Evolution of carbon fluxes during initial soil formation along the forefield of Damma glacier, Switzerland

K. Guelland · F. Hagedorn · R. H. Smittenberg · H. Göransson · S. M. Bernasconi · I. Hajdas · R. Kretzschmar

Abstract Soil carbon (C) fluxes, soil respiration and dissolved organic carbon (DOC) leaching were explored along the young Damma glacier forefield chronosequence (7–128 years) over a three-year period. To gain insight into the sources of soil CO_2 effluxes, radiocarbon signatures of respired CO_2 were measured and a vegetation-clipping experiment was performed. Our results showed a clear increase in soil CO_2 effluxes with increasing site age from 9 ± 1 to 160 ± 67 g CO_2–C m^{-2} $year^{-1}$, which was linked to soil C accumulation and development of vegetation cover. Seasonal variations of soil respiration were mainly driven by temperature; between 62 and 70 % of annual CO_2 effluxes were respired during the 4-month long summer season. Sources of soil CO_2 effluxes changed along the glacier forefield. For most recently deglaciated sites, radiocarbon-based age estimates indicated ancient C to be the dominant source of soil-respired CO_2. At intermediate site age (58–78 years), the contribution of new plant-fixed C via rhizosphere respiration amounted up to 90 %, while with further soil formation, heterotrophically respired C probably from accumulated 'older' soil organic carbon (SOC) became increasingly important. In comparison with soil respiration, DOC leaching at 10 cm depth was small, but increased similarly from 0.4 ± 0.02 to 7.4 ± 1.6 g DOC m^{-2} $year^{-1}$ over the chronosequence. A strong rise of the ratio of SOC to secondary iron and aluminium oxides strongly suggests that increasing DOC leaching with site age results from a faster increase of the DOC source, SOC, than of the DOC sink, reactive mineral surfaces. Overall, C losses from soil by soil respiration and DOC leaching increased from 9 ± 1 to 70 ± 17 and further to 168 ± 68 g C m^{-2} $year^{-1}$ at the <10, 58–78, and 110–128 year old sites. By comparison, total ecosystem C stocks increased from 0.2 to 1.1 and to 3.1 kg C m^{-2} from the young to intermediate and

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old sites. Therefore, the ecosystem evolved from a dominance of C accumulation in the initial phase to a high throughput system. We suggest that the relatively strong increase in soil C stocks compared to C fluxes is a characteristic feature of initial soil formation on freshly exposed rocks.

Keywords Glacier forefield · Chronosequence · Soil formation · DOC · Soil respiration · Carbon sources

Introduction

In the Swiss Alps, 90 % of the glaciers have exhibited a strong negative mass balance over recent decades, primarily due to rising temperatures (GOCS 2007). During glacial retreat, barren rock and debris becomes exposed, which, with time, become increasingly colonized by microorganisms and plants. The resulting chronosequences have been subject of several studies focusing on initial weathering and soil formation (Hindshaw et al. 2011; Mavris et al. 2010; White and Brantley 2003; Dümig et al. 2011; Egli et al. 2006; Kiczka et al. 2011; Wookey et al. 2002), as well as vegetation development and microbial colonisation (Becker and Dierschke 2005; Bernasconi et al. 2011; Esperschütz et al. 2011; Frey et al. 2010; Göransson et al. 2011; Lazzaro et al. 2009; Sigler and Zeyer 2002; Töwe et al. 2010; Zumsteg et al. 2012). These processes are closely linked to carbon (C) turnover and accumulation in the soil. However, while the successions of plants and microorganisms have been intensively studied, the initial development of C fluxes is still poorly understood. Studies along chronosequences of several thousands of years indicate that rates of C accumulation in soils are greatest during the initial phase of soil formation (Schlesinger 1990). Soils could, therefore, act as a C sink during the first few decades of soil development. Consequently, an improved knowledge of the development of C cycling in weakly-developed soils is essential for the quantification of soils as sources or sinks of atmospheric CO_2.

The C sources contributing to C cycling and to the build-up of soil organic matter change along glacier-formed chronosequences (White et al. 2007). Until recently, it has been assumed that the colonisation of a glacier forefield starts with autotrophic organisms (Walker and del Moral 2003) that, upon death, turn into soil organic matter (SOM) and become available to soil heterotrophs as a source of energy (Bardgett and Walker 2004). This initial order of colonisation has, however, been questioned in recent studies. Tscherko et al. (2003) and Zumsteg et al. (2012) found a fast and diverse colonisation of heterotrophs after glacial retreat, even before autotrophs had been established. Radiocarbon measurements of soil-respired CO_2 from recently ice-freed soils indicated that these first microbial communities primarily utilise ancient C (Bardgett et al. 2007). The sources of this ancient C could either be parent rock material or aeolian inputs of organic C original accumulated in cryoconite holes on the ice sheet (Hawes 2008; Anesio et al. 2010). In addition, C input from cyanobacteria could play an important role in keeping the soil C levels of initial soils from declining over time (Schmidt et al. 2008).

Accumulated soil organic matter becomes significant only at a later stage for the sustenance of soil heterotrophs. In later stages of ecosystem development, soil C models assume that there is a constant litter production and soil respiration, and hence under a stable climate, C inputs and outputs reach a "steady state" (Liski et al. 2005). In contrast to mature ecosystems under similar climatic conditions (Liptzin et al. 2009; Hagedorn et al. 2010; Warren and Taranto 2011), to the best of our knowledge there has been no field study that has assessed soil C fluxes, soil respiration and DOC leaching throughout the year during early succession in an alpine or arctic climate; partially because high alpine forefields are typically not very accessible. Soil respiration has only been measured during short campaigns in glacier forefields in Iceland, Alaska, North Norway, and Greenland (Jones et al. 2000; Nakatsubo et al. 1998; Welker et al. 2000; Wookey et al. 2002) or by incubating soil samples in the laboratory (Yoshitake et al. 2007). Consequently, the temporal evolution of the annual soil CO_2 effluxes in such systems, and the driving mechanisms behind these fluxes, are not well understood.

Soil respiration consists of multiple components principally governed by rhizosphere respiration and SOM mineralisation by soil heterotrophs. In mature ecosystems, such as grasslands (Bahn et al. 2006) and boreal forests (Högberg et al. 2001), recently assimilated CO_2 by living plants that is allocated to the rhizosphere within some days, is a major contribution to soil respiration. Along glacier forefield

chronosequences, the relative importance of different sources of soil-respired CO_2 probably changes with time due to the development of a vegetation cover, changes in plant species, and the accumulation and stabilization of SOM.

Dissolved organic carbon (DOC) leaching from soil and sorption onto mineral surfaces is most probably an important mechanism in stabilizing soil organic matter (Kaiser and Zech 1998; Kalbitz and Kaiser 2008; Sollins et al. 1996). The generation and sources of DOC in soils are, however, still uncertain in mature ecosystems (Hagedorn et al. 2004; Kaiser and Guggenberger 2000; Kalbitz et al. 2000; McDowell and Likens 1988) and have hardly been studied in initial soils. Principally, DOC is a leaching product from plants, litter, and humus and it is generated by microbial activity (Kalbitz et al. 2000), whilst root exudates may also contribute to DOC (Giesler et al. 2007). The major retention mechanism for DOC in the mineral soil is sorption to secondary oxides of Fe and Al (Kaiser et al. 1996). During soil development, the relative importance of DOC sources and sinks will change with time. For instance, for a chronosequence on volcanic bedrock, Lilienfein et al. (2004a, b) and Qualls and Bridgham (2005) showed in lab experiments that DOC sorption on mineral surfaces increases with on-going soil development through weathering but decreases again when the sorption sites become occupied. This process is, in turn, closely linked to DOC leaching from soil.

