ECOSYSTEMS

The Carbon Balance of Two Contrasting Mountain Forest Ecosystems in Switzerland: Similar Annual Trends, but Seasonal Differences

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ABSTRACT

Net ecosystem exchange (NEE) of two contrasting mountain forest types in Switzerland was measured by eddy covariance (EC) measurements at a montane mixed forest, the Lägeren forest, over 5 years (2005–2009), and at a subalpine coniferous forest, the Seehornwald in Davos, over 12 years (1997–2009). NEE was validated against annual carbon (C) storage estimates, based on biometric and soil respiration measurements as well as soil C modeling. Three different approaches were used: (1) calculation of net ecosystem production by quantifying C pools and fluxes, (2) assessment of change in wood biomass and soil C storage (ΔC), and (3) application of biomass expansion factors.

Although biometric estimates were sensitive to assumptions made for each method applied, they agreed well with measured NEE. Comparing 5 years of EC measurements available at both sites during 2005 and 2009 revealed that NEE, gross primary production (GPP), and total ecosystem respiration (TER) were larger at the Lägeren forest compared to the Davos forest, whereas soil respiration and soil C sequestration were of similar magnitudes. Both sites showed similar annual trends for NEE, GPP and TER, but different seasonal courses, due to different responses to environmental conditions (temperature, soil moisture, and radiation). Differences in the magnitude as well as in the seasonality of ecosystem CO_2 exchange could mainly be attributed to tree phenology, productivity, and carbon allocation patterns, which are combined effects of tree type (broad-leaved vs. coniferous trees) and site-specific climatic conditions. Flux differences between the two mountain sites highlight the importance of considering the role of altitude in ecological studies and modeling.

Key words: biometric inventory; eddy covariance; mountain forest; NEE; NEP; soil respiration; soil carbon sequestration; modeling.

INTRODUCTION

Mountains cover one quarter of the earth's land surface, of which 25% are forested (UNEP-WCMC 2009). Mountain forests are expected to be more strongly affected by climate change than lowland forests due to their sensitivity to warming (Schroeter and others 2005; IPCC 2007; Metzger and others 2008). In Switzerland, 30% of the land is currently covered by forests (SAEFL/WSL 2005), of which 60% grow on mountain slopes steeper than 22° (Braendli 2010). Nevertheless, the Swiss forests are among the most productive forests in Europe. They sequester about three times more C per hectare than the average European forest and 60% more than the average forest of Central Europe (SAEFL/WSL 2005; Bolliger and others 2008). Currently, 142 Mt C are stored in the whole living tree biomass and 6 Mt C in the dead wood of Swiss forests (Braendli 2010). The carbon stocks of Swiss forest soils have been estimated at 120 Mt C (Liski and others 2002). Thus, the Swiss mountain forests, as they represent two-thirds of the forested area in Switzerland, have obviously a large potential to sequester carbon. On the other hand, they hold huge amounts of C that may be released in case of further increases in extreme weather events (for example, heat waves, drought, flooding) as predicted to occur along with climate change (IPCC 2007).

The dynamics of mountain forests in response to climatic changes are, however, still very poorly understood, as most studies on the forest C cycle so far were conducted in boreal and temperate lowland forests (for example, Valentini and others 2000; Janssens and others 2003; Luyssaert and others 2007). But the often-made comparison between forests growing at high altitudes near the alpine tree line with those growing at high latitudes near the arctic timberline is typically flawed by important differences between environmental conditions at both extremes. Namely, the presence of permafrost at the arctic tree line leads to much shallower rooting depths. In addition, soil infiltration and risk of droughts may differ strongly between arctic and alpine localities, and differences in atmospheric nitrogen inputs due to differences in remoteness may result in differences in annual growth rates. In this study, we compare 5 years of simultaneous eddy covariance (EC) measurements conducted over two mountain forests that are representative for their altitudinal range in Switzerland, the Lägeren forest in the Jura Mountain range at 700 m a.s.l., and the Davos forest in the Eastern Swiss Alps at 1640 m a.s.l. Altitude can serve as a proxy for multiple factors characterizing a forest ecosystem, such as climatic conditions and growing season length, species composition and diversity, and the age of the individual trees. We ask whether productivity and C exchange patterns of forests can also be interpreted as a function of altitude.

The productivity of a terrestrial ecosystem can be assessed by micrometeorological, for example, EC, or by biometric methods. Half-hourly CO_2 fluxes, measured by the EC technique, integrate over an entire ecosystem or a representative fraction of an ecosystem within a certain spatial extent, the so-called flux footprint. The sum of CO_2 fluxes over longer periods is termed net ecosystem exchange (NEE) in the following. If measured over the same time period, the net ecosystem production (NEP) of a terrestrial ecosystem as can be determined from biometric measurements of single trees and soil respiration measurements should equal NEE measured by EC (Chapin and others 2006), when measured over short time scales, in the absence of fire, harvest, deposition and erosion, and under the assumption that loss or import of dissolved organic C in the aquatic phase is small (which is at least the case for forest ecosystems, see Kindler and others 2011).

Net ecosystem exchange, derived from EC, and NEP, derived from biometric measurements, are conceptually identical, but methodologically independent, and therefore also the sources of error are independent (Curtis and others 2002). Hence, the comparison of NEE with NEP helps to validate estimates of forests C storage (Kominami and others 2008; Keith and others 2009; Peichl and others 2010). This is thought to be especially important for EC measurements over non-ideal terrain, where uncertainties in EC budgets are expected to be larger than over flat ground, namely in cases where advection, intermittent turbulence and mesoscale effects cannot be neglected (Aubinet and others 2000; Aubinet 2008).

Furthermore, the assessment of the contribution and dynamics of the C storage of single forest compartments in relation to NEP helps to explain observed differences in C uptake patterns between ecosystems (Ehman and others 2002; Ohtsuka and others 2009). However, NEP and NEE include physiological processes that act on a wide range of time scales. Disagreements between NEP and NEE on shorter time scales (annually) were so far related to C storage and allocation processes (Black and others 2007), which become less prominent as the length of averaging period increases (Gough

and others 2008b). To address the possible role of differences in time scales of the relevant processes we complemented our EC measurements at both forest sites with biometric estimates of NEP, which include a time period of 5 years at the Lägeren and 22 years at the Davos site. Comparing temporal and spatial variability of the two forests' net C uptake, assessed by the two different approaches, we aimed at (1) validating the C exchange estimates by EC of both mountain forests, (2) identifying the annual and seasonal patterns of C exchange of both forests, (3) explaining possible differences in forest net C uptake with differences in the individual forest compartment C pools and fluxes, and (4) relating possible differences in the C uptake of both forests to their different altitudinal ranges.

MATERIALS AND METHODS

Study Sites

The study was carried out at the Lägeren forest (CH-Lae) in the Jura Mountain range and at the Davos Seehornwald (CH-Dav) forest in the Eastern Swiss Alps (Table 1). The Lägeren forest is representative of the montane zone of the Alps according to Ellenberg and Leuschner (2010), which ranges from region-specific 500 and 800 m a.s.l. up to 1,500 and 2,000 m a.s.l. The upper boundary is defined by the distribution limit of closed high forests. The montane forest zone is dominated by mixed broad-leaved and coniferous forests with beech and fir trees. The Davos Seehornwald belongs to the subalpine zone, which extends to the tree line at 2,000–2,100 m a.s.l in this region (1,700–2,400 m a.s.l. in the Swiss Alps). The term subalpine coniferous forest as defined for the Alpine region often corresponds to the internationally used term ''high montane forest''. It is dominated by spruce and pine trees and is characterized by trees in loose formation and the occurrence of krummholz. Continuous EC measurements from both sites are integrated in the global Fluxnet project database, and both sites belong to the Swiss National Air Pollution Monitoring Network (NABEL 2010).

Table 1. Environmental Characteristics of the Study Sites Lägeren and Davos

	Lägeren	Davos
Altitude (m)	682	1,639
Latitude	47°28′40.8″ N	46°48′55.2″ N
Longitude	8°21′55.2″ E	9°51′21.3″ E
Slope (°)	27	
Geographical region	Swiss Jura	Eastern Alps
Altitudinal zone	Montane	Subalpine
Mean annual air temperature (°C)[1]	7.4	3.4
Mean annual precipitation sum (mm)[1]	1000	1000
Vegetation	Mixed deciduous dominated forest	Coniferous forest
Dominant tree species	*Fagus sylvatica* L.	*Picea abies* (L.) Karst.
	Picea abies (L.) Karst	
	Fraxinus excelsior L.	
	Acer pseudoplatanus L.	
Tree age of dominant trees (years)	*F.sylvatica*: 52-155	240 (200–390)
	P.abies: 105-185	
Mean tree height of dominant trees (m)	30.6	25
Max. leaf area index (m^{2}m^{-2})	1.7–5.5	3.9
Understory	*Allium ursinum* L.	*Vaccinium myrtillus* L.
		V. gaultherioides L.
		Sphagnum sp.
pH	4.0–7.5	3.5–4.5
Soil type[2]	Rendzic leptosols	Chromic cambisols
	Haplic cambisols	Rustic podsols
Soil C stock (kg m^{-2}) in 0–20 cm	8.4–9.6[3]	9.2–11[4]

[1]*20 year average (1989–2009) calculated from MeteoSwiss (2010).*
[2]*After IUSS Working Group WRB (2007).*
[3]*Heim and others (2009).*
[4]*Jörg (2008).*

The EC flux tower at the Lägeren study site is located at 682 m a.s.l. on the south facing slope of the Jura Mountain range, which marks the northern boundary of the Swiss Plateau. The forest stand is highly diverse with respect to tree species, diameter classes and tree age. The most abundant tree species are the European beech (*Fagus sylvatica*), ash (*Fraxinus excelsior*), and Norway spruce (*Picea abies*) (Eugster and others 2007). In spring, bear's garlic (*Allium ursinum*) forms a dense understory. The southern part of the footprint area has been sustainably managed according to the forest stewardship council (FSC) since 1998; the northern part is declared as a nature reserve, where tree harvesting was discontinued more than a decade ago. Footprint modeling after Kljun and others (2004) indicates that EC fluxes include both parts of the forest in relatively equal parts.

