



NEP of a Swiss subalpine forest is significantly driven not only by current but also by previous year's weather

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Abstract. Understanding the response of forest net ecosystem productivity (NEP) to environmental drivers under climate change is highly relevant for predictions of annual forest carbon (C) flux budgets. Modeling annual forest NEP with soil–vegetation–atmosphere transfer models (SVATs), however, remains challenging due to unknown delayed responses to weather of the previous year. In this study, we addressed the influence of previous year's weather on the interannual variability of NEP for a subalpine spruce forest in Switzerland. Analysis of long-term (1997–2011) eddy covariance measurements showed that the Norway spruce forest Davos Seehornwald was a consistent sink for atmospheric CO₂, sequestering $210 \pm 88 \text{ g C m}^{-2} \text{ yr}^{-1}$ on average. Previous year's weather strongly affected interannual variability of NEP, increasing the explained variance in linear models to 53 % compared to 20 % without accounting for previous year's weather. Thus, our results highlight the need to consider previous year's weather in modeling annual C budgets of forests. Furthermore, soil temperature in the current year's spring played a major role controlling annual NEP, mainly by influencing gross primary productivity early in the year, with spring NEP accounting for 56 % of annual NEP. Consequently, we expect an increase in net CO₂ uptake with future climate warming, as long as no other resources become limiting.

ecosystem respiration (TER), has been shown to be challenging (Urbanski et al., 2007; Gough et al., 2008), and only weak links ($r^2 < 0.25$) have been found between climate variables and NEP (e.g., Gough et al., 2008). Furthermore, it is still unclear how forest NEP will respond to climate change, making predictions of this policy-relevant variable using soil–vegetation–atmosphere transfer models (SVATs) difficult and potentially inaccurate (e.g., Hanson et al., 2004; Katul et al., 2001; Richardson et al., 2007). However, due to large carbon (C) sink activities of forest ecosystems (Bonan, 2008), understanding the climate control on forest NEP and its role in the terrestrial carbon cycle is of great global importance (Stoy et al., 2009).

The challenges of SVATs to precisely model interannual NEP may arise from their focus on immediate responses of forest ecosystems to the current year's weather (Hanson et al., 2004; Urbanski et al., 2007). However, it is very likely that forest ecosystems do not only respond immediately to actual changes in environmental conditions, but can also show delayed responses to legacy-effects or climate-vegetation feedbacks. Such delayed responses to seasonal weather conditions of the previous year (hereafter referred to as previous year's weather) might include weather induced alterations of the built-up stored C in the previous year's summer and/or fall used to fuel current year's growth and metabolism (Carbone et al., 2013) and the formation of buds in the previous year's fall with the associated implications for current year's leaf area index (LAI), and thus GPP (Zweifel et al., 2006). Furthermore, the compensation of respiratory C losses due to frost damages induced in winter and spring of the previous year is yet another process possibly responsible for delayed responses. Therefore, we hypothesize

1 Introduction

Modeling and explaining interannual net ecosystem productivity (NEP) of forests, where NEP is the relatively small difference between gross primary productivity (GPP) and total

that responses to previous year's weather affect climate–vegetation feedbacks by modulating CO₂ release and/or uptake, and thus, will improve our ability to explain interannual variability of forest NEP. Such phenomena have been reported for both nonforest and forest ecosystems. Rocha and Goulden (2010) showed that negative effects on LAI and photosynthesis induced by an extreme drought in a freshwater marsh lasted for several years. Dendrochronological studies focusing on the tree scale, e.g., by Rocha et al. (2006), Pichler and Oberhuber (2007), and Babst et al. (2012), reported a significant influence of previous year's weather on current year's radial tree growth. Until now, however, little attention has been paid to the influence of such relationships on CO₂ exchange of entire forest ecosystems, and existing results have been contradictory. While Urbanski et al. (2007) suggested an influence of severe weather events from previous years on the current year's carbon uptake capacity, and thus GPP, of a mixed forest, Gough et al. (2008) showed lagged influences of environmental conditions on net primary productivity (NPP), but not on NEP.

