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Response of carbon fluxes to the 2003 heat wave and drought in three mature forests in Switzerland

Elisabeth Graf Pannatier · Matthias Dobbertin ·
Alexander Heim · Maria Schmitt ·
Anne Thimonier · Peter Waldner · Beat Frey

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Abstract The effects of the heat and drought of the summer 2003 on carbon (C) fluxes (soil CO_2 efflux, dissolved organic carbon in soil, C from litterfall and C sequestration in tree) were investigated in three mature forests in Switzerland between 2001 and 2005. Measurements of the soil matric potential (Ψ) indicated a gradient in drought intensity at the three sites (Vordemwald, Schänis, Beatenberg) with average Ψ during the summer 2003 of -75, -41 and -5 kPa, respectively. In Vordemwald where the drought was the most severe, the hourly soil CO_2 efflux declined by about 30% when $\Psi < -90$ kPa. Estimated annual soil CO_2 efflux in 2003 was about 10% smaller than effluxes in wetter years (2001, 2002 and 2004) but the differences were not significant. In Schänis and Beatenberg, no suppression of hourly soil CO_2 efflux was observed during the summer 2003. The annual efflux in 2003 at both sites was 10–15% larger than the effluxes in the other years but the differences were not significant. DOC concentrations increased during the first rewetting events after the drought in Vordemwald and in Schänis. This was mainly due to a concentration effect due to the low soil water content. Because precipitation was lower in 2003, annual DOC fluxes substantially decreased at the three sites. Carbon sequestration in tree stems in Vordemwald declined by 32% in 2003 compared to the mean 2002–2005. In Beatenberg and Schänis, tree growth responded little to the extreme summer 2003. Litterfall at the three sites showed no marked reaction to the summer 2003. Estimate of annual net ecosystem production (NEP) suggested that the stands in Vordemwald and in Schänis remained a C sink between 2002 and 2005 but that the extreme summer 2003 caused a decrease in NEP. In Beatenberg, the impact on the NEP seemed to be limited in 2003. The annual NEP in 2003 decreased with increasing drought intensity over the three sites.

Keywords C sequestration · Drought · Dissolved organic carbon · Forest ecosystem · Litterfall · Soil respiration · Tree growth · Net ecosystem production · NEP

Introduction

Heat and drought were extreme in summer 2003 in large parts of Europe. It was the hottest summer during the past 500 years in Europe (Luterbacher et al. 2004; Garcia-Herrera et al. 2010). Maximum air temperatures in June and August 2003 were particularly high.

E. Graf Pannatier (✉) · M. Dobbertin ·
M. Schmitt · A. Thimonier · P. Waldner · B. Frey
Swiss Federal Institute for Forest, Snow and Landscape
WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland
e-mail: elisabeth.pannatier@wsl.ch

A. Heim
Department of Geography, University of Zurich,
Winterthurerstr.190, 8057 Zurich, Switzerland

On most of the continent, they were more than 4°C above the reference period between 1961 and 1990 (Rebetez et al. 2006). Combined with very low precipitation, this led to an exceptionally dry summer over large parts in Europe, including Switzerland (Rebetez et al. 2006; ProClim 2005). Summer droughts and heat waves could become more frequent in Europe over the next 50–100 years as a result of global climate change (Schär et al. 2004; Fuhrer et al. 2006; Beniston et al. 2007; IPCC 2007). How forest ecosystems and carbon (C) balance respond to such extreme events is still unclear. Changes in the above- and below-ground C fluxes on a large scale could act as a feedback mechanism affecting global warming and atmospheric CO_2 levels (e.g. Niklinska et al. 1999; Cox et al. 2000).

Simulating a prolonged soil drought in a temperate deciduous forest, Borken et al. (2006) suggested that extended summer droughts can, at least temporarily, increase the storage of soil organic matter in the organic horizon. Based on eddy-covariance measurements, Jassal et al. (2008) also found that ecosystem respiration decreased more than gross primary production as a result of drought, which would result in net C storage in the ecosystem. Similar findings have been obtained in several studies (Goulden et al. 1996; Kljun et al. 2007; Krishnan et al. 2006). In contrast, Ciais et al. (2005) reported that the exceptionally hot and dry spell in the summer of 2003 caused a stronger decline in the gross primary production than in the ecosystem respiration in European forests, leading to a net annual loss of carbon. The response of the net ecosystem production (NEP) was closely related to the soil water content. Granier et al. (2007) showed that the NEP decreased with increasing drought stress at 12 European monitoring sites covering various forest ecosystem types. Jolly et al. (2005) emphasized that tree growth across the Alps was enhanced at high elevations and suppressed at low elevations in response to the extreme summer temperatures in 2003. While tree growth at high elevation benefited from an extended growing season and water availability similar to average conditions, drought stress reduced tree growth at low elevation. The divergent response of the vegetation to the heat waves across latitudes and elevations represents a key issue to assess the impact of such extreme climatic events on C sequestration on a large scale.

A great number of studies have shown that extended summer droughts have substantial impact on the processes, fluxes and organisms in forest ecosystems on short-term scales, but little is known about the relevance of these changes on annual or decadal time scales (Borken and Matzner 2008). Little information is available on the impact of the heat wave of 2003 on the components of the forest ecosystem (e.g. tree growth, foliage and fine root production, soil respiration) and on their C fluxes in the subsequent years. Borken and Matzner (2009a) suggested that changes caused by drought seemed to be of transient nature with biogeochemical process rates and fluxes returning to typical level shortly after normalization of weather conditions. In contrast, the study of Ciais et al. (2005), that focused on the short-term consequences (2002–2003), stated that long-term impacts were likely to be significant and that such events had the potential to change the long-term continental C balances.

In this study we used monitoring data of three forest ecosystems in Switzerland between 2001 and 2005 to investigate the effects of the heat wave of 2003 on major and minor carbon fluxes (soil CO_2 efflux, dissolved organic carbon (DOC) in forest soil leachates, C from litterfall and C sequestration in trees) and to assess their relevance for annual C fluxes. The C fluxes were used to assess the net ecosystem production (NEP), i.e. the net gain or loss of carbon from the ecosystem for some unit of time (1 year in this study). The three sites were located at different elevations from 480 to 1500 m a.s.l. and experienced contrasting drought conditions (severe drought, moderate drought and no water deficit) during the summer 2003.

We assumed that the extreme weather conditions of the summer 2003 affected the annual C fluxes. In particular, we hypothesized that the annual C fluxes (soil respiration, tree growth, DOC flux) and the annual NEP decreased in 2003 compared to the mean values (2001–2005) at the site exposed to the severe drought. In contrast we expected an increase of these fluxes at the two other sites where the drought was not or less pronounced.

Materials and methods

Sites

The three study sites (Vordemwald, Schänis, Beatenberg) are part of a national forest monitoring network within the framework of the Swiss Long-term Forest Ecosystem Research project LWF (e.g. Cherubini and Innes 2000; Thimonier et al. 2001). These sites are part of the Level II plots network of ICP Forests (e.g. UNECE 2008). We selected these sites according to the level of water shortage (large, small or no water deficit) in summer 2003, as calculated in a previous study of the water balance at Swiss Level II plots (Graf Pannatier et al. 2007). Vordemwald is located on the Swiss Plateau (480 m a.s.l.), Schänis in the Pre-Alps in North-Eastern Switzerland (730 m a.s.l) and Beatenberg (1510 m a.s.l) in the Pre-Alps in Central Switzerland (Heim and Frey 2004). The main characteristics of the study sites, including location, main tree species and soil type, are given in Table 1.

Sampling and measurements

Soil respiration rates were measured with an infrared gas analyzer (PP Systems EGM-4, Hitchin, Hertfordshire, UK) to monitor the change in CO_2 concentration over time in flux chambers (100 mm diameter, 150 mm high) (Zimmermann and Frey 2002). The bottom of the chamber was equipped with a deflector that prevented high fan speeds from creating erroneously high CO_2 flux values (Le Dantec et al. 1999). The chambers were set up on permanent PVC collars (4.5 cm high) (Frey et al. 2006). The respiration collars (10) were randomly located on three 20 × 20 m^2 sampling grids in the vicinity of the weather station at each site, and were inserted in the soil at a depth of 2.5 cm in autumn 2000. Using permanent collars limited soil disturbance and allowed repeated measurements at the same location over time from 2001 until 2005. Soil respiration rates were usually measured between 09:00 and 12:00 am and were repeated monthly, omitting rainy days and days with snow-covered soil. Soil respiration rates in Beatenberg were measured during the snow-free period, usually between May and November. Soil temperature was measured at 5 cm depth from the ground surface at the same time as soil respiration using a penetration probe inserted in the soil in the vicinity of the collar. In addition, it was monitored hourly at two spots in each site at a depth of 5 cm.

Soil solution was collected at eight sampling points in one 43 m × 43 m subplot (Graf Pannatier et al. 2004). It was sampled below the forest floor using zero-tension lysimetry with Plexiglas plates and at a depth of 80 cm in the mineral horizon using

Table 1 Location, climate, stand and soil characteristics of three Swiss intensive monitoring forest plots

	Vordemwald	Schänis	Beatenberg
Location and climate			
Latitude	47°16 N	47°10 N	46°43 N
Longitude	07°53E	09°04E	07°46E
Altitude (m a.s.l.)	480	730	1510
Mean annual temperature (°C)	8.4	7.0	4.7
Annual precipitation (mm)	1106	1965	1454
Stand characteristics			
Main tree species	*Abies alba*	*Fagus sylvatica*	*Picea abies*
Age of main tree species (year)	100	130	200
Canopy height (m)	32	32	23
LAI max	6.1	5.5	3
Number of trees ha^{-1} (> 12 cm at breast height)[a]	500	294	372
Basal area (m^2 ha^{-1})[a]	50.2	49.4	34.1
Mean dbh (cm)[a]	32.2	44.5	32.1
Soil characteristics			
Classification (FAO)	Dystric Planosol	Eutric Cambisol	Haplic Podzol
Humus type	Moder	Mull	Raw humus

[a] Measured during the winter 1999/2000

tension lysimetry (−50 kPa) with ceramic cups (highflow porous ceramic cups, Soil moisture Equipment Corp. Santa Barbara, USA).

Throughfall collectors were systematically distributed in two 43 m × 43 m subplots inside the forest plot. Sixteen funnel-type collectors with a 100 cm^2 opening were used for rain sampling and four buckets with a 707 cm^2 opening for snow collection during the winter (Thimonier et al. 2005).

