily model output (model) and by linear interpolation between the single CO_2 efflux data points in Fig. 2 (linear). Percent values show the contribution to the annual CO_2 efflux (November 7 to November 6; = 100%). The lower panel shows annual values based on the calendar years 2008–2012 for comparison. Statistically significant differences between linear interpolation estimates during the periods the 2007/08 until 2011/12 are indicated by different letters (ns, not significant).

occur between winter and summer (Lipson *et al.*, 2002; Schadt *et al.*, 2003), we did not observe such a pronounced shift in microbial community structure at our site (Schindlbacher *et al.*, 2011; Kuffner *et al.*, 2012). Another reason for the steady decrease of F_{soil} throughout snow cover could have been shortage of available substrate for microbial decomposition. A gradual decrease in substrate availability during winter has been reported before (Zimov *et al.*, 1996; Brooks *et al.*, 2004) and was supported by our SIR data indicating a substantial decrease in substrate availability from early to late winter (Fig. 5). Such a change in substrate availability could have easily over-ridden the effects of soil temperature considering that the absolute change in soil temperature beneath snow was small (<3 °C) and slow. We found evidence that the decrease in substrate availability might be related to the rather static soil conditions beneath snow. Active lateral transport of substrate should have been largely hindered as long as no fresh water entered the soil. Immobile decomposers might have suffered from increasing substrate shortage in their microsites. The little peaks in F_{soil} after intermediate snow melt (Fig. 2) support this explanation. Incoming meltwater could have mobilized labile substrate, thereby causing a temporary increase in F_{soil}. Similar observations after snowmelt events were made by Hirano (2005). Another cause of substrate shortage could have been decreasing root and mycorrhiza activity throughout winter (Muhr *et al.*, 2009; Subke *et al.*, 2011). Temporarily increased F_{soil} after

warm melting periods may as well be explained by temporarily increased C supply from roots or mycorrhiza. Taken together, our hypothesis (I) that snow cover determined wintertime soil temperatures and thereby drove F_{soil} was only partly confirmed. Snow cover determined soil temperatures but F_{soil} was also controlled by substrate availability (overall low F_{soil} during winter was for sure determined by overall low soil temperature).

During the 5 years, cumulative gaseous C efflux from beneath snow cover varied between 0.46 and 0.95 t ha^{-1} yr^{-1} and amounted to between 6% and 12% of the annual efflux. These values were well within the range of observations from other studies at mid-elevation forest sites (Mariko *et al.*, 2000; Hirano, 2005; Mo *et al.*, 2005; Groffman *et al.*, 2006) and confirm a first assessment of wintertime F_{soil} (ca. 12% of annual soil CO_2 efflux) at the same site during the snow-rich winter 2005/06 (Schindlbacher *et al.*, 2007). The cumulative C efflux from beneath the snow cover was largely determined by the duration of snow cover and was highest during the year with longest snow cover. However, for a quantitative assessment of the effects of changing snow cover, it was necessary to compare not only the absolute C loss during snow cover (which varied in duration) but also the soil CO_2 efflux during a fixed period of time. We chose the longest duration of snow cover during the 5 years; the 'maximum snow cover' (154 days, 7th November–8th April) as a timeframe for quantitative comparison. It allowed us to

assess how shorter and longer lasting snow cover affected the soil CO_2 efflux during this fixed period. The cumulative CO_2 efflux during the period of "maximal snow cover" ranged between 0.77 and 1.18 t C ha^{-1} yr^{-1} or between 11 and 15% of the annual CO_2 efflux. In absolute terms, the cumulative soil CO_2 efflux during 'maximal snow cover' did not differ significantly between years, but the relative contribution (15%) to the annual soil CO_2 efflux was largest during the year with the shortest winter. This is as an indication that shorter winters and shorter snow cover will increase the soil CO_2 efflux during the currently cold season. Especially as climate change may, on the long run, impose much milder winters as observed in this study. The impact of variations in current wintertime F_{soil} seems however marginal when related to the annual soil CO_2 efflux. For instance, the C efflux during the longest period of snow cover (2007/08) was only 0.21 t ha^{-1} lower than the C efflux during the same period in the year with shortest snow cover (2010/11). Considering an average annual C efflux of ca. 8 t ha^{-1} this was less than 3%. Accordingly, we did not detect any relation between snow cover duration and annual soil CO_2 efflux. Our hypothesis (II) that the annual soil CO_2 efflux was lower during years with long winters and long lasting snow cover than during years with short winters and shorter snow cover was not verified. Like the duration of snow cover, there were no effects of snow amount or snow depth on the annual CO_2 efflux either. We had expected that springtime F_{soil} would be depressed by thawing of deep snowpacks and associated delayed increase in soil temperature. In spring 2009 thawing of a deep snowpack indeed kept soil temperatures low and thereby lowered the springtime CO_2 efflux. However, in the following summer, the measured F_{soil} rates temporarily exceeded the modeled rates (Fig. 2, red arrow). This came a bit surprising as the model otherwise fitted very well. The reason for the discrepancy in measured and modeled F_{soil} could have been that the easily decomposable substrate which was left over from winter/spring was then decomposed during the following summer. However, this potentially close link between winter and warm season processes remains speculative but may deserve further investigation. In general, variations in snow cover had comparatively low impact on F_{soil} from our mid-elevation forest when compared to high-elevation (Monson et al., 2006a,b; Hu et al., 2009) or boreal forest sites (Dunn et al., 2007). Beside the less harsh winter-climate at the lower elevation, our site in the northern Alps was also characterized by frequent precipitation. Hence, at our site snow did not play a dominant role for hydrology throughout the year. In the drier Inner Alps, snow water could already be more critical in

determining annual F_{soil} and NEE. Our observations also deviate from the usually more drastically effects observed during snow-manipulation experiments; for example, the strong decrease in winter and warm season F_{soil} after snow-removal observed by Muhr et al. (2009) in a similar forest. However, in most manipulation experiments snow was removed during very cold conditions. Such a combination might at least at our site naturally not be the case in future as cold conditions and precipitation always produce snow cover.

Regarding the potential effects of climate change on snow cover at our mid-elevation temperate site, we conclude that warmer climate likely reduces the duration of winter and snow cover and thereby increases the soil CO_2 efflux during the present cold season. Since the soil CO_2 efflux during the cold season is almost an order lower than during the warm season, the quantitative effects on the annual soil CO_2 efflux are expected to be rather marginal when they are compared to potential climate change effects during the growing season (Schindlbacher et al., 2012). Effects of changing snow cover at our mid-elevation temperate forest seem of minor relevance when compared to the potential effects of changing snow cover on soil C at high altitude and high latitude biomes which are characterized by a much longer cold season, lower winter temperatures and the occurrence of permafrost (Welker et al., 2000; Zhang et al., 2001; Schimel et al., 2004; Liptzin et al., 2009; Schuur et al., 2009; Natali et al., 2011).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Relation between snow depth measurements at Achenkirch village and at the field site. Linear regression (black line) and 1 : 1 line (red).
Figure S2. Comparison of snow probe and chamber technique at low snow depth. Measurements were performed on a single day at a snow depth of 9–11 cm. Snow probe measurements were performed directly in the permanent chambers. Subsequently, snow was removed from inside and from around the chambers and the CO₂ efflux was estimated by the closed dynamic chamber method. Linear regression (black line), 1 : 1 line (red), and 95% confidence bands (blue).