In accordance with the above mentioned ecophysiological processes possibly responsible for delayed responses of forest NEP, we would expect the previous year's summer or fall to be of importance for forest NEP. If unfavorable conditions occur during these seasons, e.g., a precipitation deficit, the build-up of stored C and the formation of buds might be hampered and thus, affecting current year's NEP. Also, we expect cold winter conditions, promoting a long-lasting snow cover accumulated already in late fall of the previous year, to play an important role due to its importance for soil temperature and soil water availability in current year's spring, hence an early onset of NEP.

Here, we present a 15 yr (1997–2011) study on climate drivers of eddy covariance based NEP of a subalpine spruce forest. Based on this long-term data set, the goals of this study are (1) to identify climate drivers of NEP; and (2) to quantify the influence of previous year's weather on NEP at the Swiss FluxNet site Davos Seehornwald.

2 Materials and methods

2.1 Site description

We conducted measurements at the Swiss FluxNet site Davos Seehornwald, a subalpine coniferous forest located in the southeastern part of Switzerland (46°48′55.2″ N, 9°51′21.3″ E) at 1639 m a.s.l. The annual mean temperature at the MeteoSwiss weather station Davos Dorf, approximately 1 km southeaster of the Davos Seehornwald at 1594 m a.s.l., is 3.6 °C, and the mean annual precipitation is 1035 mm (30 yr means, 1981–2010; MeteoSwiss). The forest is dominated by Norway spruce (*Picea abies*) and shows a patchy understory of shrubs (*Vaccinium myrtillus*, *Vaccinium gaultherioides*), mosses (*Hylocomium splendens*,

Dicranum scoparium) and scattered occurrence of grasses (*Calamagrostis villosa*, *Avenella flexuosa*, *Luzula sylvatica*). Stand age of mature trees ranges from 240 to 400 yr, tree height is ca. 25 m, and leaf area index (LAI) is 3.9 m² m⁻². The soils range from Chromic Cambisols to Rustic Podzols (FAO classification; Jörg, 2008).

2.2 Climate data

Climate data used in this study were obtained from meteorological measurements on site: photosynthetic photon flux density (PPFD) (SKP 215, Skye Instruments Ltd., UK), soil temperature (TS107, Markasub, Switzerland), and global radiation data, complemented with data from the nearby MeteoSwiss weather station Davos Dorf (air temperature, vapor pressure deficit (VPD), precipitation, snow height). This enabled us to incorporate climate information in the statistical analysis of years before on-site flux measurements were available (see below). We inferred mean daily soil temperatures for two years before on-site measurements (1995, 1996) from air temperatures, using a linear regression model between the two variables for the period 1997–2011 (adjusted $r^2 = 0.69$; $p < 0.001$).

2.3 Flux measurements and data processing

Since 1997, the net ecosystem exchange (here defined as $NEE = -NEP$) of CO₂ between the biosphere and the atmosphere has been determined continuously on a 35 m flux tower using the eddy covariance (EC) method (cf. Zweifel et al., 2010; Etzold et al., 2011). From 1997 until the end of 2005, CO₂ concentrations were measured using a closed-path infrared gas analyzer (IRGA) LI-6262 (LI-COR, Lincoln, Nebraska, USA). Since the end of autumn 2005, the respective concentrations have been measured with an open-path IRGA LI-7500 from the same manufacturer. Three dimensional wind speed was measured with a three axis sonic anemometer, model Solent R2 (Gill Instruments Ltd., Lymington, Hampshire, UK), until 2006, which was then replaced by a Solent R3-50 sonic anemometer.

CO₂ concentrations, measured at 20 Hz, were post-processed with the in-house software eth-flux (cf. Mauder et al., 2008) to obtain 30 min means of CO₂ fluxes. We corrected the 30 min mean fluxes measured by the open-path IRGA for density fluctuations (Webb et al., 1980) and for self-heating of the LI-7500 instrument surface (Burba et al., 2008). Since the LI-7500 was mounted obliquely to let rainwater drip off, not the full optical path length of the sensor is subject to self-heating effects. The fraction δ of the optical path affected by self-heating was estimated at $\delta = 0.085$ based on a direct determination at a similar site (Järvi et al., 2009). We filtered corrected fluxes for unrealistically high values ($\pm 50 \mu\text{mol m}^{-2} \text{s}^{-1}$) and unfavorable atmospheric conditions such as snow, heavy rain and/or dust (window dirtiness > 70 %; open-path IRGA

fluxes only). Insufficient turbulent mixing of the atmosphere was accounted for using a u_* filter with a threshold of $u_* < 0.2 \text{ m s}^{-1}$. In addition, we filtered large unrealistic negative nighttime CO_2 fluxes. Therefore, we used a symmetric method, i.e., within a 14 d moving window, both negative and positive nighttime CO_2 fluxes outside the 14 d mean ± 1 SD (standard deviation) were dismissed. High-quality data were available between 43 % (2008) and 53 % (2002) of the time after data screening and removal of periods with instrument failures.