The Davos forest is located in the Eastern Swiss Alps at a height of 1,639 m a.s.l. The vegetation is highly dominated by Norway spruce trees (*P. abies*) with an only marginal role of larch trees (*Larix decidua*) with less than 1% abundance. The understory consists of dwarf shrubs of *Vaccinium myrtillus* and *V. gaultherioides* and dense moss mats. Site characteristics of both study sites are summarized in Table 1.

Calculation of the Carbon Balance of the Forest Sites

For both study sites forest inventory data within the footprint area of the EC flux tower were available. NEP from biometric and soil respiration measurements, as well as NEE from EC measurements were derived. For the Lägeren forest, two inventories were carried out in 2005 and 2009, and at Davos three inventories were carried out in 1988, 2006, and 2010. At the Lägeren, EC measurements were available from 2005 to 2009 and at Davos from 1997 to 2009.

Calculation of the Carbon Pools and Fluxes for NEP Estimates

The increment of live and dead material was estimated from the change in biomass between two forest inventories. To convert from tree biomass to carbon amounts, a fixed proportion of 50% C per kg of dry biomass was assumed (IPCC 2003).

Tree Volume and Biomass

Tree volume was estimated as a function of diameter at breast height (dbh) at Davos and of dbh, stem diameter at 7 m height and tree height at the Lägeren forest. Species and region-specific formulas were used to convert from dbh to volume of branches and twigs as given in Table 2. To convert from total tree volume into biomass, species specific conversion factors for wood density were applied according to Assmann (1986), except for Norway spruce in Davos. Here, analyses of the wood density of Norway spruce trees at Davos were carried out and yielded a conversion factor of 0.36 (Table 2).

Foliage and Fruit Production

We used dbh dependent functions to model the pools of foliage (Perruchoud and others 1999) and reproductive organs (Thuerig and others 2005). The gained annual estimates of foliage and reproductive litter for the Lägeren site agreed very well with measured litter fall (Ruehr and others 2010) averaged over the years 2006 and 2007 (difference $\pm$ 20 g C m^{-2} y^{-1}).

Coarse and Fine Root Production

Coarse root biomass of trees was estimated as a function of dbh (Table 2). Fine root biomass was calculated as 50% of foliage biomass (de Wit and others 2006). One main uncertainty in the fine root biomass calculation was the assumed turnover time of the fine roots. Very little is known about the turnover time of fine roots and reported values are highly variable, ranging from less than 1 year to decades (for example, Ehman and others 2002; de Wit and others 2006; Gough and others 2008b; Peichl and others 2010). Fine root turnover of the spruce trees at Davos was set to 3.33 years as found for spruce trees in Norway (de Wit and others 2006). At the Lägeren, fine root turnover was estimated from maximum fine root biomass (sequential coring) and annual fine root growth (ingrowth cores) to be 2.53 years (Ruehr, unpublished data). A recent study report that only 20% of the fine roots have a lifetime of less than 1 year, and about 80% have a lifetime of a decade or longer (Gaudinski and others 2010), which agree quite well with the turnover rates used in this study.

Understory Production

Understory litter biomass was estimated from earlier measurements at both study sites (Luescher 1991).

Soil Respiration and its Component Fluxes

Soil respiration (SR) chamber flux measurements were performed within the footprint area at the

Table 2. Methods Used to Estimate NEP

	Component	Lägeren	Davos	References
		Deciduous: species specific model parameters for beech, oak, others; Coniferous: species specific model parameters for spruce, fir, pine, other	Species specific model parameters for spruce	
	d	At 1.3 and 7 m	At 1.3 m	Assmann (1986)
	Height	Measured	–	IPCC (2003)
	WD (kg m^{-3})	Beech: 560, oak: 570, other: 520; Spruce: 390, fir: 370, pine: 400	360	Thuerig and Schmid (2008)
	C (%)	50		Braendli (2010)
	BEF	1.32 / 1.58	1.68	Braendli (2010)
	TO_{cw} (y)	Region-specific mortality, observed between NFI II (1993–1995) and NFI III (2004–2006)		[1]Ruehr, unpublished data, [2]de Wit and others (2006)
	TO_{cr} (y)	215 (90%), 25 (10%)		
	TO_{fr} (y)	$2.53^{[1]}$	$3.33^{[2]}$	
	TO_{nd} (y)	– / Spruce: 7, fir: 10, pine: 3	7	Perruchoud and others (1999)
a	BM_{bole}	$f(dbh, d7, h) * WD + V_{bark}$	$f(dbh)*WD$, Tariff function	Kaufmann (2001)
	BM_{bark}	$f(dbh)*WD$		Altherr and others (1978)
b	BM_{branch}	$f(dbh,\text{ site elevation})*WD$; spruce $= 0$		Kaufmann (2001)
b	BM_{twigs}	$f(dbh,\text{ site elevation})*WD$		Kaufmann (2001)
c	$BM_{foliage}$	$f(BM_{bole})$, litter traps	$f(BM_{bole})*TO_{nd}$, litter traps	Perruchoud and others (1999)
d	BM_{repro}	$f(dbh)$, for dbh > 20 cm		Thuerig and others (2005)
e	BM_{cr}	$f(dbh)*WD^{[1]}$	$f(dbh,\text{ stand age})*WD^2$	[1]Wutzler and others (2008); [2]Wirth and others (2004)
f	BM_{fr}	50% $BM_{foliage} *TO_{fr}$		de Wit and others (2006)
g	BM_{ustory}	Litter traps		Luescher (1991)
	SR	Chamber/modeling		Ruehr and others (2010)
h	Rh	Chambers/modeling		Liski and others (2009), Ruehr and Buchmann (2010)
i	soil C	Yasso07 soil model		Liski and others (2009)
	NPP	$a + b + c + d + e + f + g$		Curtis and others (2002)
1	NEP*	NPP-i		Curtis and others (2002)
2	ΔC	$a + b + e + j$		Curtis and others (2002)
3	NEP_{BM}	$BM_{(t + \Delta t)} - BM_{(t)} + j$		
4	NEP_{BEF}	$NEP_{BEF(t + \Delta t)} - NEP_{BEF(t)} + j$		Braendli (2010)
5	NEE	EC		Aubinet and others (2000), Baldocchi (2008)

Formulas, factors, and references used for the calculation of volume, biomass, and carbon content of several tree components, with d diameter; dbh diameter breast height; WD wood density; BM biomass; TO turnover rate in years; SR soil respiration; Rh heterotrophic soil respiration; BEF biomass expansion factors; cw coarse wood (> 7 cm, incl. coarse roots > 2 cm and bark); cr coarse roots (> 5 mm and < 2 cm); fr fine roots; repro reproductive organs; ustory understory; t point in time of biomass inventory; Δt time period between two inventories.

Lägeren site from 2006 to 2009 (Ruehr and others 2010), and at the Davos site from 2008 to 2009 (for details see Table 3). Because the Lägeren study site is rather heterogeneous, 16 plots were established, accounting for the two main soil types and associated vegetation characteristics. At the Davos study site, which is quite homogeneous, four plots were established in the EC footprint area in 2008 and one additional plot was added in 2009 (=SR$_{manual}$). In addition, each site was equipped with an automated SR chamber (=SR$_{automated}$). Details about experimental set-up, measurement routine and partitioning of root and microbial respiration flux at the Lägeren site are described in Ruehr and others (2010) and Ruehr and Buchmann (2010). At the Davos forest, respiration measurements were performed accordingly. Because root density and stone content were much higher at Davos than at Lägeren, careful soil removal was impossible and a slightly different root exclusion approach was applied for the partitioning of the soil respiration flux. Within 3 m of the SR collars, root exclusions were installed in May 2009 as follows. Around each 50 × 50-cm root exclusion treatment area trenches were dug down to 30 cm depth, thereby cutting all roots. Then, the sides of the root exclusion plots were covered by a plastic foil to prevent roots from growing back into the treatment plot from outside. At the same time, a PVC collar was inserted in the center of

each root exclusion treatment plot for later measurement of microbial respiration.

To estimate seasonal and annual soil CO_2 efflux, we used temperature response functions (Lloyd and Taylor 1994), as described by Ruehr and others (2010), and Ruehr and Buchmann (2010). At Davos, each year was divided into a summer season starting after snow melt (15 May–14 Nov) with valid SR data, and a winter season when the soils were covered with snow (1 Jan–14 May and 15 Nov–31 Dec), during which SR measurements with chambers were impossible. Originally we used temperature dependencies of SR, established during the growing season, to estimate the winter season SR. However, this resulted in unrealistically high fluxes of 0.98 ± 0.40 μmol CO_2 m^{-2} s^{-1} on average (compare with TER on average 1.70 ± 0.03 μmol CO_2 m^{-2} s^{-1}). Therefore, SR rates during the winter season were set to 0.5 μmol CO_2 m^{-2} s^{-1}, which results in 10% contribution of winter soil respiration to annual soil respiration, according to studies of soil respiration fluxes under a closed snow-cover in coniferous mountain forests (see McDowell and others 2000; Monson and others 2006; Schindlbacher and others 2007; Liptzin and others 2009).