The aim of the present study was to investigate the evolution in carbon fluxes (soil respiration and DOC leaching) with initial ecosystem development in the Damma glacier forefield, Switzerland. We measured in situ soil CO_2 effluxes and DOC leaching along the Damma glacier soil chronosequence (7–128 years) over a 3-year period. Furthermore, we determined the radiocarbon (^{14}C) content of soil-respired CO_2 to gain insight into its sources (Trumbore 2000). CO_2 derived from the mineralization of organic carbon present in the parent material, or that has been accumulating in the glacier for potentially thousands of years, will have an old ^{14}C content. On the other hand, the radiocarbon content of primary production follows the atmospheric 'bomb spike' that resulted from atmospheric nuclear bomb testing in the late 1950s and early 1960s (Levin and Hesshaimer 2000). Depending on the residence time of C in the ecosystem, this primary signal is attenuated. The ^{14}C content of respired CO_2 is a mixed signal between these different sources, fossil, SOM-, and plant-derived C, and this can therefore provide insight regarding their relative contribution to soil respiration. We also removed the aboveground vegetation by clipping to quantify the changing contribution of CO_2 recently assimilated by plants to soil CO_2 effluxes. Major controls of soil C fluxes were identified by linking measured soil C fluxes with C stocks in plants and soils and with soil weathering.

In our study, we hypothesized that:

(1) Soil CO_2 effluxes strongly increase with increasing C stocks in plants and soils during ecosystem development.

(2) The respiration of recently assimilated CO_2 through the rhizosphere increases faster with site age than heterotrophic respiration, due to a faster development of vegetation compared to soil C stocks and due to an increasing SOM recalcitrance.

(3) DOC leaching in soils initially increases with rising ecosystem C stocks but an increasing formation of reactive mineral surfaces attenuates the increase in DOC leaching with time.

Materials and methods

Study site

The study site was the forefield of the Damma glacier in the central Swiss Alps (Fig. 1); which has been investigated within the interdisciplinary BigLink project (Bernasconi et al. 2011). The glacier forefield is approximately 900 m long and extends from an altitude of 1,900–2,100 m above mean sea level (AMSL). The Damma glacier front has retreated at an average rate of approximately 10 m per year since the beginning of systematic measurement in 1921 (VAW 2011) culminating in the disconnection between the glacier and a remaining dead-ice body. The recession since the maximum stage in 1850 (during the Little Ice Age) has not been continuous, but was reversed twice throughout the past century; during 1920–1928 and 1970–1992. This resulted in the formation of two small terminal moraines in the field. Because of these re-advances of the glacier, the site chronology is neither complete nor continuous, but rather consists of three main site age groups between

Fig. 1 Location of the 18 sampling sites (*black dots*) within the BigLink grid at Damma glacier forefield, the *green C's* visualize the clipped sites next to the unclipped sampling sites. The *black dashed lines* are the moraines within the glacier forefield. The *inset map* shows the location of the Damma glacier forefield in Switzerland. The clipping experiment drawing presents the location of the clipped sites with the PVC tubes (*black squares*) for soil CO_2 efflux measurements next to the unclipped sampling sites also with the PVC tubes. (Color figure online)
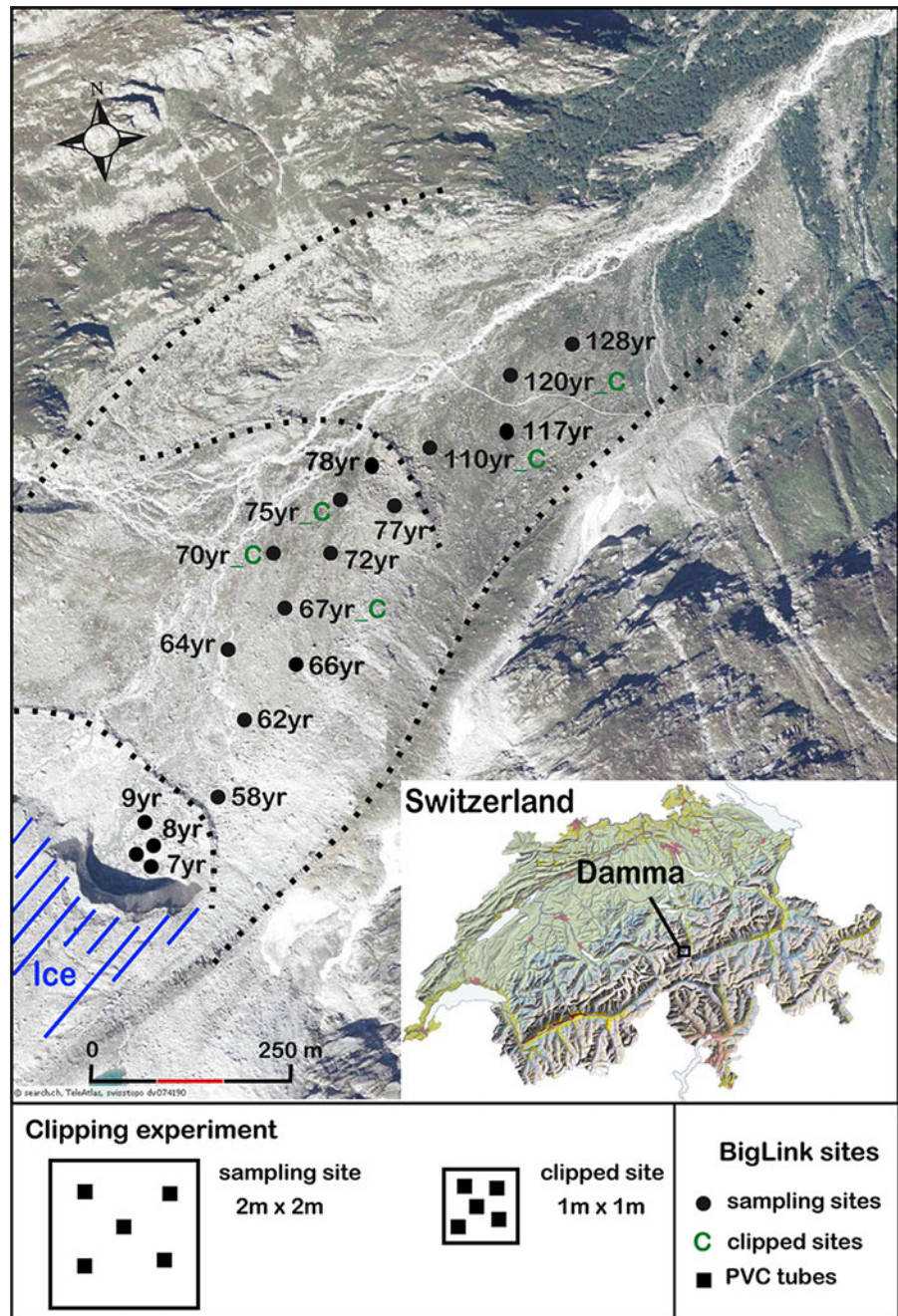
the moraines (Fig. 1): <10; 58–78, and 110–128 years. The bedrock of the glacier is the coarse-grained Central Aar granite, which is composed mainly of quartz, plagioclase, potassium feldspar, biotite, and muscovite (Schaltegger 1990). The soils in the forefield are Hyperskeletic Leptosols, ranging from Dystric (<75 year) to Eutric (78–128 year) subtypes

(Bernasconi et al. 2011; WRB 2006). The properties of topsoil are given in Table 1.