Both throughfall and soil solution samples were collected every 2 weeks between 2001 and 2005. Upon arrival of the samples in the laboratory, they were pooled and filtered (0.45 µm). The spatial heterogeneity of the chemical composition of throughfall and soil solution was also investigated at least during 6 sampling periods by analysing all samples (16 replicates for throughfall and 8 for soil solution). DOC was determined with high-temperature combustion, followed by IR detection of CO_2 (Shimadzu TOC-V_{CPH}). Measurements of DOC concentrations in throughfall started in 2002. To subtract the dilution or concentration effects of DOC concentrations in the forest floor leachates, DOC concentrations in the forest floor leachates were normalized with Cl concentrations in throughfall. Dissolved inorganic carbon (DIC) in the soil solution at 80 cm of depth was estimated in Schänis by calculating the difference of mole charges between major cations (Ca^{2+}, Mg^{2+}, Na^+, NH_4^+) and anions (SO_4^{2-}, NO_3^-, Cl^-). It was assumed that the deficit in anions represented the carbonate ions and that the main CO_2 species was HCO_3^- (Appelo and Postma 1996), since the pH of the soil solution was 8.0 on average. Cations and anions were measured in the framework of the monitoring programme LWF (Graf Pannatier et al. 2004).

The soil matric potential Ψ was measured manually every two weeks at a depth of 15 cm with 14 tensiometers in Vordemwald and 8 tensiometers in Schänis and in Beatenberg between 2001 and 2005. The measurable range varied from water saturation to −90 kPa.

Litterfall was sampled 1 m above ground with ten circular litterfall traps (diameter of 0.25 m) distributed over both 43 m × 43 m subplots. It was collected at 4-week intervals between 2002 and 2005 throughout the whole year in Vordemwald, while it was collected only during the snow-free period in Schänis and in Beatenberg. To compare data between the years, a common sampling period between April and November was used in Schänis and between May and November in Beatenberg. Litterfall samples were oven-dried (65°C) to a constant weight upon arrival in the laboratory, and then sorted into different fractions (needles or leaves, fruit and twigs). The total litterfall and the different fractions were weighed and the carbon content in the different fractions was analyzed with a CN analyzer NC 2500 (CE Instrument, Italy).

Carbon sequestration in tree stems and branches was estimated as follows: the stem circumference at breast height and the tree height of all trees with a minimum of 12 cm diameter at breast height were measured in winter 1999/2000 and 2004/2005. Permanent circumference bands had been installed on 5–10 trees of the main tree species in each plot in 2001 and were read every year in October following the vegetation season. This resulted in data on 10 silver fir and 10 Norway spruce trees in Vordemwald, 10 common beech, 10 silver fir, 5 sycamore maple and 5 European ash trees in Schänis and 10 Norway spruce trees in Beatenberg. Annual changes in basal area were also estimated (Jolly et al. 2005). The wood volume of the tree stems and branches was computed using formulae developed for the Swiss National Forest Inventory. Volume growth per ha was calculated for the 5-year period, and C sequestration was estimated using mean fresh wood densities for the different tree species and assuming 50% C content per kg wood (Solberg et al. 2009). Proportional changes in basal area were used to proportionally assess the annual C sequestration in the tree stems of each plot.

For each measured parameter, the mean of the replicates and the standard error of the mean (error bars in figures) were calculated. The instrumental errors were neglected, since they were very small compared to the other sources of uncertainty (spatial variability, model error in the next section).

Modelling of the water balance

The water balance model CoupModel (Jansson and Karlberg 2004) was used to model daily matric potential and water fluxes between 2001 and 2005 at the three sites. This is a one-dimensional model simulating water and heat dynamics in soil–plant–atmosphere systems. Input data are meteorological data, soil and plant properties. The daily meteorological data (air temperature, precipitation, relative humidity, global radiation and wind speed) came from the weather stations installed in an open area close to the study sites. Stand characteristics and soil properties were available in Walthert et al. (2003), maximal leaf area index (LAI max) in Thimonier et al. (2010) and are summarized in Table 1. The water retention curve (WRC) for each soil horizon was calculated using van Genuchten parameters determined for different classes of bulk density and texture of forest soils (Teepe et al. 2003). The saturated hydraulic conductivity (Ksat) was derived from pedotransfer functions using soil texture and bulk density (Table 76 in KA5 2005). The van Genuchten parameters and Ksat in the organic layer in Beatenberg was derived from Zuber (2007). The model was calibrated and validated with measured annual interception, daily soil temperature at 5 cm of depth and soil matric potential measured every 14 days. The results from the model were compared to the measurements using the coefficient of determination (r^2), the root mean square error (RMSE) and the mean error (ME). Output data were daily soil matric potential and soil water fluxes below the forest floor and a depth of 80 cm.

Modelling of soil respiration, DOC fluxes and data analysis

An Arrhenius-type equation (e.g. Fang and Moncrieff 2001; Reichstein and Beer 2008) was used to describe the relationship between soil respiration (soil CO_2 efflux in mg C m^{-2} h^{-1}) and soil temperature (T in K) in the topsoil:

$$\text{Soil } CO_2 \text{ efflux} = Ae^{(-E/RT)} \qquad (1)$$

where A is an Arrhenius constant, E is the apparent activation energy (KJ mol^{-1}), and R is the universal gas constant (0.008314 kJ mol^{-1} K^{-1}). We used the soil temperature recorded in the topsoil next to the collars during the CO_2 efflux measurements.

To take into account the combined influence of temperature and soil matric potential (ψ in kPa) on soil respiration, a soil moisture regulator was added to Eq. 1 according to Borken et al. (1999) and Borken et al. (2006):

$$\text{Soil } CO_2 \text{ efflux} = Ae^{(-E/RT)}(1 + b\psi) \qquad (2)$$

where b (kPa^{-1}) is an empirical fitting parameter that describes the influence of the soil matrix potential on CO_2 emissions. This model cannot describe a reduction in CO_2 emissions caused by O_2 limitation in saturated soils.

The A and E parameters of Eq. 1 (T only) were fitted until the root mean square error (RMSE) between the calculated and the mean measured CO_2 efflux was minimum. The residuals were compared to the ψ values. The A, E and b parameters of Eq. 2 (both T and ψ) were also fitted using the same method. The coefficient of determination r^2, the RMSE and the mean error were calculated for both equations and compared. The model was computed with each individual measurement of hourly CO_2 efflux ($n = 10$) to estimate the uncertainty related to the spatial variability and to calculate the standard error of the fitting parameters. The data between 2002 and 2004 were used for model calibration and the years 2001 and 2005 were used for model validation.

The daily CO_2 efflux was calculated at the three sites with Eqs. 1 or 2 depending on the influence of the matric potential on the soil respiration (Davidson et al. 1998; Martin and Bolstad 2005). The soil respiration measurements were assumed to represent the average efflux of the diel cycle since they were made between 9:00 and 12:00 (Davidson et al. 1998). No correction for diel variation was attempted since the temperature-independent component in soil respiration is still unclear (e.g. Widen and Majdi 2001; Liu et al. 2006). Input data were daily mean soil temperatures and daily matric potentials. Daily matric potentials were modelled with CoupModel. The standard error of daily soil CO_2 efflux included the spatial variability and the errors (mean relative RMSE) resulting from the modelling of the daily matric potential and the soil respiration. Annual soil CO_2 effluxes were calculated by adding the daily estimates of soil CO_2 effluxes and the annual uncertainty was the square root of the sum of daily errors. Since soil respiration in Beatenberg was measured only during the snow-free period (April–October), we added 15% to the cumulative CO_2 efflux between April and October to assess the annual soil CO_2 efflux. This estimate is an average of the relative contribution of the snow-covered seasonal flux to the annual flux found in different studies in coniferous and deciduous forests (Schindlbacher et al. 2007; Muhr et al. 2009; Liptzin et al. 2009).

DOC and DIC fluxes through the soil were calculated for each sampling period of 14 days by multiplying the concentrations with the water fluxes. Daily water fluxes were modelled with CoupModel and cumulated over the sampling period of 14 days between 2001 and 2005.

Tukey's HSD (Honestly Significantly Different) tests were performed to test the differences in annual C fluxes (cumulative soil CO_2 efflux, DOC flux, C sequestration in tree growth and C flux in litterfall) between the years (Tukey 1994). Differences were considered significant at $p < 0.05$.

Estimates of annual net ecosystem production

Similar to several studies (Curtis et al. 2002, Ohtsuka et al. 2007; Gough et al. 2008; Kominami et al. 2008), NEP was estimated with biometric measurements and defined as the change in biomass due to growth, decay and herbivory minus heterotrophic respiration and dissolved organic and inorganic carbon:

$$\mathrm{NEP} = \mathrm{L} + \mathrm{D} + \mathrm{H} - \mathrm{R_h} - \mathrm{DOC} - \mathrm{DIC} \qquad (3)$$

where L is the increment in live plant mass, D the increment in dead plant mass (detritus), H the increment lost to herbivory, R_h the heterotrophic respiration, DOC the dissolved organic carbon and DIC the dissolved inorganic carbon.

Estimates of above-ground net primary productivity were based on the annual increments of carbon stored in wood (tree stem, branches) and in the foliage (leaves, flowers, fruit etc.…) between 2001 and 2005. Annual foliage production was considered equal to the annual litterfall in the deciduous stand (Schänis) measured between 2001 and 2005. In the coniferous stands (Beatenberg and Vordemwald), a single value was used for the annual foliage production; it was determined as the average across the 5-year period of observation (2001–2005) of annual litterfall. In Beatenberg, we added the mean annual production of the ground vegetation (*Vaccinium myrtillus*), since it covered a large part (80%) of the stand (Walthert et al. 2003). It was estimated in 2005 by biomass harvest (6×1 m^2), separating the leaves from the woody parts and the mean age of the woody parts was estimated by counting the rings (Hollmann 2005).

Estimate of below-ground net primary productivity was based on allometric equations for woody roots and measurements of fine root biomass and turnover. Based on the studies of Curtis et al. (2002); Ohtsuka et al. (2005, 2009) and Kominami et al. (2008), annual increment in woody roots was estimated as 20% of the above-ground wood production. To estimate the annual production of fine roots (diameter ≤ 2 mm), we multiplied the standing crop with root turnover (Gill and Jackson 2000). Brunner et al. (2002) measured the living fine root mass in the main root zone (20 cm of depth) in Beatenberg. In Vordemwald, Brunner et al. (2004) determined the fine root biomass down to 150 cm of depth. In addition to these studies, we also measured the fine root mass in the topsoil (10 cm of depth) at the three sites. Based on the review of Brunner and Godbold (2007) and the studies of Brunner et al. (2004) and Richter (2007), a mean turnover rate (k) of 1 a^{-1} was applied in Vordemwald and Schänis and of 0.2 a^{-1} in Beatenberg. The carbon allocated to the fine root production was assumed to be 49% of the biomass (Heim and Frey 2004).