Gap-filling and partitioning of the CO_2 fluxes into GPP and TER was done using the online tool by Reichstein et al. (2005). After flux partitioning, 10 % of the daytime GPP fluxes were negative because modeled TER was lower than the measured NEE. In such cases, we set GPP to zero, and assigned the corresponding NEE to TER. The same procedure was repeated for all GPP values during nighttime (photosynthetic photon flux density $< 80 \mu\text{mol m}^{-2} \text{ s}^{-1}$).

2.4 Statistics

All statistical analyses were performed using the R statistical software, version 3.0.1 (R Core Team, 2012). In general, we used seasonal climate variables to determine which drivers exerted the greatest influence on C exchange processes at what time of the year (Table 1). The nomenclature used in the statistical analysis was composed of the abbreviation and the meteorological season of each climate variable, e.g., spring soil temperature was named *SoilTemp.spring*. We used the meteorological definition to define seasons (winter: DJF; spring: MAM; summer: JJA; fall: SON). Previous year's weather variables were denoted with “–1”, e.g., *SoilTemp.spring–1*. Accordingly, “winter–1” is the season with the longest time period between itself and current year's NEP, including December of the year before the previous year as well as January and February of the actual previous year. The current year's winter then includes the previous year's December as well as the current year's January and February. We used two subsets of data to analyze climate drivers of NEP: one with current year's weather variables only (28 variables) and one with both current and previous year's weather variables (56 variables).

The analysis itself was conducted in two steps. In the first step, we diagnosed and corrected collinearity due to interdependencies among climate variables within the two subsets of data, using the condition index (CI; Rawlings et al., 1998). CI is the square root of the ratio of each eigenvalue to the smallest eigenvalue of X , with X representing a $n \times p$ matrix of predictors (p) and with n being the sample size. A CI > 30 is critical, i.e., collinearity is present and should be corrected for (Rawlings et al., 1998; Dormann et al., 2012). Thus, we correlated each climate variable with each other and when the absolute correlation coefficient exceeded a threshold of $|r| = 0.58$, we calculated bivariate regressions between NEP and these two independent variables. We then dismissed the

Table 1. Abbreviations of the climatic variables used in this study, their descriptions and units.

Variable abbreviation	Description	Unit
<i>T2</i>	Mean air temperature at 2 m height	$^{\circ}\text{C}$
<i>T2max</i>	Maximum air temperature at 2 m height	$^{\circ}\text{C}$
<i>T2min</i>	Minimum air temperature at 2 m height	$^{\circ}\text{C}$
<i>VPD</i>	Vapor pressure deficit	kPa
<i>Precip</i>	Precipitation	mm
<i>SoilTemp</i>	Soil temperature 5 cm below ground	$^{\circ}\text{C}$
<i>PPFD</i>	Photosynthetic photon flux density	$\mu\text{mol m}^{-2} \text{ s}^{-1}$

climate variable with the lower explanatory power according to the Akaike information criterion (AIC). The chosen correlation threshold allowed fitting of linear models (degrees of freedom ≥ 1), and it was in the range of previously reported values ($|r| = 0.4$ in Suzuki et al., 2008, $|r| = 0.85$ in Elith et al., 2006). In the second step, we selected those climate variables from the collinearity-corrected data sets that resulted in the best linear regression models with 1 up to k variables, with k being the number of climate variables after collinearity correction.

We used adjusted r^2 (adj. r^2) as selection criterion for the best model and constrained the analysis of climate drivers to models with three variables at the most (see Sect. 3.2 for details). By calculating standardized regression coefficients (β ; Quinn and Keough, 2001), we determined the importance of each individual climate variable in the best models, and thus, the contribution of each climate variable to the prediction of NEP. Finally, we assessed the overall performance of the best linear regression models obtained from our first statistical approach by determining their ability to reproduce measured single-year sums of NEP. Therefore, we used the regression equations with the respective climate variables as input to recalculate annual NEP.