The climate is characterized by a short vegetation period lasting from the beginning of June to the end of September. During the remaining part of the year the glacier forefield is covered by snow. The annual precipitation amounts to 2400 mm and the mean

Table 1 Soil properties on average of the young, intermediate and old site age at 0–4 cm depths

Site age (year)	pH (CaCl$_2$)[a,b]	Bulk density (g cm^{-3})[a]	C (%)	C soil (kg m^{-2})	Fe$_0$ + Al$_0$ (g kg^{-1})[a,c]	(Fe$_0$ + Al$_0$)[a,c]/ (DOC/SOC)
10	4.6 ± 0.1	1.4 ± 0.15	0.31	0.43 ± 0.05	23.0	3.38 ± 1.54
70	4.0 ± 0.1	1.16 ± 0.16	0.80	0.93 ± 0.13	47.8	12.19 ± 3.84
120	4.1 ± 0.1	0.9 ± 0.17	2.93	2.63 ± 0.5	62.2	30.43 ± 11.88

[a] Data from Dümig et al. (2011)

[b] Soil pH measured in 0.01 M CaCl$_2$ with soil:solution ratio 1:2.5

[c] Oxalate-extractable Fe and Al

annual air temperature is 2.2 °C (Bernasconi et al. 2011). While the sites younger than 1991 are almost vegetation free, the patchy and scarce vegetation cover becomes denser between the two central moraines (1929–1991) with e.g. *Agrostis gigantea, Salix* sp. and *Deschampsia cespitosa*. Below the 1929 moraine, the forefield is fully covered with broadleaf perennials, e.g. *Rhododendron ferrugineum* L. and grasses, e.g. *Festuca rubra* L. and *A. gigantea* (Bernasconi et al. 2011).

Within the BigLink project, meteorological conditions were monitored with a weather station and the runoff from the catchment was sampled using automated water-sampling stations (Bernasconi et al. 2011).

Experimental setup

For our study, 18 plots of 2 × 2 m were selected within the BigLink grid to cover the gradient of initial soil development along the glacier forefield and to account for spatial variability (Fig. 1). Our 18 sites included 4 young sites (<10 year), 10 sites of intermediate age (58–78 year), and 4 old sites (110–128 year).

The BigLink grid was generally defined as a random sampling grid to capture the increase in age and the heterogeneity of the Damma glacier chronosequence (Bernasconi et al. 2011). It was naturally divided by the moraines into young (<10 year), intermediate (58–78 year), and old parts (110–140 year). This grid provided the sampling basis for a number of field studies within the BigLink project (Bernasconi et al. 2011; Göransson et al. 2011; Kiczka et al. 2011; Smittenberg et al. 2012). The site ages were described as 'time since deglaciation' at the time of sampling grid definition in 2007 (Bernasconi et al. 2011; VAW 2011).

Soil CO$_2$ effluxes

Measurements of soil respiration were carried out biweekly from July to September 2008, June to September 2009, and June to October 2010. To measure soil respiration, we installed PVC rings (height 5 cm, diameter 20 cm) pushed 2–3 cm into the soil at the same general locations as where soil sampling had taken place in the framework of BigLink. The CO$_2$ effluxes were measured using two identical custom-made static chambers equipped with diffusion-aspirated non-dispersive infrared gas analysers (IRGAs) and relative humidity/temperature sensors (GMP343 carbon dioxide probe, HMP75 rH/T probe; Vaisala, Vantaa, Finland). The water vapour cross sensitivity of the IRGAs was corrected online by linking it with the relative humidity/temperature sensors (Bader and Körner 2010). Soil respiration rates were calculated from the linear increase of CO$_2$-concentration during a 5 min time period.

Soil respiration during winter was determined by measuring the gradient of CO$_2$ concentrations across a snow pack, and calculating the effluxes based on Fick's law of diffusion, following Hubbard et al. (2005) and Musselman et al. (2005) (Eq. 1):

$$J_g = f\tau D \frac{P_0}{RT_0} \left(\frac{T}{T_0}\right)^{0.8l} \frac{dg}{dz} \qquad (1)$$

where J_g (μmol m^{-2} s^{-1}) is the gas flux, 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), g is the measured difference in gas concentration between soil and snow surface (μmol mol^{-1}), T is the average snow pack temperature (K), and z is depth of snow pack (m).

The porosity f was calculated from the mean density of the snow pack p (kg m^{-3}) (Eq. 2):

$$f = 1 - \frac{1}{973} \tag{2}$$

where 973 is the density of ice (kg m^{-3}). Tortousity τ was estimated as a function of porosity f (Eq. 3):

$$\tau = f^{\frac{1}{3}} \tag{3}$$

The winter fluxes were only assessed once per year because the glacier forefield is hardly accessible due to high avalanche risks, steep slopes, and hazardous passages across the dammed lake. Therefore, the soil CO_2 efflux for the snow-covered period (200 days) was estimated by extrapolating the measured data to the whole winter, which was characterised by stable soil temperatures under the continuously more than 50 cm thick snow cover.

Soil temperature was measured manually with a soil thermometer at each plot at each sampling date and continuously with temperature loggers (HOBO v2 temp logger, onset, Bourne MA, USA) at 2.5 cm soil depth in the mineral soil in all three site age groups. Soil water content was determined by the gravimetric method measuring the weight loss after drying at 105 °C; it was monitored at four sites of different age (7, 67, 110, and 120 year) in the upper 5 cm of the soils.

The relationship between soil temperature and soil respiration during summer was fitted using non-linear regression (Buchmann 2000) for each plot independently (Eq. 4):

$$y = \beta_0 e^{(\beta_1 T)} \tag{4}$$

where T (°C) is the soil temperature at 2.5 cm depth, and β_0 and β_1 are fitting parameters (IBM SPSS 19). Based on this non-linear regression, soil CO_2 efflux was calculated using measured CO_2 efflux data and continuously logged soil temperatures with a temporal resolution of 0.5 h.

To obtain the temperature sensitivity of soil respiration within each plot, Q_{10} values were calculated according to Eq. (5):

$$Q_{10} = e^{10\beta_1} \tag{5}$$

Sources of soil-respired CO_2

To estimate the sources of soil-respired CO_2 and their variation with increasing soil development, we performed both radiocarbon (^{14}C) combined with stable carbon isotope (^{13}C) analysis of soil-respired CO_2, and a vegetation-clipping experiment, where we measured the response of soil respiration to the removal of aboveground biomass (Bahn et al. 2006).