Soil C Sequestration

To estimate annual soil C storage, we used the Yasso07 soil C model (Vers. 1.0.2) (Liski and others

Table 3. Instrumentation Specifications and Measurement Details for the EC, Soil Respiration, Forest Inventory, and Meteorological Measurements at the Lägeren and Davos Site

	Lägeren	Davos
Biomass inventory		
Date of inventory	2005, 2009	1988, 2006, 2011
Size (ha)	1.48	0.66
Measured parameters	dbh, diameter at h = 7 m (D$_7$), tree height	dbh, tree height
Soil respiration	(Ruehr and others 2010)	
SR$_{manual}$: IRGA/repetitions/time period	Li-8100/n = 17/2006–2009	Li-8100/n = 5/2008–2009
SR$_{aut}$: IRGA/repetitions/time period	Li-8100/n = 1/2006–2009	Li-8100/n = 1/2008–2009
EC measurements	(Etzold and others 2010)	(Zweifel and others 2010)
Time period	2005–2009	1997–2009
Sonic anemometer	Gill solent HS	Gill solent R2 (1997–2006)
		Gill solent R3-50 (2006–2009)
IRGA	LI-7500	Li-6262 (1997–2005)
		Li 7500 (2005–2009)
Height (m)/height above canopy (m)	47/15	35/10
Data coverage: day/night (%)	62/24	84/61
Vertical CO_2 profile	Li-7000	Li-6262 (2005–2009)
Meteorological data		
Air temperature	Rotronic MP101 A	Rotronic MP400 A
Precipitation	MeteoSwiss/NABEL	MeteoSwiss/NABEL
Net radiation	Kipp and Zonen CNR1	Kipp and Zonen CNR1

2009; Tuomi and others 2009). Yasso07 simulates the stocks of soil organic C, net annual changes in these stocks, and soil microbial respiration. The model only requires basic information on weather, litter quantity and quality (chemical composition). The underlying assumption of Yasso07 is that decomposition depends on litter input type (non-woody litter and woody litter), their chemical composition (that is, waxes, sugars, cellulose, lignin) and on annual weather conditions (air temperature, temperature amplitude and precipitation). Decomposition of woody litter additionally depends on the size of the litter (for example, coarse woody litter, fine woody litter). The effects of annual weather conditions are modeled by adjusting the decomposition rates of the compartments according to their physical and chemical properties to air temperature and precipitation.

To derive woody litter estimates for the soil C model, we multiplied the woody biomass with specific lifespan estimates as given in Table 2. Litter data were linearly interpolated between forest inventory years. Outside the period covered by inventories, the same rate of change was assumed as could be determined from the closest period with data. The chemical composition of leaves, needles,

fine roots and understory litter were derived from Heim and Frey (2004). The chemical compositions of coarse woody litter (average of the chemical composition of stem wood from several tree species) resulted from values given in Liski and others (2009). The chemical composition of fine woody litter was estimated from measurements by Vavrova and others (2009).

We simulated changes in the soil C stock at Lägeren over a 10-year period (2000–2009) and at Davos over a 24-year period (1986–2011) using annual litter input with two diameter classes for wood (2 cm for fine wood, that is, twigs, bark, reproductive organs, coarse roots <2 cm; and 10 cm for coarse wood, that is bole wood and coarse roots >10 cm) and annual air temperature, the amplitude of air temperature and precipitation data. The initial soil C stocks were assumed to be in steady state, calculated from the litter input at the beginning and the mean annual temperature and precipitation over the past 20 years prior to the simulation start. For both study sites, the modeled initial soil C stocks (Lägeren: 9.6 kg m^{-2}, Davos: 9.7 kg m^{-2}) were well within the range of measured soil C stocks (Table 1). The annual soil sequestration rate of both forests was then calcu-
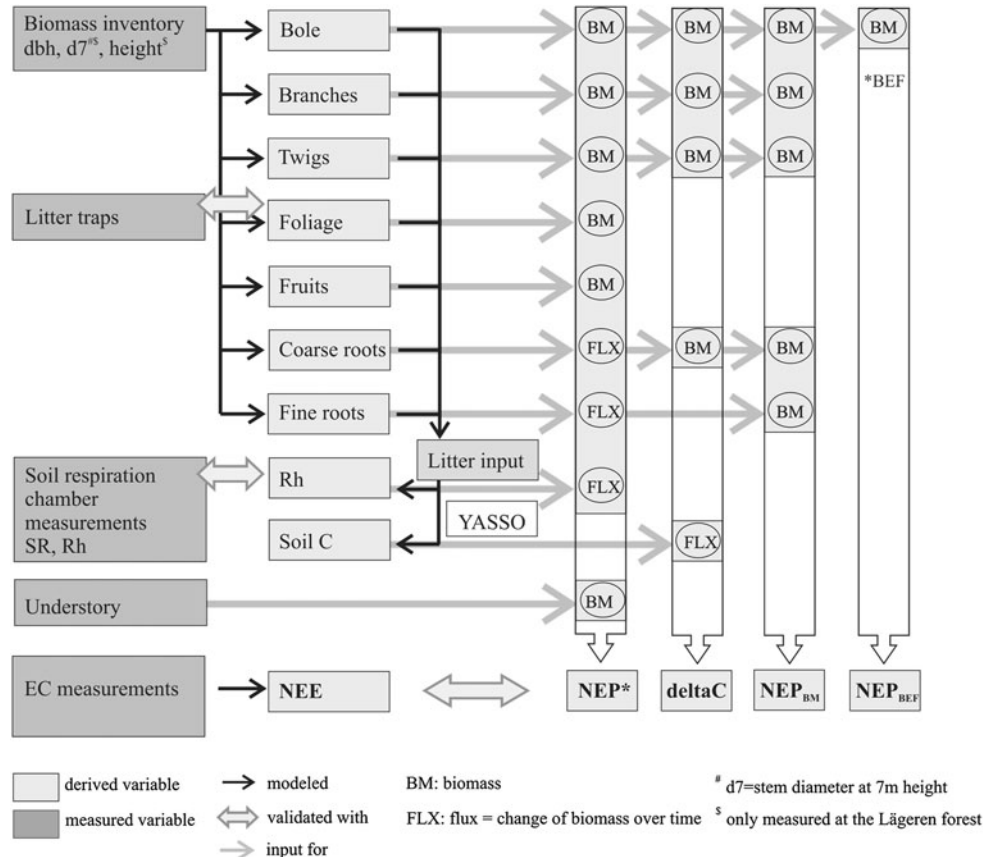

Figure 1. Flowchart for calculation of the different NEP estimates and NEE.

lated as the average of the years covered by the forest inventory.

Net Ecosystem Production (NEP)

NEP was calculated by four different approaches: NEP*, ΔC, NEP_{BM}, and NEP_{BEF} (Figure 1; Table 2).

(1) NEP*

NEP* was assessed by estimating the change of stored C in the biomass over time. This included the net gain of C by tree growth and understory production minus the loss by heterotrophic respiration (Table 2).

(2) ΔC

Assuming the loss from herbivory to be small and the annual increment of foliage and fine roots to be zero, NEP can also be expressed as the annual increment in the woody biomass and soil C storage, and is named ΔC (Curtis and others 2002).

(3) NEP_{BM}

NEP_{BM} is the change of aboveground and below-ground woody and non-woody C pools over time (Table 2).

(4) NEP_{BEF}

Tree biomass is derived from stem biomass, multiplied with biomass expansion factors (BEF). BEF extrapolate from the wood stock biomass either to aboveground or total biomass, and are region and species specific. According to the Swiss NFI, we used BEF for coniferous and broad-leafed trees, that were adapted to specific regions and altitudinal ranges in Switzerland (Table 2). NEP_{BEF} was not used to validate our EC measurements as they are regarded as uncertain themselves, but were included into the comparison as they are applied widely.

Uncertainty of NEP Estimates

The best estimates of uncertainty intervals for C pools and flux components were obtained from the literature and from comparison of modeled with measured data when available. Uncertainty estimates of C pool and flux calculations included uncertainties originating from parameter estimates of the applied models, and the uncertainties of the underlying model assumptions (such as the fine root turnover). Uncertainties for the input data (stem volume) and model parameters for branches, coarse and fine roots were set as compiled from the literature by de Wit and others (2006). This resulted in high uncertainty estimates for the carbon pools, but reduced to narrow uncertainty

intervals for the estimates of the changes in biomass (de Wit and others 2006).

The standard error of the bole volume function used for the Lägeren site is given as 0.3%, and for the tariff function used for the Davos site as 7.8% (Kaufmann 2001). Uncertainties of the annual soil C stock, of the change in the soil C stock and of microbial respiration rates originating from the parameter estimates of the soil C model Yasso07 were estimated from Monte-Carlo simulations by sampling 1,000 times the parameter estimates. Errors are presented as the 95% confidence interval. Foliage uncertainty was assessed by comparing modeled versus measured litter data at the Lägeren site (4.9% difference). The uncertainty of understory biomass was calculated as the SD of the available measurements (Luescher 1991).

The overall uncertainty of the NEP estimates results from the combined uncertainty of all included components by the error accumulation principle.

$$\delta_{NEP} = \sqrt{\sum_{1}^{n} \delta_c^2} \qquad (1)$$

with n = number of forest components included in NEP estimate and c = forest component.