Heterotrophic respiration (R_h) was assumed to be 50% of the total soil respiration (Hanson et al. 2000; Curtis et al. 2002). The contribution of R_h to total annual soil respiration has been assumed to be constant during the observation period (2001–2005), as the effect of drought on autotrophic and heterotrophic respiration is still debated (e.g. Borken et al. 2006; Nikolova et al. 2009).

In this study, the loss of leaf carbon to herbivores, nectar and pollen production, volatile organic compounds and carbon transport by vertebrates were assumed to be small at the three study sites and were neglected.

Results

Meteorological conditions and soil matric potential

The summer 2003 was drier and warmer than the other summers of the observation period (2001–2005) at the three sites (Table 2, Fig. 1). The throughfall amount cumulated from June to August was lower in 2003 than in the other years. Both mean daily air and soil temperatures from June to August were warmer (on average +3.2 and +1.6°C, respectively) in 2003 than in the other years. In Vordemwald, the summer 2005 was as dry as the summer 2003 but much cooler

Table 2 Throughfall, mean daily air and soil temperature ± standard error and mean matric potential ± standard error with number of measurement dates in brackets between June and August from 2001 to 2005

		Vordemwald	Schänis	Beatenberg
Throughfall (mm) June–August/annual	2001	300/1043	516/1779	478/1237
	2002	178/932	629/1798	614/1492
	2003	158/583	265/1165	275/772
	2004	217/795	572/1536	442/994
	2005	153/605	674/1476	418/1081
Air temperature (°C) (mean June–August)	2001	15.5 ± 0.5	16.0 ± 0.6	11.6 ± 0.7
	2002	16.6 ± 0.5	16.5 ± 0.6	12.0 ± 0.7
	2003	20.1 ± 0.4	20.1 ± 0.6	15.4 ± 0.6
	2004	16.0 ± 0.5	15.8 ± 0.6	11.4 ± 0.7
	2005	16.0 ± 0.5	15.8 ± 0.7	11.4 ± 0.9
Soil temperature (°C) (mean June–August)	2001	14.6 ± 0.2	14.3 ± 0.3	10.4 ± 0.3
	2002	14.7 ± 0.2	14.6 ± 0.3	10.7 ± 0.3
	2003	16.2 ± 0.2	16.4 ± 0.2	12.3 ± 0.2
	2004	14.3 ± 0.2	13.5 ± 0.2	9.8 ± 0.3
	2005	14.4 ± 0.3	13.7 ± 0.3	10.1 ± 0.3
Matric potential (kPa) (mean June–August)	2001	−7.2 ± 2.0 (6)	−6.6 ± 2.8 (6)	−1.4 ± 0.6 (7)
	2002	−17.1 ± 5.3 (6)	−1.6 ± 0.4 (5)	−1.8 ± 0.4 (7)
	2003	−75.2 ± 8.9 (7)	−41.2 ± 12.9 (6)	−4.8 ± 1.6 (7)
	2004	−16.1 ± 4.6 (7)	−5.6 ± 1.8 (7)	−1.8 ± 0.7 (7)
	2005	−49.4 ± 9.6 (7)	−2.8 ± 0.9 (7)	−1.7 ± 0.7 (6)

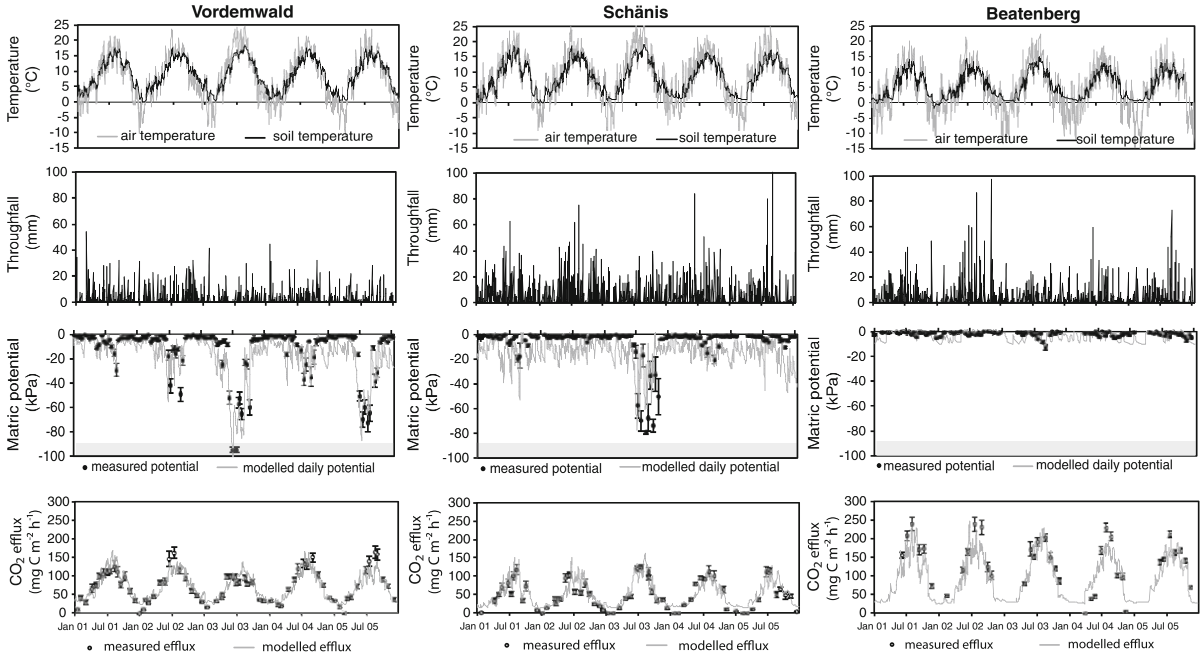

Fig. 1 Daily air and soil temperature (−5 cm soil depth), daily throughfall, measured and modelled soil matric potential (*shaded area*: below measurable range) and mean measured and modelled hourly soil CO_2 efflux in Vordemwald (modelled with Eq. 2), Schänis (modelled with Eq. 1) and Beatenberg (modelled with Eq. 1) between 2001 and 2005. *Error bars* indicate the standard errors of the measurements

(Table 2). While June 2005 was very dry (15 mm throughfall), August 2005 was the wettest (92 mm) and the coolest (14.7 ± 0.3°C) August of the observation period 2001–2005 in Vordemwald.

The measurements of the soil matric potential Ψ at 15 cm depth indicate a trend in drought severity during the summer 2003 between the three sites: the soil was the driest in Vordemwald, less dry in Schänis and remained moist in Beatenberg (Table 2 and Fig. 1). In Vordemwald, the soil was very dry from June to August 2003 with Ψ values ranging between -50 kPa and below the measurable range of -90 kPa. It was also dry during the summer 2005 but to a lesser extent than in 2003. The Ψ values ranged between -11 and -80 kPa from June to August 2005. In Schänis, the topsoil dried up with Ψ reaching -80 kPa but was not as dry as in Vordemwald. The dry period in Schänis lasted about 3 months like in Vordemwald, but started at the beginning of July, 1 month later than in Vordemwald. In Beatenberg, the soil matric potential remained close to -10 kPa during the summer 2003, indicating moist conditions.

CoupModel could reproduce quite well the observed variations in Ψ at the three sites (Table 3, Fig. 1). The dry conditions in summer 2003 and 2005 and the wet years 2001 and 2004 in Vordemwald could be well reproduced. The modelled Ψ values in Schänis reflected the dry summer 2003 and the moist conditions during the rest of the observation period. In Beatenberg, in agreement with the measurements, the modelled Ψ varied between saturation and field capacity between 2001 and 2005.

Hourly soil CO_2 efflux and relation with soil temperature and matric potenial

The measured hourly soil CO_2 efflux showed a clear seasonal pattern at the three sites between 2001 and 2005 (Fig. 1). Similar to the soil temperature, it increased at the beginning of spring, peaked in summertime and decreased in fall. In Vordemwald, the CO_2 efflux in summer 2003 (June–August) remained at a constant rather low level (89 ± 8 mg C m^{-2} h^{-1}, n = 4). These emission rates were smaller than those measured during the other summers (128 ± 19 mg C m^{-2} h^{-1}, n = 14). They were also smaller than the rates measured during the dry summer 2005 (139 ± 25 mg C m^{-2} h^{-1}, n = 3). The soil CO_2 efflux reached a high value (160 mg C m^{-2} h^{-1}) at the end of August 2005 and the beginning of September 2005. In Schänis, the hourly soil CO_2 efflux reached a maximum level of 123 mg C m^{-2} h^{-1} in summer 2003. This was the largest efflux measured during the observation period at this site. In Beatenberg, the hourly soil CO_2 efflux measured during the summer 2003 (182 ± 27 mg C m^{-2} h^{-1}, n = 3) was on average smaller than those measured in 2001, 2002 and 2004 (204 ± 33 mg C m^{-2} h^{-1}, n = 9) and similar to the mean efflux in 2005 (174 ± 35 mg C m^{-2} h^{-1}, n = 3).