For ^{14}C analysis, soil-respired CO_2 was sampled in June 2009 from the sites 7, 67, and 120 year, assuming that they are broadly representative of each of the age groups. Soil-respired CO_2 was trapped by placing a cap equipped with a rubber septum over the pre-installed PVC rings (height 5 cm, diameter 20 cm) for 2 h. From the approximately 4 L volume underneath the cap, 300 mL were drawn using a larger syringe and placed into pre-evacuated 250 mL glass bottles in order to guarantee overpressure. At the laboratory (400 m AMSL), the CO_2 was cryogenically purified on a vacuum line and flame sealed into Pyrex glass tubes, and subsequently measured for its radiocarbon content by accelerator mass spectrometry using a MICADAS system equipped with a gas ion source (Ruff et al. 2010). ^{14}C contents are reported both as percent modern carbon (pMC), i.e. relative to the ^{14}C content of the international standard (1950 AD) after background correction and $\delta^{13}C$ normalization, and as $\Delta^{14}C$ in per mil (‰), i.e. relative to the absolute atmospheric radiocarbon content (defined as 0 ‰) of the atmosphere in 1950, and that is most useful for source apportionment and carbon cycle studies (Trumbore 2000). For the determination of the stable carbon isotopic composition (expressed as $\delta^{13}C$, against international standard Vienna-Pee Dee Belemnite, VPDB) of soil respiration, a Keeling plot approach (Pataki et al. 2003) was used, i.e. time series of 12 mL gas samples were taken from underneath the capped PVC rings described above. The $\delta^{13}C$ values, as well as the CO_2 concentrations of the gas samples and ambient air, were measured with a ThermoFinnigan (Bremen, Germany, now Thermo Fisher Scientific) GasBench II, equipped with a CTC autosampler (CTC Analytics AG, Zwingen, Switzerland), Thermal Conductivity Detector, and coupled to a ConFlo IV interface and a Delta V Plus mass spectrometer (both Thermo Fisher Scientific). The samples were pressure-equilibrated just before measurement to guarantee comparable results of the concentration measurement.

The ^{14}C contents of sampled air were 'corrected' for their contribution of ambient (atmospheric) CO_2 using a two end-member model after Balesdent et al. (1988) in the following way:

The fractions of soil-derived C ($f_{soil\ CO_2}$) in the gas samples were calculated by using $\delta^{13}C$ values (Eq. 6) as follows:

$$f_{soil\ CO_2} = \frac{(\delta^{13}C_{CO_2\ sample} - \delta^{13}C_{CO_2\ atmosphere})}{(\delta^{13}C_{soil-respired\ CO_2} - \delta^{13}C_{CO_2\ atmosphere})} \quad (6)$$

where $\delta^{13}C_{CO_2\ sample}$ is the measured value of the gas samples; $\delta^{13}C_{CO_2\ atmosphere}$ is the value of the atmosphere and $\delta^{13}C_{soil-respired\ CO_2}$ is the $\delta^{13}C$ value of soil-respired CO_2 at Damma glacier forefield measured in additional measurements campaigns using the Keeling-plot approach. The soil-respired ^{14}C in the sample was calculated subsequently as follows:

$$\Delta^{14}C_{soil-respired}$$
$$= \frac{\Delta^{14}C_{sample} - (\Delta^{14}C_{atmosphere} \times (1 - f_{soilCO_2}))}{f_{soilCO_2}}$$
$$(7)$$

Where $\Delta^{14}C_{sample}$ is the measured value of the samples; $\Delta^{14}C_{atmosphere}$ is the value of the atmosphere and f_{soilCO_2} is the fraction of soil-derived C.

In the clipping experiment, we removed the above-ground biomass from areas of $1 \times 1\ m^2$ next to the BigLink sites 67, 70, and 72 year (intermediate site) as well as the 110 and 120 year (old sites) during the peak of standing biomass (end of July 2010) (Fig. 1). The youngest site was not clipped because it was free of vegetation and radiocarbon measurement during the year 2009 indicated that soil respiration consisted predominantly of 'old' pre-bomb C. In order to shade the soils as under the prevailing plant cover, the clipped sites were covered with mesh cloth commonly used for sun protection in plant nurseries. In both the clipped areas and the adjacent unclipped control areas of BigLink sites, we measured in situ soil CO_2 effluxes and soil temperatures with three to five replicates per treatment (Fig. 1).

DOC leaching

In 2009 and 2010, soil water was sampled biweekly by glass suction plates (diameter 5.5 cm, made of borosilicate glass, 1 μm pore size; Schmizo, Zofingen, Switzerland), which were flushed with 1 M HCl and then cleaned with deionized water prior to installation. In 2008, 1 year before the sampling started, the suction plates were carefully installed at a soil depth

of 10 cm, 10 cm apart from the respiration collars. The suction plates were connected to 250 mL glass bottles and an approximate suction of 400 hPa was applied manually with a 100-mL syringe to collect soil water. The sampled soil water was kept cooled during the transport to the lab, where it was filtered through 0.45 μm cellulose-acetate filters (ME25, Whatman-Schleicher & Schuell, pre-flushed with Millipore water) within 48 h of sampling. The DOC concentrations were analysed using a TOC/TN analyser (TOC-V analyzer, Shimadzu, Tokyo, Japan). Filtered deionized water used as blanks showed values of 0.22 ± 0.08 mg DOC L^{-1}. In addition, the molar absorptivity at 285 nm of DOC was determined using a Cary 50 UV-spectrophotometer (Varian, Palo Alto, USA). The specific UV absorbance (SUVA) was then calculated by dividing the measured UV absorbance (285 nm) by the DOC concentrations (mg L^{-1}). SUVA can be used as a measure for aromaticity (Chin et al. 1994), and its content of the so-called 'hydrophobic' DOC (Dilling and Kaiser 2002).

Due to the absence of soil horizons and the high gravel content of the glacier forefield, it was not possible to model the DOC flux with a common soil water flux model. Therefore, we estimated the DOC flux (g C m^{-2} day^{-1}) by using the measured DOC concentrations (DOC_{con} in mg L^{-1}) and precipitation (P in mm day^{-1}), as well as evaporation (E in mm day^{-1}, data kindly provided by M. Stähli), as an approximate water flux along the Damma glacier forefield (Eq. 8):

$$DOC_{flux} = DOC_{con}(P - E) \quad (8)$$

Results

Soil temperature and moisture

There was a distinct seasonal variation in soil temperatures (Fig. 2). During the snow-covered periods, soil temperatures at 2.5 cm depth remained almost constant at 0.1 ± 0.05 °C but increased to up to 25 °C during the summer. In contrast to the large seasonality variation, the soil temperature gradient along the forefield was small; there was no significant difference among the mean soil temperatures ($R^2 = 0.63$; $P = 0.2$). The mean annual soil temperature of the three succession stages was 3.2 ± 0.15 °C. The maximum and minimum air temperatures were 22 °C in summer and -23 °C in winter, respectively.
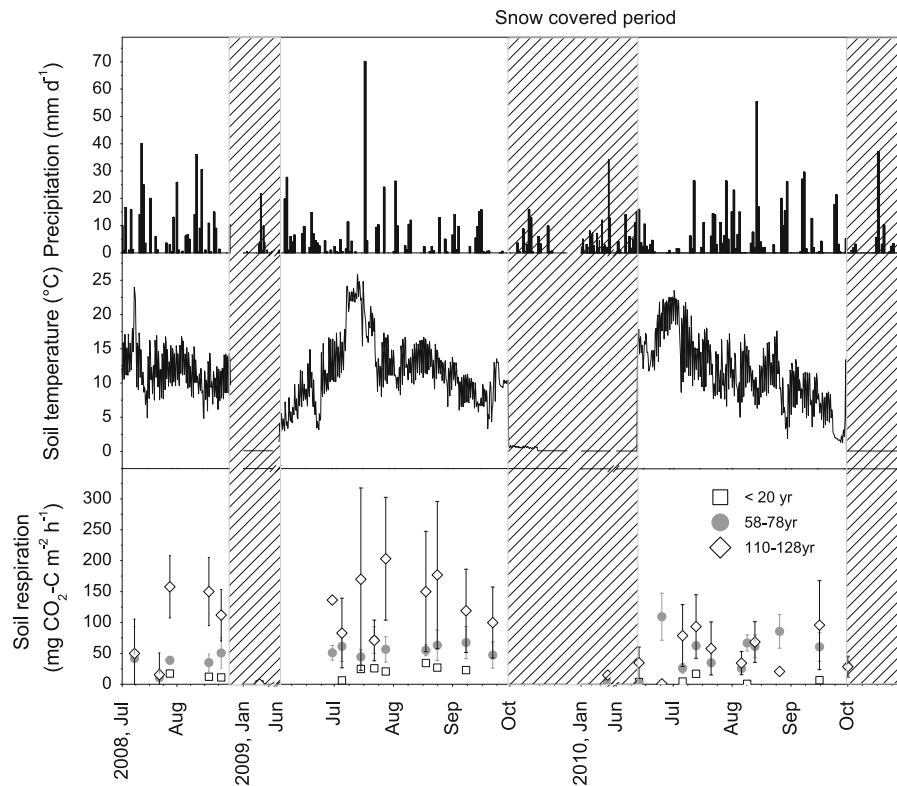
Fig. 2 Precipitation, mean soil temperature at 2.5 cm depth and soil CO_2 efflux measured along the Damma glacier forefield from 2008 to 2010. Soil CO_2 effluxes are means with standard errors of 4–5 plots