Radial Stem Increment

In addition to the NEP estimates derived from allometric relationships we calculated the annual C uptake by radial stem growth. At Davos, stem radius changes (DR = Difference in Radius over time) of Norway spruce trees were measured with twelve automated point dendrometers (ZB06, Zweifel Consulting, Hombrechtikon, Switzerland) every 10 s and averaged every 30 min (for details see Zweifel and others 2010). At the Lägeren, two automated point dendrometers (Agricultural Electronics Corporation, Tucson, AZ, USA) per tree were mounted on the north and south sides of the stems of four beeches, and two ash, fir and spruce trees. Stem radius changes were measured every 5 min and were averaged every 30 min. Each measurement was corrected for the effect of thermal expansion of the dendrometer using laboratory-derived temperature sensitivity using a linear temperature response function.

The annual C uptake determined by radial stem growth (=DR_C) was calculated as follows. Stem volume increment was derived from DR rates by applying stem volume functions (Zweifel and Haesler 2001, using a correction factor of 1). The rate of change in stem volume was converted into

the DR_C by multiplication with wood density values and then spatially extrapolated using tree species density measurements. Stem wood and phloem were assumed to contribute 85 and 15%, respectively, to the total annual stem volume increment (Zweifel and Eilmann, personal communication).

Micrometeorological Measurements

Continuous measurements of half-hourly turbulent CO_2 exchange were made with EC systems on the uppermost platform of the flux towers. Instrumentation specifications and measurement settings for each site are given in Table 3. Raw fluxes of CO_2 and water vapor were collected digitally at 20 Hz and post-processed by the inhouse software ethflux (compare Mauder and others 2008). As the planar fit method was identified as not suitable at least for the Lägeren site (Goeckede and others 2008), a 2-dimensional coordinate rotation for the wind vector for each averaging period was done: rotation of the coordinate system into the mean streamline and alignment of the vertical wind vector, so that $\overline{w} = 0$. Flux measurements were corrected for high-frequency damping losses of the instruments (Eugster and Senn 1995), and open-path infra-red gas analyzer (IRGA) measurements were additionally corrected for water vapor transfer effects (Webb and others 1980) and sensor self-heating (Burba and others 2008; Jaervi and others 2009). The resulting CO_2 flux data (F_N) were screened for quality by instrumental failure, snow, dew, or ice on the sensor, high window dirtiness of the IRGA sensor ($>60\%$), for out of range fluxes (-50 μmol m^{-2} s^{-1} $> F_N <$ 50 μmol m^{-2} s^{-1}), for $\overline{u'w'} < 0$ m s^{-1} (Eugster and others 2003), and for low friction velocity: Lägeren: $u* < 0.3$ m s^{-1} (Etzold and others 2010), Davos: $u* < 0.2$ m s^{-1} (compare Zweifel and others 2010). We removed negative night-time data and a corresponding amount of positive night-time data by a trimmed mean approach. Advection measurements at both sites indicated that horizontal advection is present at the Lägeren site, but is captured mostly by a $u*$-filter of 0.3 m s^{-1} (Etzold and others 2010). At Davos, the horizontal advection term was negligible as horizontal wind speed is very low. The $u*$-threshold of 0.2 m s^{-1} accounted for most of the observed negative nocturnal fluxes, which were attributed to the occurrence of advection.

For calculating annual C budgets, a complete data set is necessary and gaps of missing flux data have to be replaced by modeled data. Small gaps of CO_2 flux data (<2 h) were replaced by linear interpolation. Larger day-time gaps were modeled with light response curves, by relating day-time F_N to photosynthetic photon flux density (PPFD) within a moving window of variable size depending on available data points ($n = 50$) using a logistic sigmoid function according to Moffat (2010). Larger night-time gaps were modeled by temperature response functions, relating night-time F_N within a moving window of variable size depending on available data points ($n = 50$) to air temperature (Lloyd and Taylor 1994). For periods where no temperature response function could be established, as was the case for example during winter periods with temperatures below 0°C, we used a running mean approach. At the Lägeren site we observed high positive and negative fluxes (±15 μmol m^{-2} s^{-1}) during the dormant period at very low temperatures, which we interpreted as non-biotic fluxes, possibly related to weathering or dissolving processes of calcareous soil substances (compare Kowalski and others 2008; Serrano-Ortiz and others 2010) and the occurrence of fog and a stable inversion layer. We kept these data in the data set but excluded them from the gap-filling algorithm, which was used to establish light and temperature response functions. Ecosystem respiration (TER) was derived from the temperature dependencies established during the night (Reichstein and others 2005) and extrapolated to day-time conditions within a moving window of two weeks length. Gross primary production (GPP) was defined as GPP = NEE − TER.

Uncertainty of NEE

Uncertainty of NEE was computed as the random uncertainty of EC flux measurements and the uncertainty introduced by gap-filling by combining both terms in quadrature. The random uncertainty of EC measurements was calculated by the successive day approach described in Hollinger and Richardson (2005). We found the probability distribution of the random flux errors best described by the double-exponential distribution as in Hollinger and Richardson (2005). The resulting random error was on average 9.4% for the Davos data (range 3–17%) and on average 2.8% (range 1.7–3.4%) for the Lägeren data.

To assess the error caused by gap-filling we randomly produced 20% artificial gaps in each yearly time period and compared the resulted gap-filled data with the original data. We repeated this procedure 50 times and calculated the gap-filling uncertainty from the model residuals according to Aurela and others (2002). For Davos, the mean uncertainties in relation to the mean measured flux were 2.2% for day-time gaps and 9% for night-time
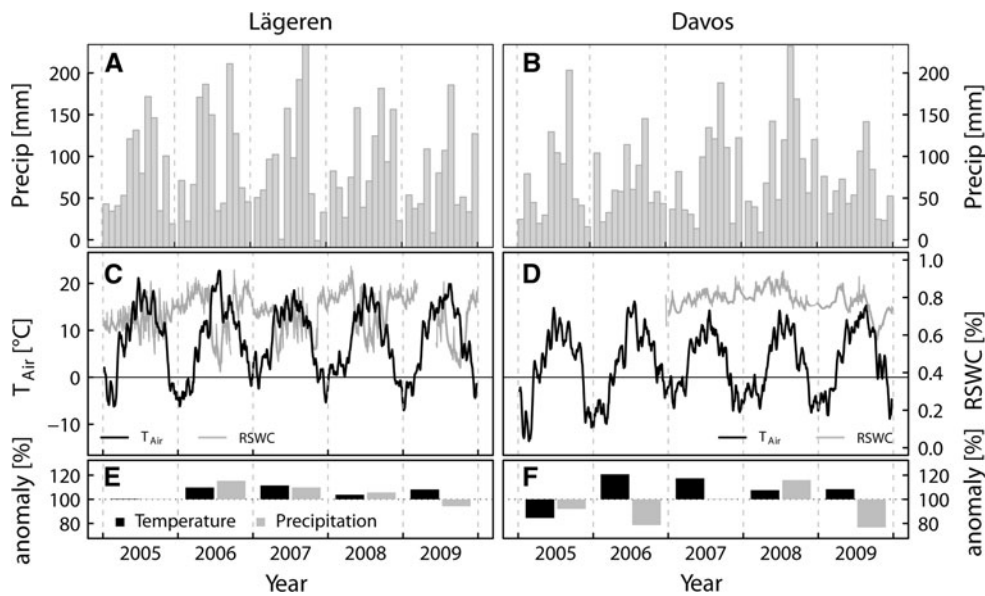
Figure 2. Climatic conditions at the Lägeren (**A**, **C**, **E**) and the Davos site (**B**, **D**, **F**) during the observation period from 2005 to 2009: Monthly precipitation sums (**A**, **B**), monthly mean air temperature and relative soil moisture content (RSWC) (**C**, **D**), and percentage anomalies of mean annual temperature (*black bars*) and mean annual precipitation sum (*gray bars*) related to the 20-year mean values (**E**, **F**).

gaps, which amounted on a yearly basis on average to 27% (range 11–50%) and ± 28 g C m^{-2} y^{-1} depending on the gap-frequency and flux magnitude. For the Lägeren, the mean uncertainties were 0.92% for day-time gaps and 1.5% for night-time gaps. Applied to all gap-filled periods, these uncertainties resulted in 6% (range 4.1–7.8%) and ± 26 g C m^{-2} y^{-1} per year. For the annual sums of TER and GPP we applied a maximum error of ± 25% (Desai and others 2008).

Meteorological Data

Standard meteorological variables, such as air temperature and radiation components were measured on the uppermost platform of the flux tower (Table 3). Additional meteorological data were obtained from the National Air Pollution Monitoring Network NABEL (precipitation), the Swiss Federal Office of Meteorology and Climatology MeteoSwiss (long-term meteorological data).

RESULTS

The Lägeren and Davos forests are two contrasting mountain forest types, representative for their altitudinal range in Switzerland. The following differences between the Lägeren and Davos forests are considered the most important: (1) much cooler climate at Davos site compared to Lägeren, (2) high species diversity at Lägeren compared to the predominance of spruce trees at Davos, and (3) the age of the trees. At Davos most of the trees are much older than those at the Lägeren site (see Table 1).

Climate Conditions

The mean daily course of temperatures for the Davos and the Lägeren sites were nearly identical but mean monthly temperature values at Lägeren were almost constantly 5°C higher than at Davos (Figure 2, linear regression of mean monthly temperatures: $R^2 = 0.92$, $P < 0.01$). In contrast, annual sums as well as seasonal patterns of precipitation differed between sites (linear regression of monthly precipitation sums: $R^2 = 0.32$, $P < 0.01$), with a more distinct seasonality of precipitation at the Davos forest (Figure 2A, B). For both sites mean annual temperatures in the years 2006–2009 were above the long-term (20 years: 1989–2009) average, whereas the year 2005 was comparably cool, especially at the Davos site. Although the long-term annual precipitation sums were in the same range (Table 1), annual precipitation patterns differed. At the Lägeren site, the observation period was wetter compared to the long-term average. At the Davos forest, only the year 2008 was wetter than the long-term average, the years 2006 and 2009 received less than 80% of the long-term mean annual precipitation. Whereas the Lägeren forest received the largest amount of precipitation in 2006 and only the summer months were dry, the Davos forest experienced one of the driest and also warmest years within the study period.