The variations in hourly soil CO_2 effluxes were mainly explained by changes in soil temperature. Using Eq. 1, the soil temperature explained 79, 84 and 72% of the variation in CO_2 efflux in Vordemwald, Schänis and Beatenberg, respectively (Table 4). In Vordemwald, the residuals between calculated and observed CO_2 effluxes varied mainly between -20 and $+20$ mg C m^{-2} h^{-1}, except during the summer 2003 where the calculated CO_2 efflux was overestimated (Fig. 2). The residual was close to zero at the beginning of the dry period with $\Psi < -90$ kPa (23 June 2003) but increased 5 days later (27 June 2003) to about 40 mg C m^{-2} h^{-1}, indicating that the soil CO_2 efflux could not be solely explained by the soil temperature. The residual decreased to zero during the first rewetting event. Residuals of about -50 mg C m^{-2} h^{-1} were

Table 3 Statistical performance of the modelling of soil matric potential (ψ) at 15 cm of depth at the three sites including the coefficient of determination (r^2), the root mean squared error (*RMSE*), the mean error of estimate (*ME*), the average of measurements between 2001 and 2005 with standard error in brackets and number of measurements (*n*)

Site	r^2	RMSE (kPa)	M.E. (kPa)	Mean measured (kPa) (standard error)	*n*
Vordemwald	0.84	9.6	−5.5	−13.0 (1.7)	131
Schänis	0.59	13.0	−8.6	−7.0 (1.4)	120
Beatenberg	0.34	2.97	−0.03	−2.0 (0.19)	97

Table 4 Non-linear regression results of soil respiration related to soil temperature only (Eq. 1) and soil temperature and matric potential (Eq. 2) at the three study sites with estimates of parameters *A* (Arrhenius constant), *E* (apparent activation energy), and *b* (moisture regulator) and their standard error in *brackets*

	Calibration: 2002–2004							Validation: 2001 and 2005			
	r^2 (*n*)	Mean error (mg C m^{-2} h^{-1})	RMSE (mg C m^{-2} h^{-1})	RMSE in % of mean flux	*A*	*E* (kJ mol^{-1})	*b* (kPa^{-1})	r^2 (n)	Mean error (mg C m^{-2} h^{-1})	RMSE (mg C m^{-2} h^{-1})	RMSE in % of mean flux
Vordemwald											
Equation 1	0.79* (40)	0.98	19.09	27	2.61×10^{13} (1.04×10^{12})	62.7 (2.2)		0.88* (28)	−1.89	16.88	22
Equation 2	0.89* (40)	0.91	13.83	19	9.51×10^{15} (3.80×10^{14})	76.4 (2.8)	0.0045 (0.0006)	0.88* (28)	3.09	15.54	20
Schänis											
Equation 1	0.84* (38)	1.57	15.72	31	5.40×10^{17} (2.16×10^{16})	86.9 (3.4)		0.90* (23)	10.57	16.04	33
Equation 2	0.85* (38)	1.55	15.53	31	1.82×10^{17} (7.28×10^{15})	84.3 (3.2)	−0.0017 (0.0016)	0.91* (23)	9.22	14.79	31
Beatenberg											
Equation 1	0.72* (24)	2.06	37.01	29	4.00×10^{16} (1.60×10^{15})	78.3 (3.0)		0.83* (13)	−26.03	32.36	21
Equation 2	0.74* (24)	2.20	35.51	28	4.89×10^{17} (1.96×10^{16})	84.0 (3.1)	0.020 (0.013)	0.86* (13)	−23.13	29.55	19

The coefficient of determination r^2 (* $p < 0.001$) with number of observations in brackets (*n*), the mean error of the estimate, the root mean squared error (*RMSE*) of the estimate are given for the calibration period (2002–2004) and for the validation period (2001 and 2005) calculated at two measurement dates (16.7.02 and 24.8.05), indicating that the soil temperature model underestimated the CO_2 efflux at these two dates. In Schänis, the residuals between calculated and observed CO_2 effluxes varied mainly between −20 and +20 mg C m^{-2} h^{-1} from 2001 to 2005, also during the summer 2003. In Beatenberg, the residuals varied between −60 and +60 mg C m^{-2} h^{-1} from 2001 to 2003 and did not show any anomaly during the summer 2003. The residuals were distributed symmetrically with a mean close to zero, also between water saturation and field capacity at −6.3 kPa (shaded area in Fig. 2, left).

When Ψ was included in the regression (Eq. 2), the coefficient of determination r^2 reached 0.89 in Vordemwald with a root mean square error (RMSE) of 14 mg C m^{-2} h^{-1} (Table 4). The *b* coefficient of 0.0045 kPa^{-1} indicates that a decrease in matric potential (increasing drought) reduces the soil CO_2 efflux. In Schänis and Beatenberg, r^2 and RMSE remained similar to those determined with Eq. 1. The parameter *b* in Schänis was negative, meaning that

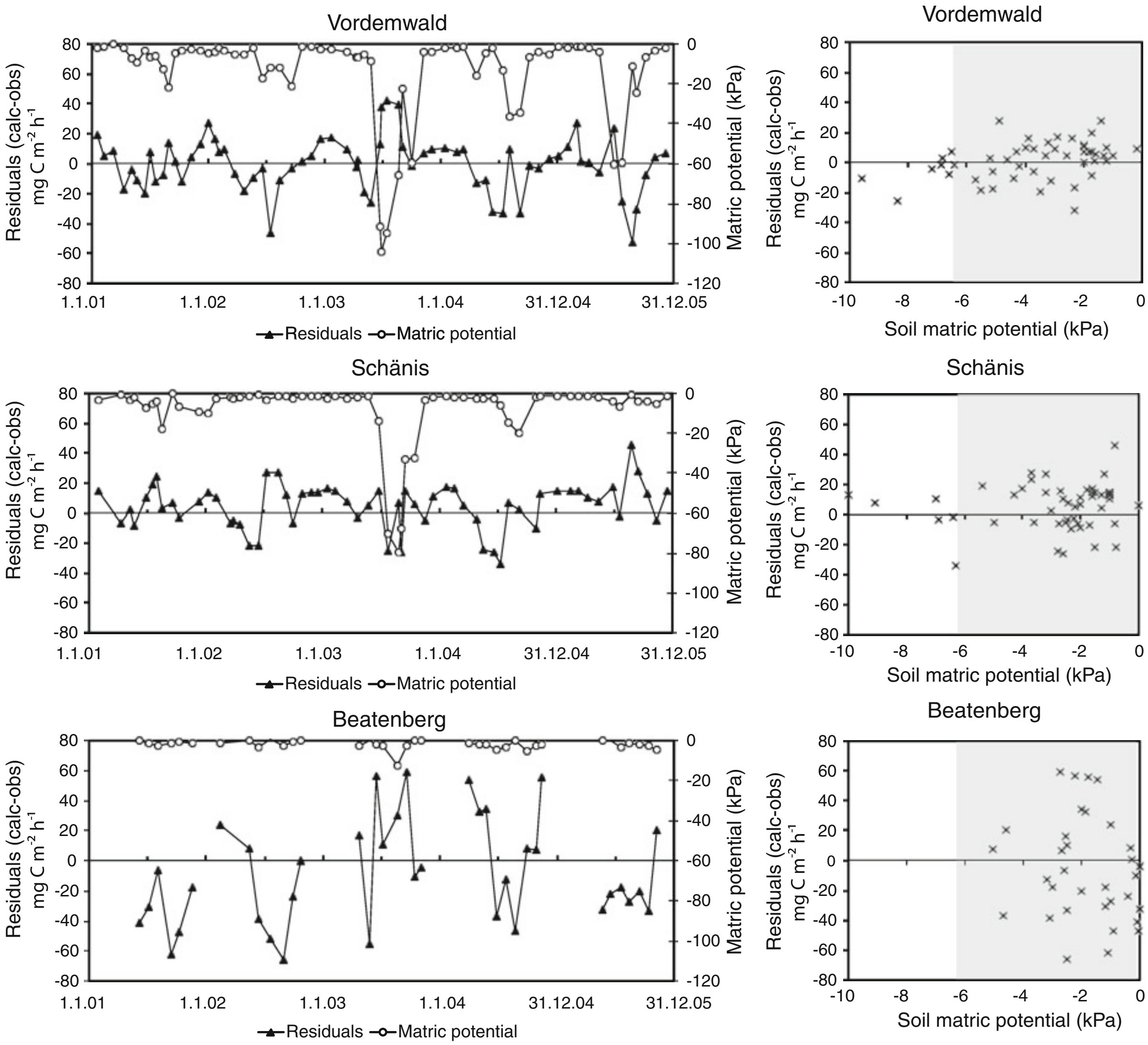

Fig. 2 Matric potential and residuals between soil CO_2 efflux estimated with soil temperature (Eq. 1) and measured soil CO_2 efflux at the three study site. The graph on the right-hand side illustrates the residuals in relation to the matric potential in moist conditions between saturation and field capacity at −6.3 kPa (*shaded* area)

the soil CO_2 efflux increased with the matric potential. However, due to the large uncertainty of the estimate (Table 4), the soil matric potential could be neglected in the regression. In Beatenberg, the b parameter was large (0.020 kPa^{-1}), indicating that soil respiration strongly decreased with decreasing Ψ values (increasing drought). Because of the large uncertainty of the estimate (Table 4), it was concluded that the matric potential did not affect the soil respiration in Beatenberg. The parameters A and E were lower in Vordemwald than those estimated in Schänis and Beatenberg.

Estimates of the cumulative soil CO_2 effluxes

Based on the coefficients presented in Table 4, the daily soil CO_2 efflux was modelled using both soil temperature and modelled soil matric potential data (Eq. 2) in Vordemwald and only soil temperature (Eq. 1) in Beatenberg and Schänis (Fig. 1).

The daily soil CO_2 effluxes cumulated over the summer (June–August) and annual effluxes between 2001 and 2005 are illustrated in Fig. 3. The error bars represent the uncertainty related to the modelling of the matric potential and the soil CO_2 efflux and to the spatial variability of the soil respiration (see method section). Significant differences ($p < 0.05$) between the effluxes (annual or summer) in 2003 and those estimated in the other years were indicated with different letters in Fig. 3.

In Vordemwald, the soil CO_2 efflux cumulated over the hot and dry summer 2003 (232 ± 48 g C m^{-2}) was smaller than the summer efflux in 2001 (280 ± 30 g C m^{-2}), 2002 (259 ± 30 g C m^{-2}) and 2004 (263 ± 29 g C m^{-2}) but slightly larger than the summer efflux in 2005 (217 ± 36 g C m^{-2}). However, the differences in effluxes between 2003 and the other years were not significant ($p < 0.05$). Similarly to the summer efflux, the annual efflux was lower in 2003 (572 ± 68 g C m^{-2}) than in 2001 (665 ± 54 g C m^{-2}), 2002 (638 ± 54 g C m^{-2}), 2004 (619 ± 52 g C m^{-2}) but was similar to the annual efflux of 2005 (573 ± 58 g C m^{-2}). Again the differences were not significant at $p < 0.05$.

In contrast, the soil CO_2 efflux in Schänis was higher during the summer 2003 (260 ± 35 g C m^{-2}) than during the summer 2001 (205 ± 27 g C m^{-2}), 2002 (209 ± 26 g C m^{-2}), 2004 (183 ± 23 g C m^{-2}) and 2005 (185 ± 24 g C m^{-2}) but only the difference with 2004 was significant. Also the annual soil CO_2 efflux was larger in 2003 (490 ± 48 g C m^{-2}) than in 2001 (435 ± 41 g C m^{-2}), 2002 (442 ± 41 g C m^{-2}), 2004 (411 ± 38 g C m^{-2}) and 2005 (431 ± 40 g C m^{-2}) but the difference between 2003 and the other years were not significant.