Precipitation showed an irregular distribution with single peaks reaching up to 70 mm day^{-1}, but without clear seasonal variation (Fig. 2). During the main growing season (July 1–September 30), precipitation amounted to 330 and 490 mm in 2009 and 2010, respectively.

The volumetric soil moisture content was on average between 6.6 ± 0.5, 23.2 ± 0.01 and 8.8 ± 0.7 vol.% for the 10, 70 and 120 year old sites; therefore it can be assumed the sandy soils were mostly unsaturated in the upper 10 cm.

Soil CO_2 efflux along the chronosequence

Overall, average soil respiration rates increased along the glacier forefield from 13.9 ± 2.6 to 103.8 ± 10.3 mg CO_2–C m^{-2} h^{-1} at the young and the old site. Soil respiration rates exhibited a clear seasonal pattern (Fig. 2) and correlated with soil temperature. An exponential equation (Eq. 4) gave a better fit for the relationship between soil respiration and soil

temperature than the linear regression. The R^2 of the regression ranged between 0.5 and 0.7 ($P < 0.05$) with the exception of the sites 66, 72, 77, 78 and 118 year, which had $R^2 < 0.3$. The Q_{10} values were 4.5 at the young, 3.4 ± 0.5 at the intermediate and 3.4 ± 0.9 at the old sites, with a high variation within the site age groups. They did not show a consistent change along the chronosequence. The measured soil CO_2 effluxes in summer 2009 were higher than in summer 2010 (Fig. 2), although this was not statistically significant, which can be attributed to lower temperatures at the sampling days in 2010.

During winter, CO_2 concentrations within the snowpack increased linearly from the snow surface to the soil at all site ages, indicating that soil respiration was on-going under the snow cover, even at soil temperatures of 0.1 ± 0.05 °C (Fig. 3). The soil CO_2 efflux rates during the winter showed a consistent increase along the chronosequence but they amounted on average to less than 11 % of the summer rates. However, their contribution to the annual effluxes was
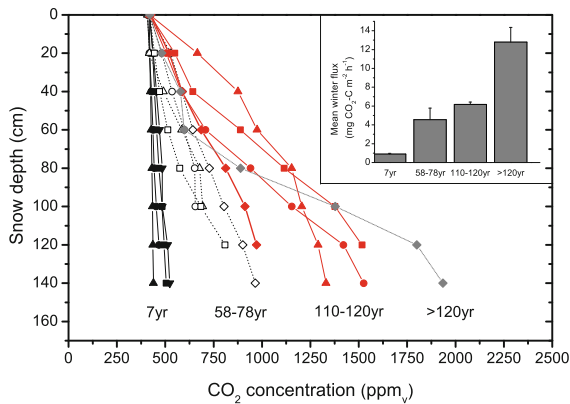
Fig. 3 CO_2 concentration profile under snow and mean winter CO_2 efflux of three site age groups from single winter CO_2 efflux measurements in March 2010

Fig. 4 Development of soil C stocks and plant biomass with site age (Smittenberg et al. 2012). Cumulative seasonal CO_2 efflux (July–Sep. 2009) and DOC flux (July–Sep. 2009) along Damma glacier forefield

between 30 and 38 % (Table 3) due to the long duration of the snow period.

The annual soil CO_2 effluxes increased significantly with increasing site age ($R^2 = 0.84$; $P < 0.05$) from the youngest soils above the 1992 moraine to the most developed soils below the 1,928 moraine (Table 3). The young site (<10 year) showed a low annual flux of 9 g CO_2–C m^{-2} $year^{-1}$, while the highest CO_2 effluxes were observed at the old site with approximately 160 g CO_2–C m^{-2} $year^{-1}$. Soil respiration varied strongly within each age group, with coefficients of variation ranging between 20 and 56 %. Plant biomass C (aboveground + root), soil C stocks, and ecosystem C stock measured in the same sites correlated significantly with site age ($R^2 = 0.77$, 0.76, 0.77, and 0.85), but not with soil respiration, although all variables increased along the glacier forefield (Fig. 4). The ratio between total ecosystem C stocks and soil C fluxes (soil respiration and DOC leaching) decreased with increasing site age along the glacier forefield (Table 3).

Sources of soil-respired CO_2

Radiocarbon analysis

Stable and radiocarbon isotopic results are presented in Table 2. The samples show $\Delta^{14}C$ values of sampled air slightly below modern at the 7 year old site and slightly above modern for the 70 and 120 year old sites. Using the $\delta^{13}C$ values of the gas samples used for
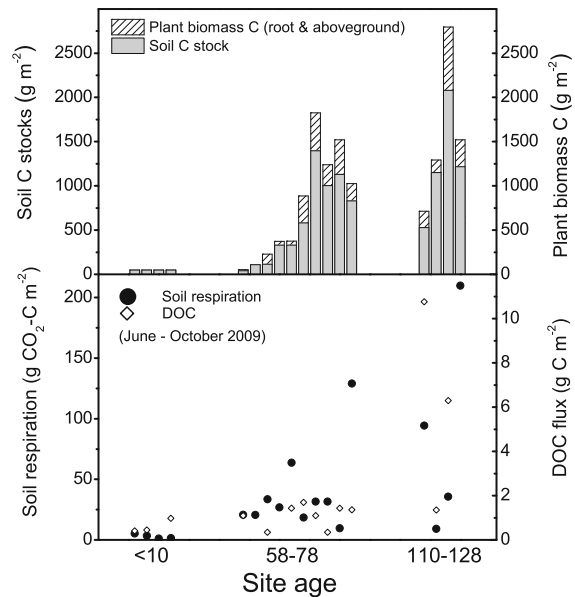
the ^{14}C measurement, an atmospheric $\delta^{13}C$ value of -9.3 ‰, and soil-respired CO_2 values of -23.1 to -26.6 ‰ (Table 2) in Eq. (6) described above, one arrives at an approximate contribution of CO_2 originating from soil respiration of 32–63 % (Table 2). Using this as input data in the mixing model of Eq. (7), together with atmospheric radiocarbon values from the same year, the ^{14}C content of the soil-respired $^{14}CO_2$ can be estimated (Table 2). However, due to insufficient replication, no robust measure of uncertainty can be given, but the data can be used semi-quantatively.