3 Results

3.1 Annual carbon dioxide flux and intra-annual patterns

The subalpine coniferous forest was a net CO_2 sink throughout the measurement period from 1997 until 2011. Annual sums of net CO_2 uptake ranged from 54 (1997) to 336 $\text{gC m}^{-2} \text{ yr}^{-1}$ (2009), with a 15 yr average of $210 \pm 88 \text{ gC m}^{-2} \text{ yr}^{-1}$ (mean ± 1 SD) (Fig. 2) and we did not find a significant trend towards increasing NEP within the measurement period ($p = 0.08$). On average, cumulative C losses exceeded CO_2 uptake ($|\text{TER}| > \text{GPP}$) from the beginning of the year until the beginning of May (mean date ± 1 SD: 8 May ± 23 d). Typically, at the end of March (27 March ± 16 d), when air temperature was still below zero and the soil was snow-covered (Fig. 1), photosynthesis

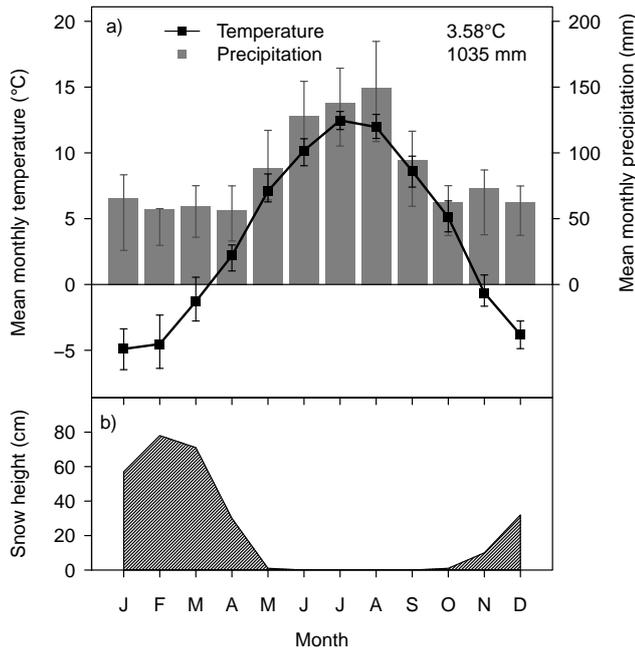


Fig. 1. Mean monthly air temperature and precipitation (a) and mean monthly snow height (b) at the Davos site for the reference period 1981–2010 (MeteoSwiss). Vertical bars indicate the interquartile ranges. Mean annual temperature and mean annual precipitation for the period 1981–2010 are given in the top right corner.

compensated respiration and the cumulative NEP began to increase until the beginning of November (6 November ± 15 d), when it reached its maximum. At this time, monthly temperatures fell below zero, with only a shallow snow cover present (Fig. 1). The temporal pattern of cumulative NEP in 2001 differed substantially from all other years (Fig. 2). Photosynthesis started to dominate already at the end of February (25 February 2001), and a positive cumulative NEP was reached in mid-March (12 March 2001), almost two months earlier than in other years. The early compensation by photosynthesis and onset of net C uptake were the result of an early warm period from the end of February until the beginning of April, with air temperatures more than 2 °C higher than average (1.7 °C in 2001 vs. a mean of -0.5 °C from 1981 to 2010). Consequently, the year 2001 showed the second highest net carbon uptake during the measurement period with an annual NEP of $314 \text{ g C m}^{-2} \text{ yr}^{-1}$, only slightly lower than the maximum net carbon uptake in 2009, since a long cold spell in spring 2001 caused a stagnation and even a slight decrease of NEP for about three weeks in April 2001.