The C Balance of the Two Forest Sites

EC measurements, as well as biometric estimates indicate that both sites were significant C sinks (Figure 3; Tables 4, 5). Hereby, annual sums of
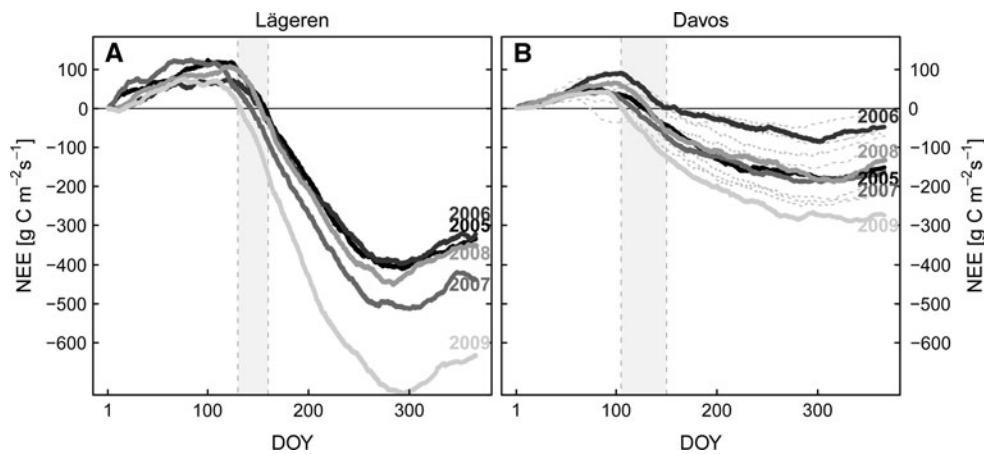
Figure 3. Cumulative NEE for **A** the Lägeren and **B** the Davos forest for the years 2005–2009. For the Davos site, NEE of previous measured years (1997–2004) is shown by *gray dotted lines*. *Gray areas* indicate the range of DOY_0, the compensation point when the net C uptake balances the net C losses that accumulated since the beginning of the calendar year.

Table 4. Mean Annual C Budgets (NEE, GPP, TER), Derived from EC, Soil SR and Rh, Derived from Soil Respiration Chamber Measurements, Soil C Derived from Soil C Modeling (Yasso07), and Carbon Uptake by Radial Stem Increment (DR_C) for the Lägeren and the Davos Forest

	Lägeren	Timespan	Davos	Timespan
NEE (Mg C ha^{-1} y^{-1})	−4.15 (±0.56)	2005–2009	−1.53 (±0.54)	2005–2009
GPP (Mg C ha^{-1} y^{-1})	−18.30 (±4.48)	2005–2009	−10.38 (±2.54)	2005–2009
TER (Mg C ha^{-1} y^{-1})	+13.83 (±3.38)	2005–2009	+8.85 (±2.16)	2005–2009
SR (Mg C ha^{-1} y^{-1})	+8.90 (±0.46)	2006–2009	+9.18 (±0.83)	2008–2009
Rh (Mg C ha^{-1} y^{-1})	+5.07 (±0.48)	2007, 2008	+4.23 (±0.07)	2008–2009
Soil C (Mg C ha^{-1} y^{-1})	−0.23 (±0.10)	2005–2009	−0.50 (±0.07)	2005–2009
DR_C (Mg C ha^{-1} y^{-1})	−3.75(± 1.13)	2006–2007	−1.15 (± 0.35)	2006–2007

NPP, NEP, NEE, GPP, TER, Rh, as well as DR_C were higher at Lägeren compared to Davos during the years 2005–2009 (Table 4). Annual soil respiration was, however, of the same order of magnitude at both sites and soil C sequestration rates were higher at the Davos site.

The overall aboveground C pool (derived from allometric estimates) of the Lägeren forest (178.2 Mg C ha^{-1}) was larger than at Davos (105.3 Mg C ha^{-1}), but with reversed results in the belowground pools (Table 5). As a corollary, the aboveground C turnover at Lägeren (6.11 Mg C ha^{-1} y^{-1}) was more than double the rate observed at Davos (2.85–3.07 Mg C ha^{-1} y^{-1}), whereas the belowground C turnover was higher at Davos. A higher NPP of the Lägeren forest, but an almost identical respiration flux at the Lägeren and Davos sites then led to higher net C uptake capacity at Lägeren compared to Davos. We did not expect to find similar annual SR rates at both study sites as the Davos forest is subject to a much cooler climate than the Lägeren forest. But this finding can be explained by the higher temperature sensitivity of SR at the Davos forest: SR rates at Davos (SR$_{automated}$: R_{ref} = 4.19, SR$_{manual}$: R_{ref} = 4.38) doubled those

at the Lägeren forest (SR$_{automated}$: R_{ref} = 1.91, SR$_{manual}$: R_{ref} = 2.22) for a temperature range between 5 and 10°C for 2008 and 2009 (Figure 4).

Biometric versus Meteorological Estimates of Forests' C Storage

At both sites, NEE derived from EC measurements agreed with NEP estimates (Table 5). In general, NEP* was the lowest of all NEP estimates at both sites. At the Lägeren site, C uptake derived from NEE (4.35 Mg C ha^{-1} y^{-1}) was higher than calculated NEP* (3.07 Mg C ha^{-1} y^{-1}), but was very close to estimates of ΔC (4.29 Mg C ha^{-1} y^{-1}) and NEP$_{BM}$ (4.34 Mg C ha^{-1} y^{-1}). NEP$_{BEF}$ (5.14 Mg C ha^{-1} y^{-1}) was higher than all other estimates. At the Davos site, NEP estimates of the two time periods investigated were in the same range (differences: −0.14 to 0.61 Mg C ha^{-1} y^{-1}). All NEP estimates indicate a slightly higher yearly net uptake during the years 2006–2010, compared to the time period 1988–2006, except NEP$_{BEF}$. NEE measurements were available from 1997 to 2009. For the time period from 1997 to 2006 EC measurements yielded 1.17 Mg C ha^{-1} y^{-1} carbon uptake, which is lower

Table 5. Mean Pools (in Mg C ha⁻¹) and Fluxes in (Mg C ha⁻¹ y⁻¹) of the Major Components of NPP and Net Ecosystem C Storage for the Two Forest Sites in Switzerland

	Lägeren		Davos		
	Mean C pool	Mean yearly C flux 2006–2009	Mean C pool	Mean yearly C flux 1988–2006	Mean yearly C flux 2006–2010
Trunk	137.5 (±2.1)	2.40 (±0.05)	81.5 (±6.3)	1.08 (±0.02)	0.92 (±0.04)
Branches + twigs	36.5 (±5.1)	1.29 (±0.03)	15.4 (±2.0)	0.16 (±0.01)	0.15 (±0.01)
Foliage + fruits	4.2 (±0.2)	2.42 (±0.02)	8.4 (±0.40)	1.61 (±0.02)	1.99 (±0.04)
Aboveground	178.2 (±23.3)	6.11 (±0.19)	105.3 (±16.5)	2.85 (±0.89)	3.07 (±0.19)
Understory		*0.40 (0.33–0.43)*		*0.24 (0.22–0.25)*	*0.24 (0.22–0.25)*
Woody root	34.2 (±7.9)	0.38 (±0.01)	45.3 (±10.0)	0.51 (±0.01)	0.49 (±0.02)
Fine root	1.8 (1.6–2.7)	0.72 (0.72–0.73)	3.87 (3.5–5.8)	1.07 (1.07–1.09)	1.33 (1.33–1.36)
Belowground	36.0 (26.9–55.8)	1.10 (±0.02)	49.17 (37.5–75.5)	1.58 (1.55–1.65)	1.82 (1.75–1.90)
NPP		7.63 (±0.29)		4.67 (4.50–5.04)	5.13 (4.75–5.52)
Rh (modeled)		4.55 (±0.27)		3.96 (±0.14)	4.32 (±0.15)
Soil C		0.22 (±0.17)		0.13 (±0.08)	0.50 (±0.07)
NEP*		3.07 (2.96–3.19)		0.71 (0.62–0.81)	0.90 (0.78–1.02)
ΔC		4.29 (4.14–4.44)		1.90 (1.65–2.16)	2.06 (1.78–2.62)
NEP$_{BM}$		4.34 (4.18–4.50)		1.78 (1.54–2.02)	2.15 (1.86–2.74)
NEP$_{BEF}$		5.14 (5.03–5.25)		1.69 (1.65–1.73)[1]	1.55 (1.52–1.62)
NEE		−4.35 (±0.56)		−1.17 (±0.61)[1]	−1.53 (±0.54)[2]

[1]1997–2005.

[2]2006–2009.