The ^{14}C content of respired CO_2 at the 7 year old site (that became ice-free in 2000 AD) was well below modern ($\Delta^{14}C = -68.1$). In contrast, respired CO_2 from the older succession stages had positive $\Delta^{14}C$ values very close to that of the present-day atmosphere ($\Delta^{14}C = 46.2$, data kindly provided by Ingeborg Levin, pers. communication).

Clipping

The vegetation-clipping experiment conducted to identify the contribution of 'new' plant-derived C to soil respiration showed that soil CO_2 effluxes increased within the first week after the removal of

Table 2 Measured and calculated radiocarbon contents and $\delta^{13}C$ values of sampled, respectively soil-respired CO_2 for young, intermediate and old successional stage along the Damma glacier forefield in summer 2009

ETH lab no.	Site age (year)	pMC sample	$\Delta^{14}C$ sample (‰)	$\delta^{13}C$ sample (‰)	$\delta^{13}C$ soil-respired (‰)[b]	Fraction soil-respired CO_2 sample (%)[d]	^{14}C soil resp. (pMC)[c]	^{14}C soil resp. $[\Delta^{14}C$ (‰)][c]
38571	7	100.1 ± 2.02	−5.8	−15.8	−23.7	45	97.77	−68.1
38572	70	104.1 ± 1.45	41.0	−17.4	−23.1	63	106.01	38.0
38573	120	103.4 ± 2.47	33.6	−19	−26.6	32	103.5	6.8
Atmosphere			46.2[a]		−9.3			

pMC percent modern carbon

[a] Data kindly provided by Ingeborg Levin (pers. communication)

[b] Calculated after Keeling plot approach Pataki et al. (2003) from separate samples (raw data not given)

[c] Calculated using Eqs. (6) and (7) mentioned in the text

the aboveground biomass; this was mainly attributed to the disproportional increase of soil temperature in the clipped plots as compared to the unclipped plots (on average +4.5 °C, data not shown). We corrected this temperature effect, which caused a 100 % increase of the flux, by calculating 'theoretical respiration' rates for the control sites using the temperatures of the clipped sites, and applying the temperature dependency (Eq. 4) of the control sites (Bahn et al. 2006). After temperature correction, the soil respiration was 40–89 % lower in the clipped than in the unclipped sites in all soil ages during the 6 weeks after clipping. In general, the clipping of the intermediate sites had a stronger effect on soil respiration as compared to soil respiration following clipping at the old site (Fig. 5): on average 68 versus 46 % in the intermediate and old sites, respectively. At the youngest sites, where the plant cover was below 5 % (and where we did not clip the vegetation), we assumed a negligible contribution by plants.

DOC leaching

The average concentrations of DOC at 10 cm soil depth ranged from 2.6 to 32.2 mg L^{-1}, with the lowest concentrations observed at the young site and the highest at the oldest site (Fig. 6). The cumulatively DOC leached 10 cm depth from July to September increased from 0.4 ± 0.02 to 7.4 ± 1.6 g C m^{-2} along the glacier forefield (Table 3). In contrast, the specific UV absorbance at 285 nm used as a measure of DOC aromaticity did not increase clearly with site age and ranged between 0.001 and 0.036 L mg C^{-1} cm^{-1}
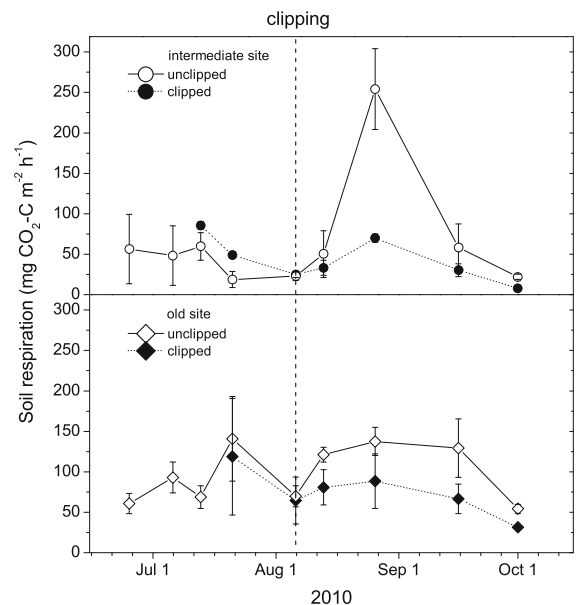

Fig. 5 Effects of clipping the aboveground vegetation, corrected to a common temperature at the intermediate and old sites of Damma glacier forefield in 2010. Soil CO_2 effluxes of the clipped and unclipped sites are means with standard errors of 4 or 5 plots

(Table 3). The concentrations of DOC were not related to soil temperature and did not show a distinct temporal pattern over the summer season.

DOC concentrations and fluxes correlated significantly with site age ($P < 0.01$; Fig. 4) as well as with plant C ($P < 0.05$). Soil C stocks increased along the chronosequence as the other variables but they were not significantly related to the DOC concentrations and fluxes.
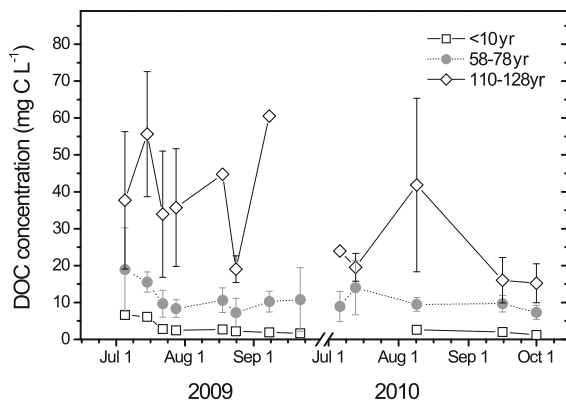
Fig. 6 DOC concentration measured along the Damma glacier forefield in 2009 and 2010. DOC concentrations are means with standard errors of 4 or 5 plots

Discussion

Increasing soil CO_2 efflux along the chronosequence

Soil respiration along the glacier forefield increased strongly with C accumulation in plant biomass and soil, supporting our hypothesis of an accelerated respiratory activity with ongoing ecosystem development. Our finding is in agreement with studies in high arctic ecosystems, where measured soil CO_2 efflux rates increased with the time since deglaciation in North-Western Greenland and Svalbard (Jones et al. 2000; Nakatsubo et al. 1998). In contrast, in North Iceland, Wookey et al. (2002) observed highest soil CO_2 effluxes close to the glacier front, while soil respiration rates decreased with increasing soil age. The measured CO_2 efflux rates in these arctic studies were, however, smaller than in our study. Although the arctic

chronosequences included sites that had been ice-free for more than 250 years, the soil CO_2 efflux rates in the arctic reached only up to 42 mg C m^{-2} h^{-1} (Jones et al. 2000; Nakatsubo et al. 1998; Wookey et al. 2002), which was comparable with the soil respiration rates at the 70-year old sites of the Damma chronosequence. Possible reasons for the higher CO_2 efflux rates of our alpine glacier forefield could be higher temperatures, with an annual mean of 2.2 °C compared with −11.6 °C in Greenland (Jones et al. 2000), and a faster ecosystem development after glacier retreat in the Alps than at higher latitudes (Becker and Dierschke 2005; Nilsen et al. 1999). A comparison with mature ecosystems under similar climate conditions shows that our measured soil CO_2 effluxes at the oldest sites (approximately 2,000 m AMSL) were 2.5 times lower than at an unglaciated alpine treeline (2,180 m AMSL) (Hagedorn et al. 2010), suggesting that soil CO_2 effluxes will increase further with continuing ecosystem development.