Across all 15 yr, the intra-annual pattern of daily mean NEP showed a steep increase from the beginning of spring (March–May) until they peaked around mid-May (Fig. 3), the time in year when air temperature was well above zero and the snow cover had disappeared (Fig. 1). This increase in mean daily NEP from the beginning of spring was mainly

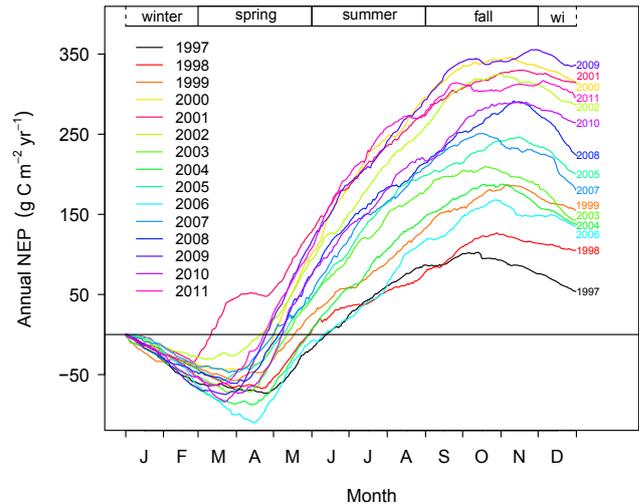


Fig. 2. Annual NEP of the Davos Seehornwald spruce forest for the measurement period 1997–2011. Seasons are defined according to their meteorological definition (winter: DJF; spring: MAM; summer: JJA; fall: SON).

driven by an increase in photosynthetic CO_2 uptake (Pearson's product moment correlation coefficient (r) for spring GPP vs. spring NEP = 0.98), while TER remained more or less constant at a low base level until about May. Spring time NEP alone accounted for 56 % of annual NEP at the Davos site. With the sharp increase of TER at the end of May, daily mean NEP slowly decreased, yet stayed positive since GPP outperformed TER until the end of October. Between November and mid-April of the following year, daily mean NEP of the Davos site was negative. Although photosynthesis did occur at the Davos site during winter, TER always exceeded GPP (Fig. 3).

3.2 Climate drivers of net ecosystem productivity

At the Davos site, 20 % of interannual variability of NEP during the period 1997–2011 could be explained with two out of a maximum of three climate variables from the current year (Fig. 4a). However, also including climate variables from the previous year in the analysis (Fig. 4b), and thus accounting for a response of NEP to previous year's weather, further increased the explained interannual variance, reaching 53 % (limiting the analysis to three variables, see Sect. 2.4). These results were highly consistent, also if only two variables were used from the data set with previous year's weather or if the collinearity threshold was chosen in such a way that both initial variable subsets (without and with previous year's weather) had the same number of variables (data not shown). Using more than three independent variables would further increase the explained variance of NEP for the data set with current and previous year's weather (Fig. 4b, hatched area), yet, strongly overparameterizing the linear models in relation to the dependent variable (i.e., 15 yr). Therefore, we limited

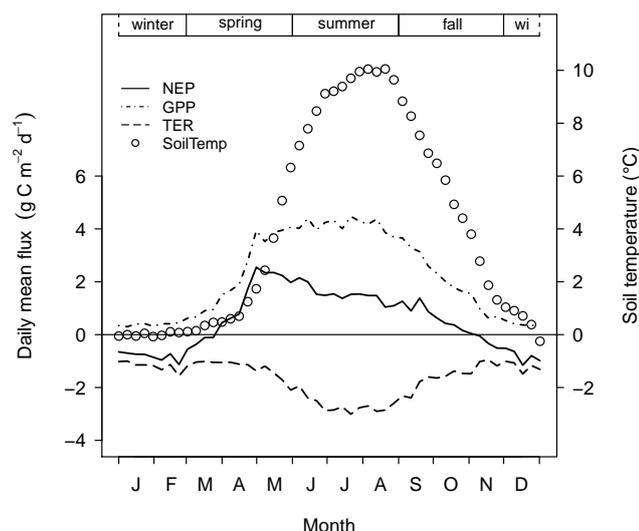


Fig. 3. Smoothed mean daily sums of NEP, GPP and TER as well as smoothed mean daily soil temperature at 5 cm depth of the Davos Seehornwald spruce forest for the measurement period 1997–2011. Smoothing was done by fitting a local polynomial regression (LOESS) to the original mean daily values, using a 7 and 18 d smoothing window for the fluxes and the soil temperature, respectively. Seasons are defined according to their meteorological definition (see Fig. 2).

all our analyses to a maximum of three independent variables.