Annual net C storage was calculated (1) as NEP by allometric functions (NEP*), (2) as the change in C pool size (ΔC), (3) as difference between the C pools of 2009 and 2006 (NEP$_{BM}$), (4) as NEP$_{BEF}$, and (5) as NEE from EC measurements. Cursive letters indicate constant values. The error estimates are maximum error margins for NPP components, 95% confidence intervals for SR, Rh and soil C, and cumulative gap-filling and random error for NEE estimates. In case of symmetric errors, we specified the estimated uncertainty range, in case of asymmetric errors the upper and lower margins.
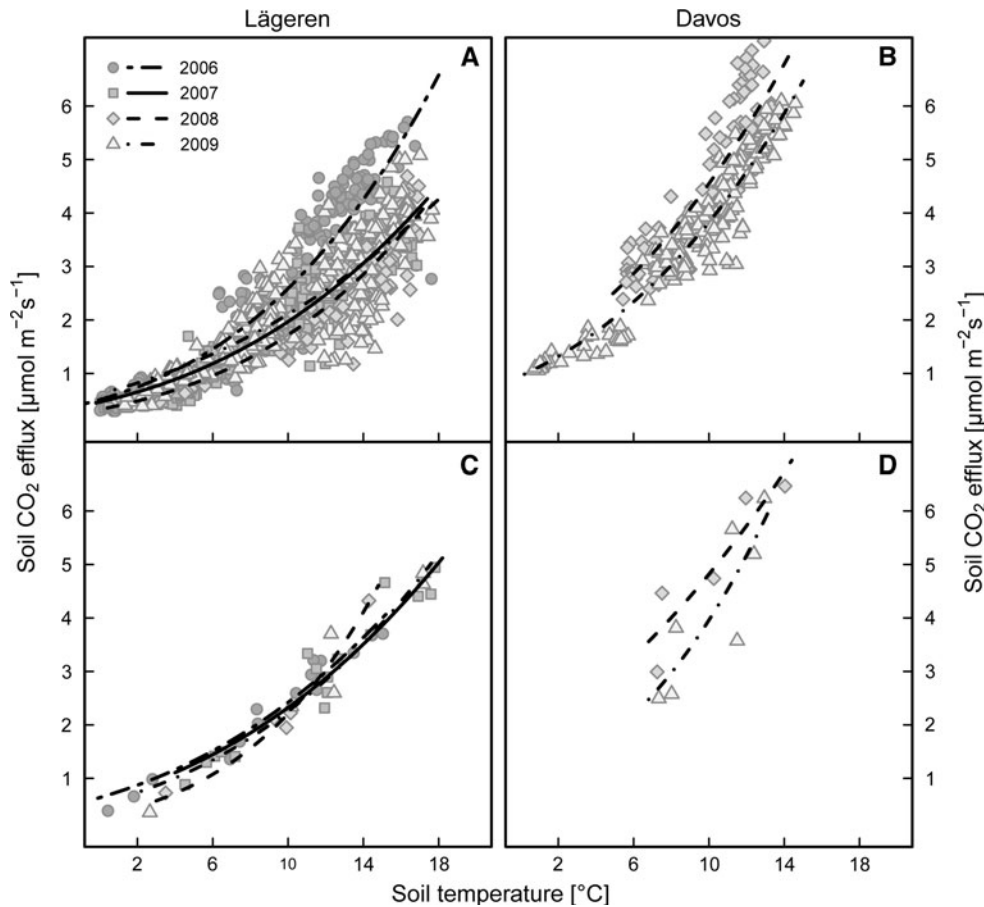
Figure 4. Temperature dependency of soil respiration at the Lägeren (**A**, **C**) and Davos (**B**, **D**) forests. Shown are daily averages for $SR_{automated}$ and campaign averages for SR_{manual}, as well as fitted lines of the Lloyd–Taylor function for each study year. Please note that SR data in 2006 are only given for non-water-limiting periods (volumetric soil moisture > 15%).

than ΔC, NEP_{BM}, and NEP_{BEF}. Recall that these estimates covered a different time period than the EC measurements and hence may not exactly reflect the same growth conditions. NEE from 2006 to 2009 (-1.53 Mg C ha^{-1} y^{-1}) compared well to NEP (0.9–2.15 Mg C ha^{-1} y^{-1}) for the time period from 2006 to 2010.

Temporal Patterns of C Uptake

During 2005–2009, NEE of the Lägeren forest ranged from -366 to -662 g C m^{-2} y^{-1} (mean: -415 g C m^{-2} y^{-1}), and in the Davos forest from -47 to -274 g C m^{-2} y^{-1} (mean: -154 g C m^{-2} y^{-1}). Overall, the inter-annual variability (coefficient of variation, CoV, defined as the variance normalized by the mean) of NEE at the Davos forest was higher than at the Lägeren (CoV$_{Davos}$ = 0.53; CoV$_{Lägeren}$ = 0.31). Nevertheless, both forests showed similar annual trends of net CO$_2$ uptake with lowest rates for the year 2006, high uptake in 2007, and an extraordinary high net uptake in 2009 (Figure 3). Although the annual sums of NEE from both forests showed similar temporal patterns (lin-

ear regression model NEE$_{Lägeren}$ against NEE$_{Davos}$: adj. R^2 of 0.71, $P = 0.05$), monthly sums were only weakly related (adj. $R^2 = 0.48$, $P < 0.01$) due to different seasonal patterns: In general, the curvature of cumulated NEE (NEE$_{Cum}$) was much flatter at the Davos site compared to the Lägeren site, both during winter and summer (Figure 3). The winter respiration compensation point DOY$_0$ (=NEE$_{Cum}$ crosses the zero-line) occurred nearly 1 month earlier at the Davos forest (mean: DOY 128) than at the Lägeren (mean: DOY 147). Thus, lagging the Davos data by 1 month, cross correlation analysis revealed a close correlation between monthly sums of both forests ($R = 0.80$, adj. $R^2 = 0.67$, $P < 0.01$), and net sums integrating over 2 months were also closely related (adj. $R^2 = 0.70$, $P < 0.01$).

For both forest sites, DOY$_0$ had a high explanatory value for the resulting annual net uptake (Davos: adj. $R^2 = 0.71$, $P < 0.01$ for 1997–2009 and $R^2 = 0.87$, $P = 0.01$ for 2005–2009; Lägeren: adj. $R^2 = 0.92$, $P < 0.01$, for 2005–2009). The later start of the photosynthetic activity of the Lägeren trees was compensated during summer, when the slope of NEE$_{Cum}$ was much steeper at Lägeren
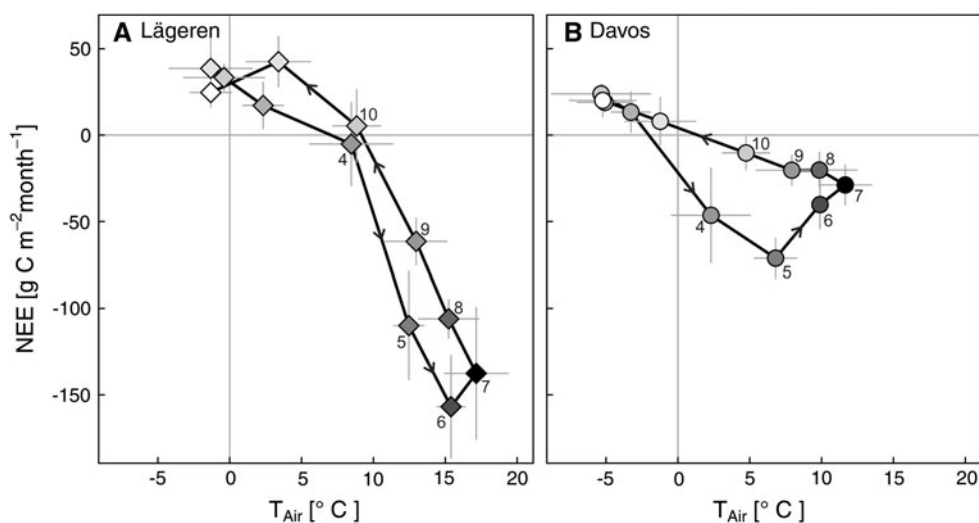
Figure 5. Mean monthly sums of NEE in relation to mean monthly air temperature. Values are means ± SE. *Numbers* indicate the respective month of the year.

(mean: -3.7 g C m^{-2} day^{-1}) compared to Davos (mean: -1.1 g C m^{-2} day^{-1}). In general, at Davos the highest monthly net uptake was already achieved during April/May, whereas at Lägeren the summer months (June/July) yielded the highest monthly net uptake rates (Figure 5). The Davos forest yielded even higher net uptake rates during spring than the Lägeren forest, although spring temperatures were comparably lower. During summer, monthly temperatures still increased at the Davos site, but C uptake decreased. The seasonal course of cumulative net uptake per month in relation to monthly averaged air temperature resulted in a hysteresis plot with a counterclockwise spin (Figure 5). In contrast, the net uptake of the Lägeren forest increased exponentially with increasing temperature and a less pronounced hysteresis.

The Response of Carbon Uptake to Environmental Drivers

Mean daily NEE of both forests responded differentially to daily temperature, relative soil moisture content (RSWC, Reichstein and others 2005), and PPFD (Figure 6). Net uptake of the Lägeren forest increased with temperature and PPFD, peaking and declining at highest values. Under non-temperature limiting conditions the net flux at the Lägeren showed no relation to soil moisture up to a threshold of 0.8% RSWC, above which a pronounced increase of mean daily NEE (that is, decrease of net uptake) was observed. The net uptake at the Davos forest showed only a weak response to temperature and PPFD, and remained rather constant above a temperature of 4°C and PPFD of 300 μmol m^{-2} s^{-1}. The net uptake increased with

increasing soil moisture, especially when winter and spring data with temperatures below 4°C were included.