Our estimates of annual soil CO_2 effluxes contain a high uncertainty due to the infrequent winter measurements caused by the general inaccessibility and the high avalanche risk. Yet, our winter measurements are the first reported for a glacier forefield. They show the same increase with site age as during the summer (Fig. 3). Under the permanently thicker snow cover than 50 cm, soil temperatures were almost stable at 0.1 ± 0.05 °C (Fig. 2) suggesting that the temporal variability of soil respiration was probably low. This is supported by Monson et al. (2006), who found low variation in soil CO_2 effluxes at almost constant soil temperatures underneath the snow during continuous winter measurements in a subalpine forest. Assuming that the measured winter CO_2 effluxes were

Table 3 Annual soil respiration (SR annual), seasonal soil respiration (June–Sep.; SR season), seasonal leached DOC (June–Sep.) in 2009, and total ecosystem C accumulation

Site age (year)	SR annual (g C m^{-2} year^{-1})	SR season (g C m^{-2})	Leached DOC (g C m^{-2})	SUVA (L mg C^{-1} cm^{-1})[a]	Ecosystem C accumulation (g C m^{-2} year^{-1})[b]	Ecosystem C accumulation/soil C fluxes[c]
7	8.6 ± 1.1	5.3 ± 0.7	0.41 ± 0.02	0.002 ± 0.001	100	11
58–78	66.6 ± 16.6	45.0 ± 8.6	1.60 ± 0.56	0.027 ± 0.02	150	2
110–128	160.5 ± 66.7	113.2 ± 49.1	7.39 ± 1.59	0.017 ± 0.04	60	0.4

[a] Specific UV absorbance at 285 nm

[b] Plant biomass, organic layer and mineral soil 0–10 cm, data from Smittenberg et al. (2012)

[c] Ratio between ecosystem C accumulation (g C m^{-2} year^{-1}) and soil C fluxes (g C m^{-2} year^{-1})

representing the winter effluxes over the entire snow-covered period, the winter CO_2 efflux contributed to between 30 and 38 % of annual soil respiration. This is in the higher range of values measured in other ecosystems such as alpine tundra (1–27 %; Brooks et al. 1997); subalpine meadows (30 %; Liptzin et al. 2009) or subalpine forests (12 %; Schindlbacher et al. 2007). The relatively high importance of winter respiration in this glacier forefield could be attributed to the long-snow covered period (7 months) and the thick snow-cover, which effectively insulated soils and resulted in unfrozen and thus, relatively 'warm' soils.

Cumulative seasonal soil respiration, plant biomass, and soil C stocks all increased with site age (Fig. 4), which supports our hypothesis (1) that CO_2 effluxes increase with ecosystem development. However, soil respiration rates were not significantly correlated with the plant biomass or soil C of the same site, which we mainly attribute to the small-scale heterogeneity of the glacier forefield, where the parameters could not be measured exactly at the same point.

Sources of soil-respired CO_2

In this study, we applied two approaches to gain insight into the sources of soil-respired CO_2: the analyses of radiocarbon content and the removal of aboveground vegetation by clipping. The $\Delta^{14}C$ value of the youngest site, deglaciated only in 2000 AD, was clearly negative. Yet, organic C assimilated over the last decade must contain ^{14}C concentrations that equal that of the atmosphere over that time period, i.e. with positive $\Delta^{14}C$ values. We therefore conclude that there must be a significant contribution of pre-bomb C to the young site. This finding is similar to that of Bardgett et al. (2007), who showed that ancient C was the primary source for initial soil respiratory activity in recently ice-freed soils of the crystalline metamorphic Ödenwinkelkees glacier in Austria. The likely source of this old C is either remnants of fossil soil C that may have been present thousands of years ago, or supra-glacial C, aerosols and dust being deposited on the glacier over the last centuries to millennia (Hawes 2008; Anesio et al. 2010). The dominance of older C in soil-respiratory activity contradicts the general assumption that soil autotrophs primarily drive microbial activity in initial soils (Walker and del Moral

2003). Indeed, PLFA measurements of Esperschütz et al. (2011) show that heterotrophs are already dominant in the very young soils of the Damma forefield. Genetic profiling and sequencing of clone libraries by Zumsteg et al. (2012) indicated that bacterial diversity was high and did not change along the soil chronosequence of the Damma glacier. However, fungi shifted from an *Ascomycota*-dominated community in young soils colonizing rocks to a more *Basidiomycota*-dominated community in old soils either living in association with plants or decomposing litter. At the oldest site, the ^{14}C content of soil-respired CO_2 is virtually the same as that of the present-day atmosphere, while that of the intermediate site showed slightly elevated values (Table 2). This suggests that respired CO_2 at these sites is mainly derived from recently assimilated C, but mixed with CO_2 derived from SOM of a few decades old, when atmospheric ^{14}C contents were more strongly affected by nuclear bomb testing. The additional contribution of CO_2 mineralized from SOM that accumulated before the 1950's may explain the lower ^{14}C contents of the oldest site compared to the intermediate site. Any respiration derived from ancient C, as observed for the youngest site, appears to be strongly diluted by respiration of recent C.

The clipping experiment supports this conclusion; the removal of aboveground vegetation led to a fast decrease of soil respiration corrected for temperature at the intermediate and old sites (Fig. 5), which is in agreement with clipping studies in alpine meadows (Bahn et al. 2006) as well as in grasslands (Craine et al. 1999). In the Damma forefield, the experimental clipping induced a decline in soil respiration of up to 90 % at the intermediate site and 56 % at the old site within two weeks, which demonstrates that CO_2 assimilated by plants and allocated to the their roots contribute significantly to soil CO_2 efflux (Fig. 5). These fractions very likely underestimate the root-derived respiration, as the decomposition of fine roots and carbohydrate reserves still releases CO_2 (Bahn et al. 2006).

The results of the clipping experiment in conjunction with the ^{14}C analysis of soil-respired CO_2 indicate a changing contribution of root respiration and heterotrophically respired CO_2 from SOM to the total soil CO_2 efflux along the glacier forefield. However, our findings confirmed only partly our second hypothesis that respiration of recently assimilated CO_2

through the rhizosphere will increase faster than heterotrophic respiration. (1) In the initial phase, plants are absent and soil respiration originates primarily from 'ancient' SOM and maybe from soil autotrophs. (2) In later stages, soil-respired CO_2 consists of a mixture of recently assimilated C and a few decades old SOM. The higher clipping effect at the intermediate sites (58–78 year) than at the older sites (110–128 year) suggests that the contribution of rhizosphere respiration to the total soil CO_2 effluxes peaks after a number of decades and declines thereafter. The likely reason for this pattern could be the accumulation of SOM with prolonged soil evolution, whose mineralisation contributes increasingly to soil respiration.