Similarly to Schänis, the soil CO_2 efflux in Beatenberg was higher during the summer 2003 (387 ± 38 g C m^{-2}) than during the summer 2001 (348 ± 35 g C m^{-2}), 2002 (352 ± 35 g C m^{-2}), 2004 (298 ± 31 g C m^{-2}) and 2005 (303 ± 32 g C m^{-2}). Only the differences with 2004 and 2005 were significant. The annual soil CO_2 efflux was also higher in 2003 (785 ± 75 g C m^{-2}) than in 2001 (738 ± 71 g C m^{-2}), 2002 (731 ± 71 g C m^{-2}), 2004 (679 ± 67 g C m^{-2}) and 2005 (700 ± 69 g C m^{-2}) but the differences between 2003 and the other years

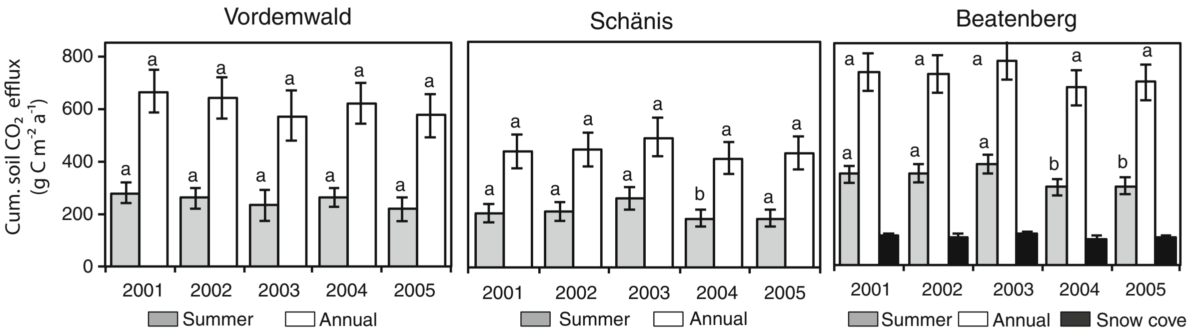

Fig. 3 CO_2 effluxes cumulated over the year (annual), the summer (June–August) and during the snow cover period (only in Beatenberg) estimated with Eq. 2 (function of soil temperature and matric potential) in Vordemwald and Eq. 1 (function of soil temperature) in Schänis and Beatenberg. *Error bars* indicate the standard errors of the estimated effluxes. Significant differences ($p < 0.05$) between the years in annual and summer effluxes are indicated with *different letters*

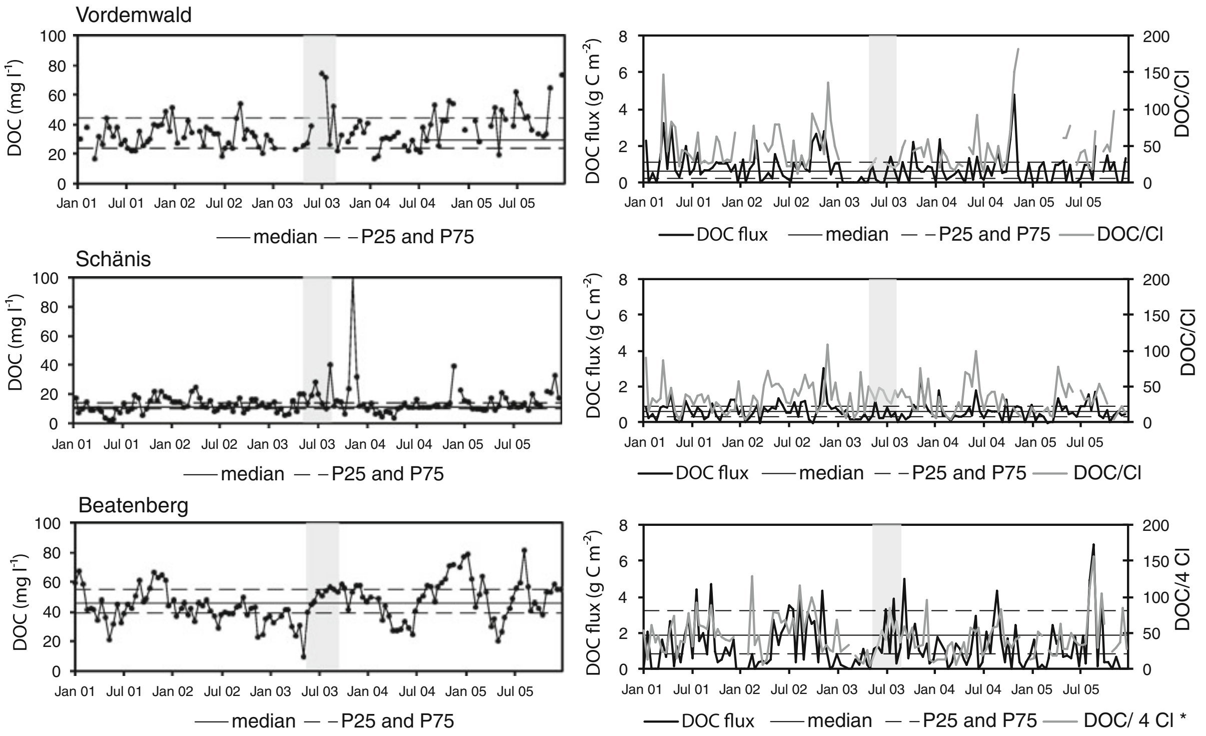

Fig. 4 DOC concentrations, DOC normalized with Cl in throughfall (DOC/Cl) and 14-day DOC-fluxes below the forest floor in Vordemwald, Schänis and Beatenberg (2001–2005). *Solid* and *broken lines* indicate the median and the 25th (P25) and 75th (P75) percentiles of summer DOC concentrations and fluxes (2001–2005). *Shaded area* June–August 2003. DOC/4 Cl in Beatenberg: for scale purposes, the Cl concentrations in throughfall were multiplied by 4 to normalize DOC

were not significant. The estimated soil CO_2 efflux cumulated over the snow-cover season (15% of annual soil emission) varied between 102 and 118 g C m^{-2}, which corresponds to the mean CO_2 efflux found in several coniferous ecosystems during that period (Liptzin et al. 2009).

The standard errors of the cumulated soil CO_2 efflux varied between 10 and 25% of the cumulated effluxes. The largest errors were calculated in 2003 during the dry phases in Vordemwald and Schänis due to the uncertainty related to the soil matric modelling. The spatial variability of the soil CO_2 effluxes contributed on average to 70% of the total error (data not shown).

Dissolved organic carbon from the forest floor

DOC concentrations and fluxes are illustrated in Fig. 4. The median, the 25th and 75th percentiles of summer DOC concentrations and fluxes indicate the range of values usually observed between June and August from 2001 to 2005.

In Vordemwald, no soil solution could be collected in June 2003 because of very low precipitation (3 mm in 4 weeks) and very dry conditions in the soil. After some rain events in July, it was possible to sample soil solution again and the DOC concentrations from the forest floor were found to be much higher (70 mg l^{-1}) than the 75th percentile of DOC concentrations measured during the summers 2001–2005 (44 mg l^{-1}) (Fig. 4). DOC decreased in September and October 2003 to values ranging between 20 and 30 mg l^{-1}. Since the increase in DOC concentrations in summer 2003 might be due to the low soil water content (concentration effect), we normalized the data with a conservative element (Cl in throughfall). DOC/Cl ratios and biweekly DOC fluxes remain at a low level during the summer 2003 and the following months (Fig. 4).

In contrast to Vordemwald, soil solution samples in Schänis could be collected during the whole summer 2003. DOC concentrations were similar to those measured in the other years (Fig. 4). Concentrations peaked in mid-June 2003 (28 mg l^{-1}) and mid-August 2003 (40 mg l^{-1}) and were higher than the normal range of concentrations usually measured during the summer (Fig. 4). Biweekly DOC fluxes and DOC/Cl ratios remained low during that period.

In Beatenberg, soil solution could be collected during the whole summer 2003. DOC concentrations in the Oa horizon were in the range of values usually measured during the summers 2001–2005 (Fig. 4). Biweekly DOC fluxes increased in summer 2003 to the same extent as they did during the previous summers. A clear annual pattern of DOC concentrations and fluxes could be observed between 2001 and 2005, with low values in May during snowmelt, an increase in DOC during the summer until December and a decrease between December and May (Fig. 4).

The annual DOC fluxes from the forest floor varied strongly from year to year at the three sites (Fig. 5). The lowest annual DOC flux of the observation period (2001–2005) was assessed in 2003. In Vordemwald, the annual fluxes varied from 13 to 26 g C m^{-2} a^{-1}, in Schänis from 13 to 20 g C m^{-2} a^{-1} and in Beatenberg from 16 to 44 g C m^{-2} a^{-1} (Fig. 5). The annual fluxes of 2003 represent between 40 and 80% of the highest annual DOC fluxes, usually observed in 2002 at the three plots. In Vordemwald and in Schänis, the annual DOC fluxes from the forest floor were in 2005 as low as those assessed in 2003.

The annual DOC fluxes below the litter layer were much larger than the annual DOC input from throughfall at the three sites (Fig. 5), indicating that DOC was mainly produced and mobilized in the soil organic layer. The differences in DOC input from throughfall between the years were smaller than 4 g C m^{-2} a^{-1}, except in Vordemwald where the DOC input was much higher in 2003. A high input of DOC (11 g C m^{-2}) was measured at the beginning of July 2003 in Vordemwald, just before firs shed a large amount of needles (data not shown).

There was almost no DOC output at a soil depth of 80 cm in Vordemwald and Schänis, suggesting that the DOC leached from the organic layer had been retained in the soil or mineralized. In Beatenberg, the DOC output was large (on average 10 g C m^{-2} a^{-1}) in all years except in 2003 (5 g C m^{-2}).