DISCUSSION

Three main issues were observed in the similarities and differences in the CO_2 budgets of the two forest ecosystems: (1) Biometric NEP estimates support NEE measurements by EC, (2) annual trends of NEE are similar among the Lägeren and Davos forest, but with intra-annual differences, and (3) the activity of trees is the main driver of forest CO_2 budgets. Based on that, we ask the question of how the latitudinal gradient of European forest C uptake (Valentini and others 2000) translates to altitudinal differences within a small geographic domain.

Biometric NEP Estimates Support NEE Measurements by EC

As NEE and NEP are methodologically independent the comparison of both estimates helps to validate the calculations of ecosystem C budgets, because both approaches are associated with large uncertainties and sources of errors (Curtis and others 2002; Keith and others 2009). Both estimates show that each of the forests is a persistent carbon sink. NEE derived from EC measurements agreed with biometric NEP estimates and deviations between both estimates (Lägeren: 0.5–30%, Davos: 38–64%) lay in the range reported by other studies (for example, Curtis and others 2002; Black and others 2007; Gough and others 2008b; Peichl and others 2010). However, estimates of NEP were already variable themselves, depending on the approach that was applied. Thus, NEP estimates differed by
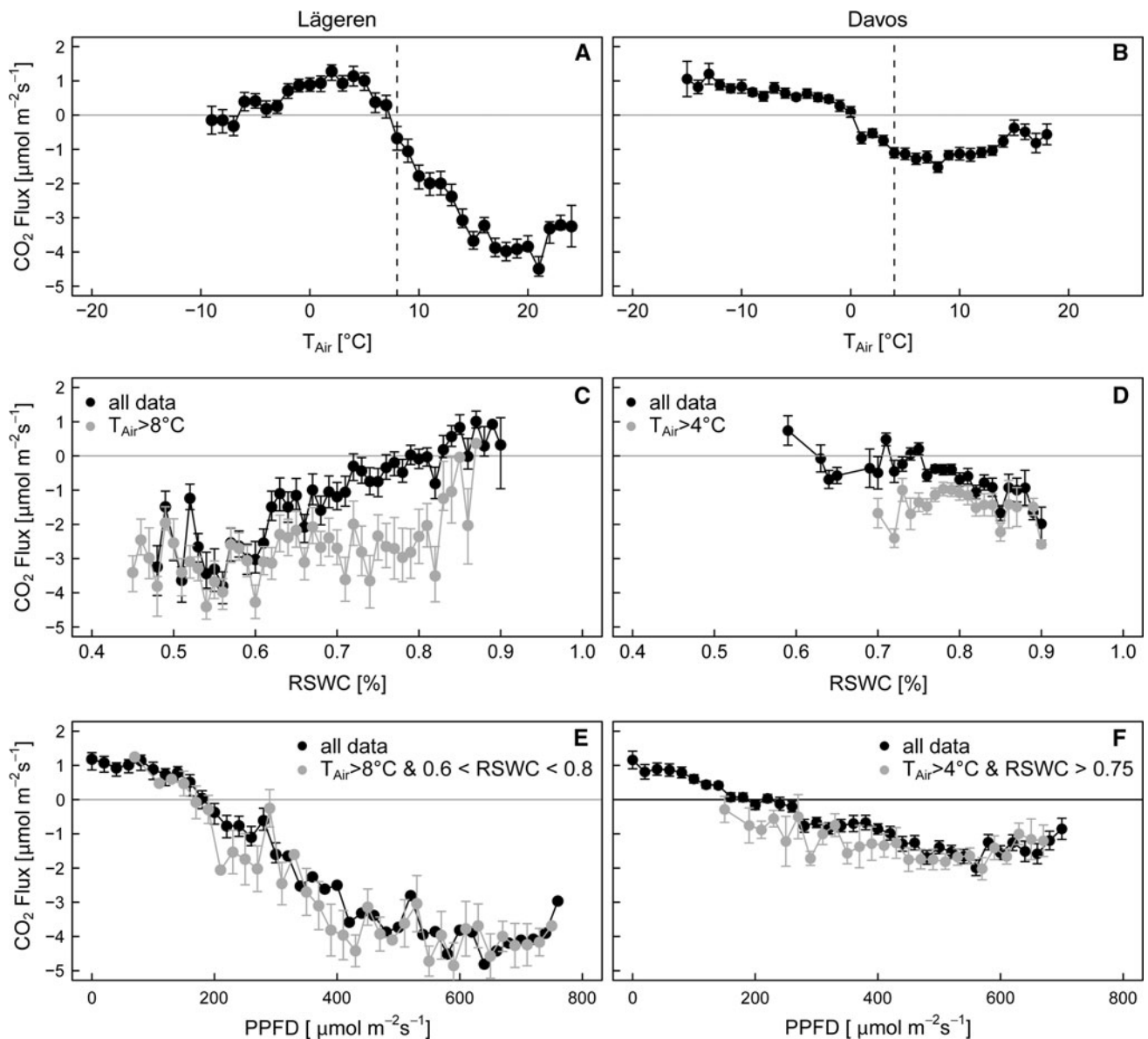
Figure 6. Mean daily CO_2 flux in response to mean daily air temperature (T_{Air}), bin-averaged in 1°C classes (**A**, **B**), in response to relative soil moisture content (RSWC), bin-averaged in 1% classes (**C**, **D**), and in response to photosynthetic photon flux density (PPFD), bin-averaged in 20 µmol m^{-2} s^{-1} classes (**E**, **F**) for the Lägeren site (**A**, **C**, **E**) and the Davos site (**B**, **D**, **F**). Values are means ± SD for the years 2005–2009.

127 g C m^{-2} y^{-1} (±17% variability) at the Lägeren site and by 119 g C m^{-2} y^{-1} (±39%) for 1988–2006 and 125 g C m^{-2} y^{-1} (±37%) for 2006–2010 at the Davos site, but no systematic trend of relationships between NEP and NEE could be observed. The relationships of NEP to NEE are thought to differ with forest type, stand age and species composition (Black and others 2007). Black and others (2007) concluded that NEP calculations based on the mass-balance approach (ΔC, NEP$_{BM}$, and NEP$_{BEF}$) overestimate NEP due to unaccounted soil decomposition losses. NEP* on the other hand,

does not include the C flux to mycorrhiza, accounting for up to 20% of host photosynthates (Smith and Read 1997) or the exudation of C from roots to the soil, which can account for 0.5–5% of the net fixed C (Farrar and others 2003), and therefore likely underestimates NEP. NEP$_{BEF}$ compared well with other NEP estimates at the Davos site, but was significantly higher than all other NEP estimates at the Lägeren site. The ratio of TER/GPP based on the NEP$_{BEF}$ estimate for the Lägeren site results in 0.63. Using a ratio of TER/GPP of 0.74 as a reference for European forest ecosystems (Luyssa-

ert and others 2009) would indicate that BEF may overestimate the productivity of forests. The simple approximation of NEP from dbh and only one scaling factor may be especially problematic for such diverse forests as the Lägeren with a huge variety of species, growth forms and spatial differentiations. In addition, BEF do not account for the different turnover times of the individual tree compartments. We conclude that BEF are useful for estimating forest productivity on large scales as for the UNFCCC accounting, when detailed investigations are difficult to carry out. However, they should be applied with great care, especially for broad-leaved or mixed forest stands.

Our comparison of the different approaches clearly identifies crucial areas for future research to further improve our understanding of the forest carbon cycle and to yield reliable estimates of carbon sequestration. The largest uncertainty in our NEP estimates originates from modeling the belowground C dynamics, and especially those of fine roots (compare Curtis and others 2002; Gough and others 2008a; Braendli 2010). Considering these uncertainties the IPCC even recommends using only aboveground BEFs for national inventories (Loewe and others 2000). Furthermore, for mountain forest sites with a long winter season, the cumulative winter fluxes are an important component in budget calculations, but they are difficult to quantify, and hence impose a large uncertainty on NEP* estimates. Without giving a specific recommendation on the best method for estimating the annual C storage because no clear trend could be observed, we note that NEP* is the most comprehensive approach, but is associated with the highest uncertainties, mainly introduced by the C flux calculations. ΔC and NEP_{BM} are much easier to derive as the non-woody pools are neglected. In our study, they provided robust estimates which compared well with the NEE estimates. Thus, ΔC and NEP_{BM} appear to be useful and easily applicable tools to get a rough estimate of NEP. However, if the research interest is in the dynamics and contributions of the single forest compartments, then a more sophisticated approach (such as NEP*) is needed.

Temporal Patterns of Net Uptake

In general, C budgets of the Davos forest were more variable than those of the Lägeren forest, but both forest sites showed similar trends of annual net uptake during 2005–2009 (Figure 3). This was surprising as the sites were exposed to different climatic conditions between 2005 and 2009 (Figure 2) and responded differentially to environmental variables (Figure 6). Whereas the daily net uptake of the Lägeren was strongly enhanced by temperature and incoming radiation under sufficient moisture conditions, the daily net uptake of the Davos forest was only weakly related to temperature or to PPFD. Thus, we could not detect a temperature limitation of the photosynthetic activity of the Davos trees as was a priori expected for a subalpine site with low annual temperatures. Instead, the net uptake was rather decoupled from seasonal temperature variations, and the highest net uptake rates were observed during April and May under very low temperature conditions, whereas during the warmer summer period comparably low net uptake rates were observed (Figure 5). The temperature uncoupling during the spring snow melt period is also seen in the soil moisture response curve (Figure 6), where net uptake increases with increasing RSWC, which mainly reflects an increasing RSWC during the spring snow melt. The high importance of the spring period and of the availability of snow melt water on annual NEE was already shown for the subalpine forest site Niwot Ridge by Monson and others (2005) and Hu and others (2010). The temperature decoupling of subalpine ecosystems should be taken into account in ecosystem modeling, in which usually temperature response functions are applied.