DOC leaching increases faster with soil age than soil respiration

The leaching fluxes of DOC at 10 cm soil depth were small compared with soil respiration. Only 2–5 % of the C losses from soils throughout the summers of 2009 and 2010 were leached as DOC. In support of our third hypothesis, we found rising DOC fluxes with ongoing soil development, which most probably resulted from the accumulation of SOC along the soil chronosequence. The soil organic C stock, and thus the pool for DOC generation, was up to 40 times higher at the oldest sites compared with the recently deglaciated part of Damma glacier forefield (Smittenberg et al. 2012). The DOC concentrations of the 120 year old sites, averaging 38 mg DOC L^{-1}, were in a comparable range as those found in mature alpine ecosystems under similar climatic conditions (Hagedorn et al. 2010; Müller et al. 2009). In contrast to soil respiration, where the rates were less than half of the ones from mature alpine soils, this suggests that there will be only a small further increase in DOC leaching with continuing ecosystem development. The comparison with mature alpine ecosystems also supports our third hypothesis of an attenuating DOC leaching due to the formation of reactive mineral surfaces. Along the forefield of the Damma glacier, the time for weathering was probably too short for the formation of reactive mineral surfaces, which could retain DOC. This assumption is in agreement with the controlled leaching experiments in the laboratory with up to 1,200 years old volcanic soils by Lilienfein et al.

(2004b) and Qualls and Bridgham (2005). They found increasing DOC leaching until site ages of 250 year as a result of increasing SOM content, but a decrease thereafter due to a stronger adsorption to soil minerals. In ecosystems of different land-uses across Europe, Kindler et al. (2011) observed that DOC retention in the mineral soil is inversely related to the ratio between soil organic carbon and oxalate-extractable Fe and Al oxides. While SOC controls the DOC production, the Fe and Al oxides affect DOC retention (Kaiser et al. 1996). Along the forefield, SOC content increased five times more than the poorly crystalline Fe and Al oxides (Table 1), suggesting that increases in DOC production are greater than increases in DOC adsorption by mineral surfaces (Table 1). Physical fractionation of SOM along the glacier forefield by Smittenberg et al. (2012) supports this pattern. The SOC increase with increasing soil age was primarily related to an increase in 'light' SOM, and not to increases in 'heavy' mineral bound SOM, suggesting that C accumulation proceeds faster than the formation of reactive surfaces that could potentially act as DOC sinks and lead to mineral-associated SOM.

The comparison of DOC leaching and soil respiration indicates that the significance of DOC leaching to C losses from the topsoil increases towards the oldest soils of the chronosequence (Table 3). The reason for the more rapid increase in DOC leaching rates compared to those observed in soil respiration might be the apparently slow formation of C stabilizing reactive surfaces through weathering which results in small DOC retention and in high proportions of 'labile' SOM. Our conclusions are consistent with results of a controlled leaching experiment with various soil horizons conducted by Kaiser et al. (1996). They demonstrated that the net release in DOC from soils exhibits a natural threshold, turning net DOC sinks into net DOC sources above certain SOC concentrations and below certain concentrations of Fe and Al oxides. In contrast, respiratory activity, and hence CO_2 production, increases continuously with increasing SOC contents and occurs even at very low SOC contents (Kirschbaum 2000).

C fluxes and C accumulation in initial ecosystems

In conjunction with measured ecosystem C stocks, our C flux data indicates that the ecosystem in Damma
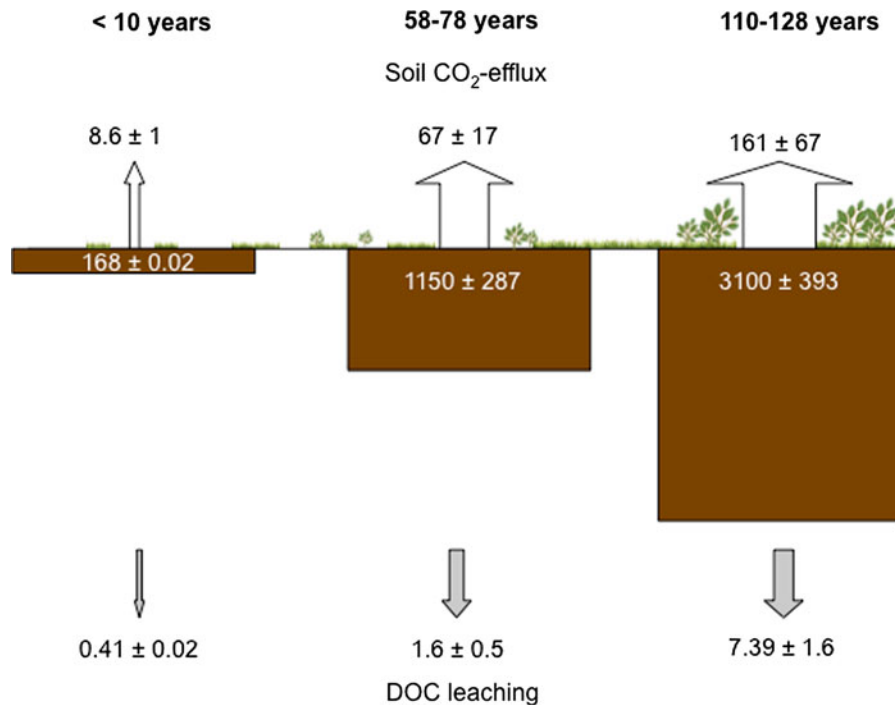
Fig. 7 Schematic representation of the evolution of C fluxes (g C m^{-2} year^{-1}) and total ecosystem C stocks (g C m^{-2}, data from Smittenberg et al. 2012) along the Damma glacier forefield. *Note* soil C fluxes and C pools are not proportionally to their sizes

glacier forefield has become less efficient with respect to C storage during its development (Fig. 7). We found a continuous increase of soil C fluxes along the forefield, while the total ecosystem C accumulation decreased relative to the soil C fluxes (Table 3). The ecosystem C stocks were on average 0.2, 1.1, and 3.1 kg C m^{-2} at the youngest, intermediate and oldest part, respectively (Smittenberg et al. 2012). However there were distinct exponential increases in between the moraines, especially in the young and intermediate parts of the chronosequence. From these data Smittenberg et al. (2012) calculated annual net ecosystem C accumulation rates, which were 100, 150, and 60 g C m^{-2} year^{-1} in the young, intermediate and old sites. By comparison, the C losses from soils by soil respiration and DOC leaching increased from a mere 9, to 70 and finally to 170 g C m^{-2} year^{-1} along the three stages of soil formation. This implies that the ecosystem evolved from a dominance of C accumulation in the initial phase to one with a relatively high turnover, i.e. a high throughput system. We suggest that the relatively high C accumulation as compared to C fluxes is a characteristic feature of initial soil formation on freshly exposed rock material.

Conclusions

Our assessment of soil C fluxes, soil respiration and DOC leaching, along the chronosequence of the glacier forefield, showed that:

1. There is a general increase of soil respiration with site age, which is linked to increasing plant biomass and SOC stocks.
2. Soil temperature is a main driver of the seasonal variation of soil respiration, while soil moisture did not have a measurable influence. Measurement campaigns in winter suggest that 30–38 % of the annual CO_2 efflux is respired during the approximately 200 day long snow covered season.
3. The origin of soil-respired C changed with soil age. While heterotrophic respiration of ancient C dominates the low fluxes in the very young soils, new plant-fixed C becomes the main source for soil respiration at the 58–78 year-old sites. With ongoing soil development and SOM accumulation, the contribution of heterotrophic respiration to soil CO_2 efflux increases again.

4. DOC leaching increased with site age due to the faster development of SOC stocks as a DOC source compared to the rate of formation of reactive mineral surfaces acting as DOC sinks. This increase in DOC leaching is faster than in soil respiration.

5. Over the course of a century, ecosystem evolution at the high alpine Damma forefield appears to evolve from a system dominated by C accumulation in the initial phase to one that is characterized by high throughput.

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