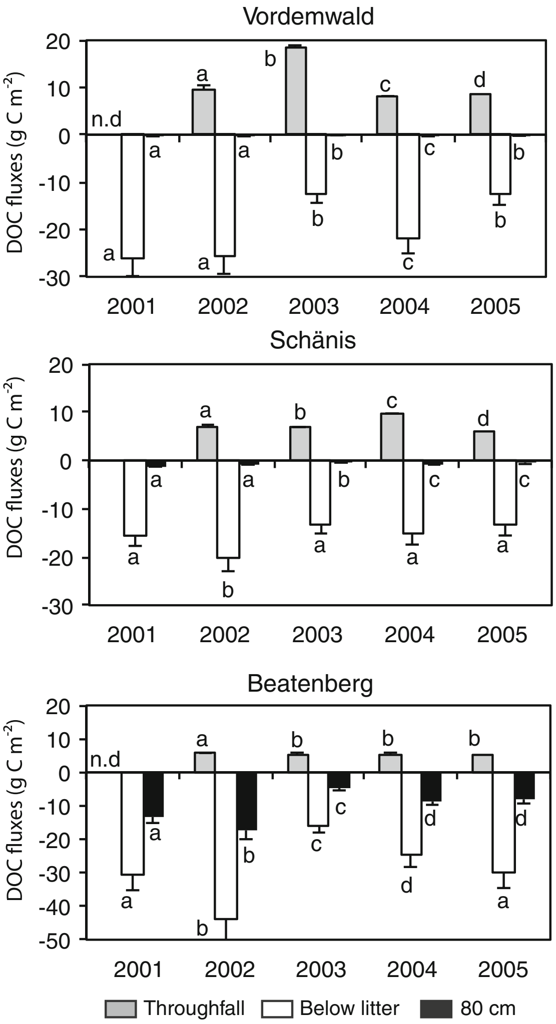

Fig. 5 Annual DOC fluxes in throughfall, soil solution from the forest floor and at a depth of 80 cm in Vordemwald, Schänis, Beatenberg (2001–2005). *Error bars* indicate the standard error of DOC fluxes. Significant differences ($p < 0.05$) between the years are indicated with *different letters*

Tree production

Tree growth in Vordemwald strongly decreased by 32% in 2003 compared to the mean tree growth measured between 2002 and 2005 (Fig. 6a). In Schänis, a reduction of 15% was measured, while in Beatenberg tree growth was 13% larger in 2003 than the mean tree growth 2002–2005. Variations in the C sequestration in stems and branches are illustrated in Fig. 6b. Compared to the mean C sequestration between 2002 and 2005 (387 g C m^{-2}) in Vordemwald, C sequestration decreased to 262 g C m^{-2} in 2003. In Schänis, C sequestration in 2003 (196 g C m^{-2}) was slightly lower than the mean C sequestration between 2002 and 2005 (231 g C m^{-2}). In Beatenberg it increased slightly

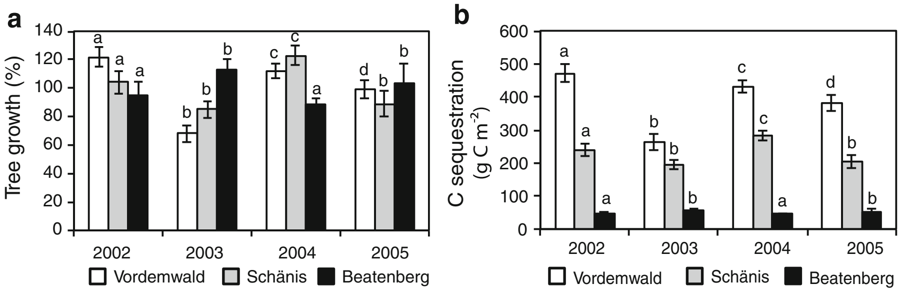

Fig. 6 **a** Tree growth in % of the mean tree growth between 2002 and 2005 (100%). **b** Carbon sequestration in tree stems between 2002 and 2005 in Vordemwald, Schänis and Beatenberg. *Error bars* indicate the standard error of tree growth and C sequestration. Significant differences ($p < 0.05$) between the years are indicated with *different letters*

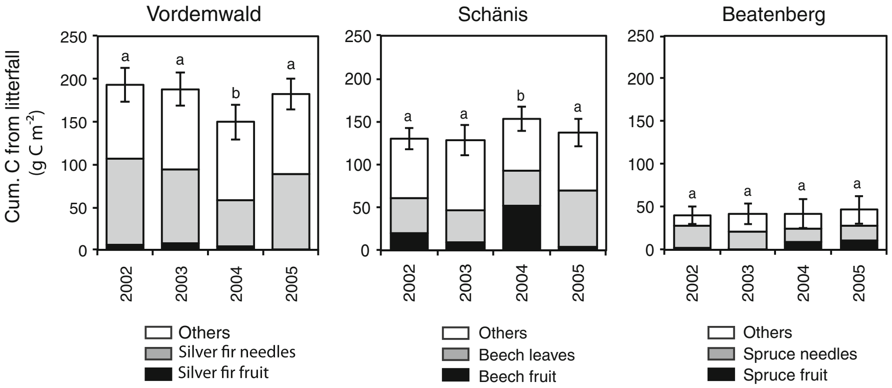

Fig. 7 Cumulated C from litterfall (needles or leaves of the main tree species, fruit of main tree species and total litterfall) cumulated from January to December in Vordemwald, from April to November in Schänis, and from May to November in Beatenberg (2002–2005). *Error bars* indicate the standard error of total litterfall. Significant differences ($p < 0.05$) between the years are indicated with *different letters*

to 58 g C m^{-2} in 2003. The mean C sequestration 2002–2005 was 51 g C m^{-2}.

As illustrated in Fig. 7, the carbon input from annual litterfall in Vordemwald in 2003 (188 g C m^{-2}) was similar to the flux measured in 2002 (193 g C m^{-2}) or in 2005 (182 g C m^{-2}). In contrast it was much lower in 2004 (149 g C m^{-2}). During the dry summers 2003 and 2005, a large amount of needles fell already in July, while they usually fall between July and October (data not shown). In Schänis, the total litterfall cumulated from April to November was quite similar each year (129–137 g C m^{-2}), except for 2004 (153 g C m^{-2}). The large total litterfall during that year was due to a large production of beech fruit (Fig. 7). In Beatenberg, the total litterfall cumulated between May and November was similar from 2002 to 2005 (40 g C m^{-2}), but fruit from Norway spruce was more abundant in 2004 and 2005.

Estimate of annual net ecosystem production

The estimates of the various C budget components between 2002 and 2005 at the three sites are presented in Table 5. The errors estimated for the annual net primary production (NPP) and net ecosystem production (NEP) were derived from the errors calculated for each annual C flux. They include the spatial variability and the uncertainty of the models used to assess the cumulative soil CO$_2$ effluxes.

Estimated annual NPP was on average the largest in Vordemwald (816 ± 36 g C m^{-2} a^{-1}), mainly because of the high tree productivity, intermediate in Schänis (577 ± 28 g C m^{-2} a^{-1}) and very low in the old spruce stand in Beatenberg (264 ± 15 g C m^{-2} a^{-1}). Estimated heterotrophic respiration was on average the highest in Beatenberg

Table 5 Estimate of annual net ecosystem production (*NEP*) between 2002 and 2005 at the three forest sites with standard error of estimates in *brackets* and difference (Δ) between the annual C fluxes in 2003 with the mean of fluxes in 2002, 2004 and 2005

C budget component (g C m^{-2} a^{-1})	2002	2003	2004	2005	Δ
Vordemwald					
(a) Wood (stem + branches)	471 (27)	262 (24)	432 (19)	382 (25)	−166
(b) Foliage	*174 (18)*	*174 (18)*	*174 (18)*	*174 (18)*	*0*
(c) Understory	na	na	na	na	na
(d) Woody roots = 0.2 × (a)	94 (9)	52 (5)	86 (9)	76 (8)	-33
(e) Fine root (biomass: 178 g C m^{-2}; k = 1 a^{-1})	*178 (18)*	*178 (18)*	*178 (18)*	*178 (18)*	*0*
(f) NPP (a + b + c + d + e)	917 (37)	666 (35)	870 (32)	810 (44)	−200
(g) Total soil respiration	638 (54)	572 (68)	619 (52)	573 (58)	−38
(h) Heterotrophic respiration = 0.5 × (g)	319 (27)	286 (34)	310 (26)	287 (29)	−19
(i) DOC + DIC	0.40 (0.06)	0.10 (0.01)	0.30 (0.05)	0.20 (0.02)	−0.2
NEP (f–h–i)	598 (47)	380 (49)	561 (42)	524 (47)	−180
Schänis					
(a) Wood (stem + branches)	239 (18)	196 (14)	283 (15)	205 (21)	−46
(b) Foliage	130 (12)	129 (18)	153 (14)	137 (16)	−11
(c) Understory	na	na	na	na	na
(d) Woody roots = 0.2 × (a)	48 (5)	39 (4)	57 (6)	41 (4)	−9
(e) Fine roots (biomass; 163 g C m^{-2}; k = 1 a^{-1})	*163 (16)*	*163 (16)*	*163 (16)*	*163 (16)*	*0*
(f) NPP (a + b + c + d + e)	580 (27)	527 (28)	656 (26)	546 (31)	−67
(g) Total soil respiration	442 (41)	490 (48)	411 (38)	431 (40)	62
(h) Heterotrophic respiration = 0.5 × (g)	221 (21)	245 (24)	206 (19)	216 (20)	31
(i) DOC + DIC	20.7 (0.9)	6.7 (0.3)	15.0 (0.6)	11.1 (0.6)	−9
NEP (f–h–i)	338 (34)	275 (37)	435 (33)	319 (37)	−89
Beatenberg					
(a) Wood (stem + branches)	48 (5)	58 (4)	45 (2)	53 (7)	9
(b) Foliage	*41 (13)*	*41 (13)*	*41 (13)*	*41 (13)*	*0*
(c) Understory	*97 (10)*	*97 (10)*	*97 (10)*	*97 (10)*	0
(d) Woody roots = 0.2 × (a)	10 (1)	12 (1)	10 (1)	11 (1)	2
(e) Fine roots (biomass: 325 g C m^{-2}; k = 0.2 a^{-1})	*65 (7)*	*65 (7)*	*65 (7)*	*65 (7)*	*0*
(f) NPP (a + b + c + d + e)	261 (18)	273 (18)	257 (18)	267 (19)	11
(g) Total soil respiration	731 (71)	785 (75)	679 (67)	700 (69)	82
(h) Heterotrophic respiration = 0.5 × 5 (g)	366 (36)	393 (38)	340 (34)	350 (35)	41
(i) DOC + DIC	17.5 (2.6)	4.9 (0.7)	8.4 (1.3)	8.1 (1.2)	−6
NEP (f–h–i)	−122 (40)	−125 (42)	−91 (38)	−91 (39)	−23

Italic numbers are constant between 2002 and 2005 since they were estimated only once during the observation period

na not available. The values are assumed to be small

Δ = Annual C fluxes in 2003 minus mean annual C fluxes of 2002, 2004 and 2005

(359 ± 25 g C m^{-2} a^{-1}), intermediate in Vordemwald (284 ± 31 g C m^{-2} a^{-1}) and the lowest in Schänis (208 ± 25 g C m^{-2} a^{-1}). Carbon losses through DOC and DIC were small (maximum of 21 g C m^{-2} a^{-1}) at the three sites compared to heterotrophic respiration.