The net uptake at the Davos forest started about 1 month earlier compared to the Lägeren forest. Interestingly, monthly sums of NEE of the Lägeren and Davos forest were closely related by lagging the Davos data by 1 month or by integrating NEE over 2 months. Thus, over a longer time period (such as 2 months) the influence of climatic conditions on the forests' net uptake may be overridden by intrinsic forest dynamics (Richardson and others 2007). Despite the highest uptake rates during summer at the Lägeren forest, DOY_0 (the ecosystem turns from a source to a sink) also had high predictive power for annual NEE. Thus, the period during which the ratio of GPP and TER is changing, is most critical for the annual NEE, introducing high uncertainties into global change scenarios, as the spring period is expected to undergo large changes, for example, of snow coverage, lengthening of the vegetation period, or increase of snow melt days (Appenzeller and others 2008).

Activity of Trees as Main Determinant for Forest C Budgets

NPP, NEP, NEE, GPP, TER, as well as DR_C were strongly increased at Lägeren compared to Davos, whereas Rh was only slightly larger (Tables 4 and 5).

Thus, differences in the C balance of the two forests, namely the higher productivity of the Lägeren forest, can mainly be attributed to differences in tree physiology at the two sites (that is, growth, water balance, phenology, and respiration), resulting from different climate conditions, the dominating tree functional type of the vegetation cover (coniferous vs. broad-leaved) and the age of the trees. The predominating influence of tree dynamics on the CO_2 budget of the Davos forest was already shown in Zweifel and others (2010). They found a remarkably close relationship between NEE and continuously measured stem radius changes, which integrates growth and tree water relation processes. It was concluded that tree water relations and stem growth are representative for the productivity of the Davos forest, and that other ecosystem components, such as understory vegetation and SR, are acting most likely in phase with the measured trees.

SR was of similar magnitude at both sites despite different temperature conditions, due to higher temperature sensitivity of SR at the Davos forest (Figure 4), likely caused by the relatively high photosynthetic activity of the Davos conifers already under low temperature conditions (Figures 5, 6) and coupled to this (Janssens and others 2001; Hoegberg and Read 2006) also high respiration rates. This pattern was confirmed by a larger belowground tree C pool and an increased belowground C allocation at the Davos forest compared to the Lägeren (Table 5). Similar observations were made at three Swiss forests of different altitudinal

ranges (subalpine, montane, lowland). At the subalpine site, the lowest aboveground tree growth was measured, but the highest fine root C pool and the highest rates of root respiration (compare Graf Pannatier and others 2010). Thus, the importance of belowground tree processes apparently increases with increasing altitude.

C Uptake as a Function of Altitude?

Valentini and others (2000) suggested respiration as the main determinant of the C balance of European forests. They found a decreased net uptake of European forests with increasing latitude, whereas GPP remained rather constant. We tested whether this hypothesis holds true also for increasing altitude, as the Alpine altitudinal gradient is often considered comparable to the latitudinal gradient of the Northern Hemisphere, for example, with respect to temperature (Koerner 1999), but with substantial differences, for example, in light intensity, day length, duration of the growth period, or soil temperature conditions. Figure 7 puts both sites in context with others compiled by Valentini and others (2000). During 2005–2009, the mean net uptake of the Davos forest was significantly lower compared to the Lägeren forest (Table 4). And whereas NEE of the Lägeren matches the regression line in Figure 7A nearly perfectly (4.15 Mg C ha^{-1} y^{-1} at 47°N), NEE of Davos (1.17 Mg C ha^{-1} y^{-1} at 46°N) is not representative for its latitudinal range, but fits well
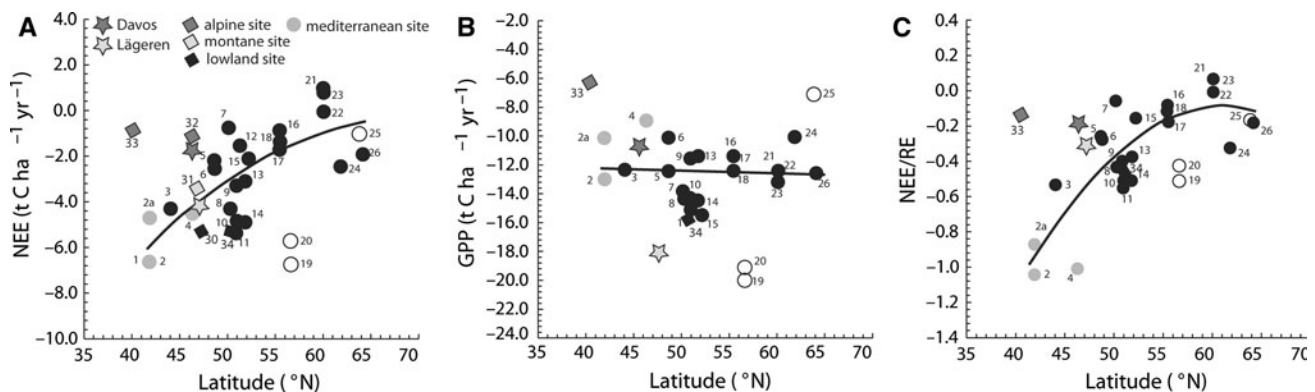

Figure 7. European forest CO_2 budgets (NEE (**A**), GPP (**B**), and the ratio NEE/TER (**C**)) as a function of latitude (modified from Figures. 1, 2, 3 in Valentini and others (2000); new mountain forests and/or Swiss forest sites are inserted as *diamonds*, the Lägeren and Davos sites as *stars*; Mediterranean mountain sites already included in Valentini and others (2000) were modified as *gray circles*). *Open circles* intensively managed plantations. The *numbers* 1–26 are as in Valentini and others (2000). Added sites are: #*30* Vordemwald (480 m a.s.l, Switzerland); #*31* Schänis (730 m a.s.l., Switzerland); #*32* Beatenberg (1510 m a.s.l, Switzerland); #*33* Niwot Ridge (3050 m a.s.l., U.S.); #*34* Hainich (440 m a.s.l, Germany). Adapted by permission from Macmillan Publishers Ltd: Nature (Valentini and others), copyright (2000). Additional data were obtained from Graf Pannatier and others (2010) (#30–32); Sacks and others (2007) (#33); Knohl and others (2008) (#34).

in C budgets of forests north of 55°N (Figure 7A, see also Luyssaert and others 2007). This is also the case for other alpine forest sites in Switzerland (#32 in Figure 7A) and outside Europe (#33), whereas the Swiss montane forest site Schänis (#31) is comparable to the Lägeren site. Mediterranean forests at higher altitudes (#2,2a,4), however, have a much higher net uptake compared to the alpine forests of the temperate zone and to lowland Mediterranean forests with NEE ranging from 90 to 551 g C m^{-2} y^{-1} (compare Baldocchi and others 2010). An increasing net uptake with increasing altitude was also shown for ecosystems (desert, savannah, woodland, and forest) in southwestern North America by Anderson-Teixeira and others (2011). In these regions, the carbon uptake capacity of ecosystems at low altitudes is limited by hot and/or dry conditions, whereas subalpine ecosystems benefit from low temperatures and ample moisture. In contrast, the annual net uptake of subalpine forests in the temperate zone is mainly determined by the forest's spring net uptake capacity and the snow water availability during this period (Hu and others 2010).

Similarly, GPP at the Lägeren forest is much higher than at Davos (Figure 7B). Note that the carbon uptake by GPP is presented with a negative sign, and in this case most negative values mean a high carbon uptake by GPP. Whereas the Davos forest ranges among the sites with lowest GPP, the Lägeren forest has a higher mean GPP than most of the sites included in Valentini and others (2000). Although being large in this context, mean GPP (ca. $-1,800$ g C m^{-2} y^{-1}) at the Lägeren is comparable to estimates for other forests in Europe not included in Valentini and others (2000), such as the old-growth beech forest Hainich in Germany (-1670 g C m^{-2} y^{-1}, Knohl and others 2003), the spruce forest Tharandt ($-1,845$ g C m^{-2} y^{-1}, Gruenwald and Bernhofer 2007) or a broad-leaved deciduous woodland in England ($-2,100$ g C m^{-2} y^{-1}, Thomas and others 2011). In fact, Swiss forests, and especially those of the Central Plateau, to which the Lägeren borders, have been reported to be the most productive forests in Europe due to favorable growth conditions (SAEFL/WSL 2005; Braendli 2010). This is also reflected by tree sizes that reach a maximum of 42.2 m at the Lägeren (Eugster and others 2007). In comparison, GPP at Davos is rather low, but still significantly higher compared to the subalpine forest Niwot Ridge in the Colorado Rocky mountains (Figure 7B), which is explainable by the shorter growing period and the zero GPP during winter at the Niwot Ridge site (Sacks and others 2007). The ratio of NEE to TER of the Davos and Niwot Ridge site is in the same range, but higher than at the other forests at similar latitudes, indicating an increasing importance of respiration at higher altitudes (Figure 7C).

Differences between the forest C budgets at the Lägeren and at the Davos forests correspond to the latitudinal gradient found for the C balance of European forests, with altitude perceived as a proxy for changing environmental conditions, and an increasing tree age (SAEFL/WSL 2005). However, the relationship of NEE to altitude may not be the same for all vegetation zones and regions (for example, temperate, mediterranean, and tropical). This emphasizes the need to account for the altitudinal range of ecosystems in modeling approaches when aiming at a better understanding of forest ecophysiological processes, especially in response to climate change, which is predicted to be most pronounced in alpine regions.

ACKNOWLEDGMENTS

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