Estimated annual NEP was on average the largest in Vordemwald (516 ± 46 g C m^{-2} a^{-1}), intermediate in Schänis (342 ± 35 g C m^{-2} a^{-1}) and the lowest in Beatenberg (−107 g ± 40 C m^{-2} a^{-1}).

In Vordemwald, the annual NEP in 2003 (380 ± 49 g C m^{-2}) was about 30% lower (−180 g C m^{-2})

than the average of the annual NEP of 2002, 2004 and 2005 (Table 5). In Schänis, the annual NEP in 2003 (275 ± 37 g C m^{-2}) was 25% smaller (-89 g C m^{-2}) than the average of the NEP in the other years. In Beatenberg, the annual NEP in 2003 (-125 ± 42 g C m^{-2} a^{-1}) was about 20% lower (-23 g C m^{-2}) than the average of the annual NEP of the other years.

Discussion

Effects of the 2003 drought and heat wave on soil carbon dioxide emissions

The soil respiration at the three study sites reacted differently to the heat wave in 2003 depending on the drought intensity. In Vordemwald, the hourly soil CO_2 efflux declined by about 30% during the dry summer 2003 (soil matric potential $\Psi < -90$ kPa), compared to the values measured at the same soil temperatures but at field capacity (e.g. in summer 2004). The modelled daily Ψ in summer 2003 reached -110 kPa (Fig. 1) suggesting that soil respiration might considerably drop at these Ψ values. The less pronounced drought in Schänis with Ψ values until -80 kPa in August 2003 did not lead to a reduction of the soil respiration. In Beatenberg, the soil remained moist during the summer 2003 (-2 kPa $< \Psi < -12$ kPa) and soil respiration reacted mainly to soil temperature. Many studies have shown the influence of the soil water content or the matric potential in the soil surface layer on the soil respiration (e.g. Orchard and Cook 1983; Davidson et al. 1998; Gaumont-Guay et al. 2006). Davidson et al. (1998) found a decline in soil respiration rates only after the matric potential had fallen below -500 kPa in a temperate mixed hardwood forest. Orchard and Cook (1983) found a drop of 50% in heterotrophic respiration between -500 and -1500 kPa but they reported a decline of 10% in heterotrophic respiration already when the matric potential fell below -10 kPa. Gaumont-Guay et al. (2006) also reported that soil respiration was strongly reduced when the matric potential fell below field capacity. Davidson et al. (1998) reported that matric potential is a more appropriate expression of water content than either volumetric or gravimetric water content since it provides an expression of water availability to plants and micro-organisms and it is applicable to all soil textures. However, the measurement of the matric potential is challenging since no single sensor can cover the entire range from water saturation to the wilting point (Durner and Or 2005). Since the soil at the three study sites was usually moist, conventional tensiometers (measurable range until -90 kPa) were used but they were not suited for the summer 2003 in Vordemwald. To overcome this issue, the matric potential was derived from the volumetric soil water content in many studies (e.g. Davidson et al. 1998; Lavigne et al. 2004) but the results depend on the accuracy of the soil water retention curve.

The modelled hourly soil CO_2 efflux reflected the seasonal variations of the measured effluxes at the three sites (Fig. 1, Table 4). The application of both Eqs. 1 and 2 to the data collected in 2001 and 2005 validated the parameters assessed for the period 2002–2004 since the coefficient of determination r^2 increased and the relative root mean square error (RMSE) decreased (Table 4). The model presented in Eq. 2 was selected because it was applied to a drought experiment in a temperate forest in Central Europe (Borken et al. 1999), in similar conditions to those prevailing at our sites. It cannot fit a decrease in CO_2 emissions caused by O_2 limitation in water-saturated soils. However the residuals illustrated in Fig. 2 indicate that the modelled soil CO_2 emissions were not overestimated between water saturation and field capacity. A good coefficient of determination could be reached with Eq. 2 in Vordemwald ($r^2 = 0.89$). In Schänis and in Beatenberg, the uncertainty related to the soil moisture regulator (*b* parameter) was very large and therefore the soil respiration was modelled with the soil temperature only. A multiplicative model using both soil water potential and soil temperature (Davidson et al. 1998; Lavigne et al. 2004) was also applied to our data and provided the same r^2 and RMSE (data not shown). Both types of model indicated a stronger influence of soil temperature in Schänis and Beatenberg (larger *E* parameter) than in Vordemwald.

The comparison between the modelled and measured soil CO_2 efflux (Fig. 1) shows some anomalies. For instance, the model underestimated the high soil CO_2 efflux (160 mg C m^{-2} h^{-1}) in Vordemwald at the end of June 2002 and August 2005. There was no drought stress ($\Psi > -25$ kPa) and the soil temperature could not explain completely these high values

(Fig. 2). The high emission rates in June 2002 could be explained by the rapid increase in soil temperature (from 12 to 17°C in 10 days) and the moist soil conditions (−10 kPa), which likely enhanced the biological activity. The high emission rates at the end of August 2005 were measured after 2 weeks of cool and wet weather. The soil was rewetted from −65 to −11 kPa, which probably caused an increase in soil respiration.

While the hourly soil CO_2 efflux reacted to the dry soil conditions (<−90 kPa) in Vordemwald, the effect of the drought was less clear when considering the cumulative summer and annual soil CO_2 effluxes. Although the cumulative effluxes were lower in 2003 and 2005 than those assessed in the other years, the differences were not significant, because of the uncertainty of the estimates (10–15% of annual efflux). The error includes the spatial variability ($n = 10$) and the uncertainty related the model (mean relative RMSE) of the soil respiration and matric potential. This suggests that the extreme summer 2003 did not have a substantial impact on soil respiration on the seasonal and annual scale. The standard error of the mean annual CO_2 efflux was in the same order of magnitude as the decline caused by drought reported in several studies. For instance, Martin and Bolstad (2005) found a reduction of 15% in annual soil respiration caused by a summer drought of 81 days in a broadleaf forest of northern Wisconsin. Borken et al. (1999) reported that a prolonged summer drought of 172 days followed by a rewetting period of 19 days in a Norway spruce plantation in the German Solling research area did not affect the annual soil respiration rate during the first year of the experiment.

Borken and Matzner (2009b) suggested, based on a review of the present literature, that prolonged summer drought and subsequent wetting will reduce soil C mineralization on the annual scale because relatively short wetting pulses generally cannot compensate for low mineralization rates during the drought periods. Our data suggest that the intensity, the timing and the duration of the summer drought and the soil temperatures before and after the drought have more influence on the annual soil CO_2 effluxes. Our data showed that the combination of drought and cold and wet periods like in summer 2005 decreased the annual CO_2 efflux (572 ± 94 g C m^{-2} a^{-1}) as much as the summer drought in 2003 (573 ± 83 g C m^{-2} a^{-1}). The summer 2005 was marked by a dry period in June/July, followed by a cool and wet August (the coldest August registered during the observation period), resulting in low cumulative CO_2 efflux. The increase in CO_2 efflux at the beginning of September 2005 following the rewetting period was not large enough to compensate the low emission rates of the preceding months. Figure 1 indicates that the soil respiration was slightly underestimated at the beginning of September. However this underestimate approximates 14 g C m^{-2} for September, which would result in an annual soil CO_2 efflux of 587 g C m^{-2} in 2005. This is still similar to the efflux estimated in 2003 (difference not significant at $p < 0.05$).

The heat wave in summer 2003 and the absence of drought stress at the higher sites (Schänis and Beatenberg) increased the cumulative soil CO_2 efflux. Especially the summer efflux in 2003 was significantly higher at both sites (on average +20% in Beatenberg and +30% in Schänis) than those measured in the other years. However the differences between the years strongly diminish when considering the annual effluxes, which illustrates the importance of the soil respiration during the other seasons. In Beatenberg, the soil respiration during the snow-cover season has been estimated to be 15% of the annual soil emission based on Liptzin et al. (2009). However, since the depth and the duration of the snow cover vary from year to year at the site (from 90 to 130 days snow cover yearly during the observation period), the cumulative soil CO_2 efflux likely varied between the winters. The measurements of the soil respiration during the winter would provide more accurate results. Because of the large heterogeneity in snow depth and in snow density at the site, a large number of measurements should be performed.

Effects of the 2003 drought and heat wave on dissolved organic carbon

It has been shown in many studies that DOC concentrations increase following rewetting after dry periods (see e.g. the review of Kalbitz et al. 2000). Rates of decomposition in dry soils tend to be reduced, which might cause microbial products to accumulate. This, together with cell death and lysis, can contribute to high DOC concentrations in the soil leachate after dry periods. Lundquist et al. (1999) also suggested that the increase in DOC following a drought in two agricultural soils might be caused by the release of organic substrates from roots. In Vordemwald and in Schänis, we observed an increase in DOC concentrations in the forest floor in summer 2003 during rewetting. But we interpret this increase as a concentration effect due to the low amount of water in the soil (Fig. 4). Indeed the biweekly DOC fluxes remained low and the DOC/Cl ratios indicated that there was no enrichment in DOC in the soil solution compared to the chloride in throughfall. Kalbitz et al. (2000) reported that water fluxes are greatly responsible for seasonal changes in concentrations of DOC.

Due to the low precipitation amount and water fluxes in 2003, the annual DOC fluxes in 2003 were lower at the three sites than were the fluxes during the wet years like 2001, 2002 or 2004. This is consistent with the overview of Michalzik et al. (2001), who showed that annual fluxes of DOC in forest floor leachates were positively correlated to annual precipitation in temperate forests. Borken et al. (1999) found no increase in annual DOC flux at a soil depth of 10 cm after a prolonged summer drought followed by a short rewetting period in a Norway spruce plantation. Prechtel et al. (2000) and Hentschel et al. (2007) reported that the cumulative DOC fluxes in undisturbed columns containing organic and mineral horizons from a mature Norway spruce stand were not altered by drying and wetting treatments.

Effects of the 2003 drought and heat wave on tree production

The response of tree growth and carbon sequestration in tree stems to the drought and heat wave in 2003 depended strongly on the soil water availability at the site. A marked reduction of 32% in growth and C sequestration (-125 g C m^{-2} compared to the mean 2002–2005) was measured at the site that experienced a pronounced drought (Vordemwald). A slight decline of 15% (-35 g C m^{-2} compared to the mean 2002–2005) was recorded in Schänis, where the drought was less severe than in Vordemwald. In contrast, a slight increase of 13% ($+7$ g C m^{-2} compared to the mean 2002–2005) was observed at the higher altitude site (Beatenberg), where soil water was available and air temperatures were higher than average. These contrasting responses to the heat wave were also observed in other studies in Switzerland (Jolly et al. 2005) and in Europe (Ciais et al. 2005; Garcia-Herrera et al. 2010). Satellite-derived photosynthetic activity across the Alps and in situ forest growth measurements at 15 sites across Switzerland revealed a pattern of growth enhancement at high elevations and growth suppression at low elevations in response to the extreme summer temperatures in 2003 (Jolly et al. 2005). Relative changes in tree growth at the 15 sites were correlated to the soil water availability (Graf Pannatier et al. 2007). Tree growth in 2004 seemed to recover from the drought in Vordemwald and in Schänis with values over 100% of the mean growth between 2002 and 2005 (Fig. 6a).

The direct effect of the drought 2003 on litterfall in Vordemwald was a premature shedding of silver fir needles in July 2003, which is a frequent response of coniferous stands to drought (Bréda et al. 2006). The decrease in the annual litterfall of fir needles in 2004 in Vordemwald is difficult to explain. It does not match the findings of several studies that have analyzed the factors controlling annual variations in litter production. Bille-Hansen and Hansen (2001) showed that litterfall from Norway spruce in seven Level II plots of ICP-Forests in Denmark increased after a severe summer drought. In a study considering litterfall data from 64 sites across Europe, Berg and Meentemeyer (2001) showed that litterfall from conifers (pine, spruce and fir) was strongly related to the annual evapotranspiration. The temperature and the amount of precipitation during the year of needle formation also influence litter production since these factors control the mass and size of the developed needles and thus the later litterfall (Bille-Hansen and Hansen 2001).

In Schänis, the litterfall of beech leaves remained constant during the observation period and did not show any reaction to temperature or soil water availability. In contrast to the rather constant litterfall of beech leaves in Schänis, the litterfall of beech fruit varied during the observation period. It was particularly high in 2004 compared to the other years measured (2001–2005). These observations contrast with previous findings showing that the litterfall of leaves during mast years is lower than the litterfall in years with little or no fructification (e.g. Eichhorn and Paar 2000; Ziegler 2004; Bréda et al. 2006). The high fructification observed in Schänis might be related to the heat wave in 2003. Eichhorn et al. (2005) showed that over 80% of the beech trees in Germany exhibited a heavy mast production in 2004, which was the highest figure since 1990. There is ample evidence that sunny, warm and dry summers, especially in July, favor fruit production in the following spring (Hilton and Packham 2003; Schmidt 2006).

No direct effect of the heat wave in 2003 could be observed on the litterfall production in Beatenberg. Since stem growth increased in 2003 compared to the mean growth between 2002 and 2005, it can be hypothesized that needle production also increased, leading to more needle litterfall when the spruce trees will shed the needles formed in 2003.

Potential impacts of the 2003 drought and heat wave on the annual NEP

The range of annual NEP estimated at the three study sites (from −125 to 598 g C m^{-2} a^{-1}) is comparable to the range of NEP determined by Granier et al. (2007) at 12 eddy covariance sites across Europe (from −102 to 782 C m^{-2} a^{-1}). Similarly to our forest sites, most stands in the study of Granier et al. (2007) were mature or old stands with LAI varying between 2.3 and 7.2. Several studies in temperate deciduous and coniferous forests also reported NEP ranging between 140 and 350 g C m^{-2} a^{-1} (e.g. Ohtsuka et al. 2007; Ohtsuka et al. 2009; Pregitzer and Euskirchen 2004; Jassal et al. 2008). The NEP estimate in Beatenberg was negative but close to zero, suggesting that the stand was a small C source or almost carbon neutral. This could be explained by the advanced age of the stand (about 200 years), since old forests might reach a steady state with respect to carbon cycling or might be C sources (e.g. Melillo et al. 1996; Hyvönen et al. 2007).

Our estimates of annual NEP suggest that the stands in Vordemwald and in Schänis remained a C sink between 2002 and 2005 but that the drought caused a strong decrease in NEP, especially in Vordemwald where the drought was severe. The reduction was mainly due to a decrease in the annual NPP, in particular in Vordemwald where a strong decline in C sequestration in tree stem was measured (Table 5). Indeed, the extreme summer temperatures in 2003 suppressed tree growth at low elevations across the Alps (Jolly et al. 2005). Based on our NEP estimates at the three sites, the decline in the annual NEP in 2003 was related to the drought intensity. The measurement and the modelling of the soil matric potential ψ showed us a trend in drought intensity: the soil was the driest in Vordemwald, less dry in Schänis and remained moist in Beatenberg (Table 2 and Fig. 1). The severe drought in Vordemwald resulted in a strong decrease in NEP, while in Schänis where the drought was less pronounced, the reduction was moderate. Granier et al. (2007) reported that the drought effect on annual NEP over 12 eddy covariance forest sites across Europe was variable from site to site, eight of them showing a lower NEP in 2003 as compared to 2002. The decline between both years varied from 50 to 305 g C m^{-2} at the eight sites, which is in the same range as estimated in Vordemwald (−218 g C m^{-2}) and in Schänis (−63 g C m^{-2}). Granier et al. (2007) also found that the NEP increased in 2003 or remained constant at three sites not affected by the drought. Similarly we found no NEP reduction between 2002 and 2003 in Beatenberg where soil water was easily available during the summer 2003. The changes in NEP between 2003 and the other years were small (< 35 g C m^{-2} a^{-1}) in Beatenberg, suggesting a limited impact of the heat wave on the NEP. The NEP in 2004 seemed to recover from the 2003 drought in Vordemwald and Schänis. The estimated values were much higher than those in 2003, which mainly resulted from enhanced C sequestration in trees in 2004 (Table 5). Tree growth at both sites was likely enhanced because of the moist soil conditions (Table 2).

Large uncertainties are related to the annual NEP estimate (Table 5). The decrease in NEP in 2003 in Vordemwald is 3–4-fold larger than the error, which suggests that the decline is very likely. In Schänis, the decline in NEP is only twice larger than the error, which makes the decrease less certain. In Beatenberg, the errors are in the same range as the annual variations. The errors presented in Table 5 include the spatial variability and the errors of the soil respiration model but do not take into account the uncertainty of the estimates of the fine root production or the fraction of heterotrophic respiration to total soil respiration. We assumed that heterotrophic respiration was 50% of the total soil respiration (e.g. Hanson et al. 2000; Curtis et al. 2002) and that the fraction of heterotrophic respiration did not change between 2002 and 2005. Indeed, the effect of drought on autotrophic and heterotrophic respiration is not clear. Nikolova et al. (2009) found that autotrophic respiration in a beech forest accounted for 45–55% of the total soil respiration independent of the soil water regime, while it was significantly reduced during drought in spruce and amounted to only 25% of the total soil respiration. In contrast, Borken et al. (2006) found that summer drought primarily decreased heterotrophic respiration in the O horizon in a mixed deciduous forest. A sensitivity analysis with different fractions of heterotrophic to total soil respiration (25, 50 and 75%) between 2001 and 2005 and two scenarios reproducing a reduction and an increase in the fraction of heterotrophic respiration (±25%) in 2003 was performed in Vordemwald and in Schänis. All scenarios in Vordemwald resulted in a decline (from -28 to -333 g C m^{-2}) in NEP in 2003 compared to the mean NEP of 2002, 2004 and 2005 (data not shown). In Schänis a reduction of 25% of the heterotrophic fraction in 2003 would result in an increase in the NEP in 2003.

The losses of dissolved C (DOC and DIC) from the soil were generally small and constituted minor fluxes in the C budget. However, in Schänis and Beatenberg, the output of DOC and DIC in wet years like in 2002 represented 5–10% of the estimated heterotrophic respiration, which represents a non-negligible fraction of the C loss from the soil.

Conclusions

The main results of this study can be summarized as follows:

- The intensity of the response of hourly soil respiration to the drought depended on the soil water availability and the soil temperature. Hourly soil respiration during the summer 2003 was suppressed in Vordemwald when the soil matric potential was <-90 kPa. In Schänis where the drought was less severe ($\Psi > -80$ kPa) and in Beatenberg where the soil was moist, hourly soil respiration was not reduced. The cumulative (summer and annual) soil CO_2 effluxes in Vordemwald were lower in 2003 than the values in the other years but the differences were not significant. The heat wave of the summer 2003 in Schänis and Beatenberg resulted in higher cumulative soil CO_2 efflux during the summer 2003 but did not affect significantly the annual efflux.
- DOC concentrations increased during the first rewetting events after the drought in Vordemwald and in Schänis. The high concentrations were mainly due to a concentration effect due to the low soil water content. Because precipitation was lower in 2003 than in the other years of the observation period (2001–2005), the annual DOC fluxes from the forest floor and the DOC output at a depth of 80 cm substantially decreased at the three sites. However, DOC losses generally constituted a minor C flux from the ecosystem at the three sites.
- C sequestration in tree stems responded markedly to the 2003 drought and heat wave. They were strongly reduced in Vordemwald where the drought was the most severe, whereas they increased in Beatenberg where soil water was available and air temperatures were higher than average. Tree growth strongly increased in 2004 in Vordemwald and Schänis, suggesting that the effect of the drought was limited to the year 2003.
- Litterfall data did not show a marked reaction to the drought apart from premature shedding of needles in Vordemwald in 2003 and high fructification in Schänis in 2004.
- Our estimate of annual NEP suggests that the stands in Vordemwald and in Schänis remained a C sink between 2002 and 2005 but that the drought caused a strong decrease in NEP, especially in Vordemwald where the drought was severe. In 2004, the NEP appeared to recover from the 2003 drought at both sites. In Beatenberg, the stand seemed to be almost carbon neutral. The changes in NEP between 2003 and the other years were small, suggesting a limited effect of the heat wave in 2003 in Beatenberg. The NEP in 2003 decreased with increasing drought at the three sites.

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