Regardless of which subset was analyzed (with current year's weather only or with both current and previous year's weather), soil temperature of current year's spring (*SoilTemp.spring*) was identified as the most influential driver of NEP (Table 2). NEP always increased with increasing soil temperatures. Winter irradiance was ranked second for the subset with current year's weather only, always with a negative effect on NEP ($\beta = -0.34$ and -0.42 for models with two and three independent variables, respectively; Table 2). When previous year's weather was included, minimum air temperature of the previous year's spring (*T2min.spring-1*) was the second most important variable, also with a strong positive effect on NEP, similar to soil temperature ($\beta = 0.68$ and 0.70 for models with two and three independent variables, respectively). For both subsets, the third explanatory variable was only of minor importance (*PPFD.fall-1*, $\beta = -0.30$; Table 2) and did not increase the explained interannual variability of NEP significantly.

3.3 Modeling of annual net ecosystem productivity

We used the best linear regression models with current year's weather only and with both current and previous year's weather (two and three independent variables, respectively; Table 2) to compare their performance to measured single-year NEP (1997–2011; Fig. 5). The model with both cur-

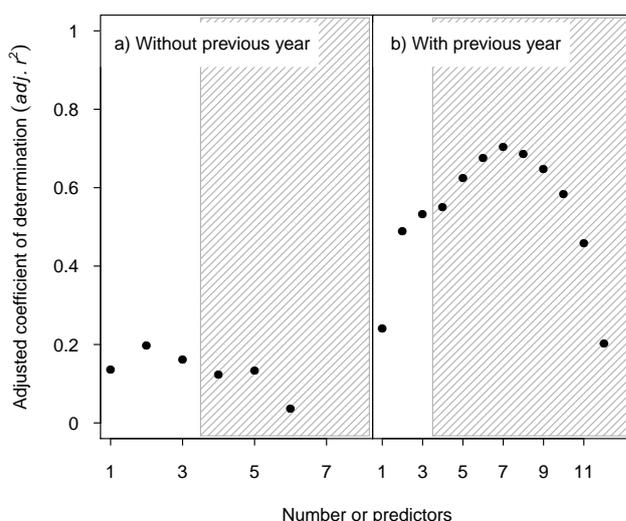


Fig. 4. Number of predictors used in the model's NEP vs. climatic variables (1997–2011) against the adjusted coefficient of determination ($\text{adj. } r^2$) for the data subsets with current year's weather only (a) and with both current and previous year's weather (b) of the Davos Seehornwald spruce forest. Hatched areas in (a) and (b) indicate overparameterized models.

Table 2. Linear regression coefficients, p values, and β coefficients for individual variables of the best models for NEP with up to three variables with current year's weather only and with both current and previous year's weather included as well as $\text{adj. } r^2$ and p values for the entire model (p_{mod}). Previous year's weather variables are denoted with “-1”.

Variable	Coefficient	p	β	$\text{adj. } r^2$	p_{mod}
Models with current year's weather only					
Intercept	578.23	0.0139	–		
<i>SoilTemp.spring</i>	49.65	0.0913	0.44		
<i>PPFD.winter</i>	-3.12	0.1811	-0.34	0.20	0.1051
Models with current and previous year's weather					
Intercept	583.93	0.0464	–		
<i>SoilTemp.spring</i>	101.96	0.0022	0.90		
<i>T2min.spring-1</i>	75.93	0.0059	0.70		
<i>PPFD.fall-1</i>	-1.81	0.1708	-0.30	0.53	0.0094

p and β are valid for each independent variable.

$\text{adj. } r^2$ and p_{mod} are valid for the entire model.

rent and previous year's weather was substantially better able to reproduce the interannual variability than the one without (current and previous year: $\text{adj. } r^2=0.53$ vs. current year only: $\text{adj. } r^2=0.20$, Table 2), and also showed smaller confidence intervals (Fig. 5a, b). Focusing on single years, the linear model with year's weather only over- or underestimated measured annual NEP anomalies by more than $50 \text{ g C m}^{-2} \text{ yr}^{-1}$ for 10 of the 15 yr – this model only performed well in five years (1997, 1999, 2003, 2010, and 2011) (Fig. 5c). In contrast, the linear model including current and previous year's weather performed well in 11 out of 15 yr –

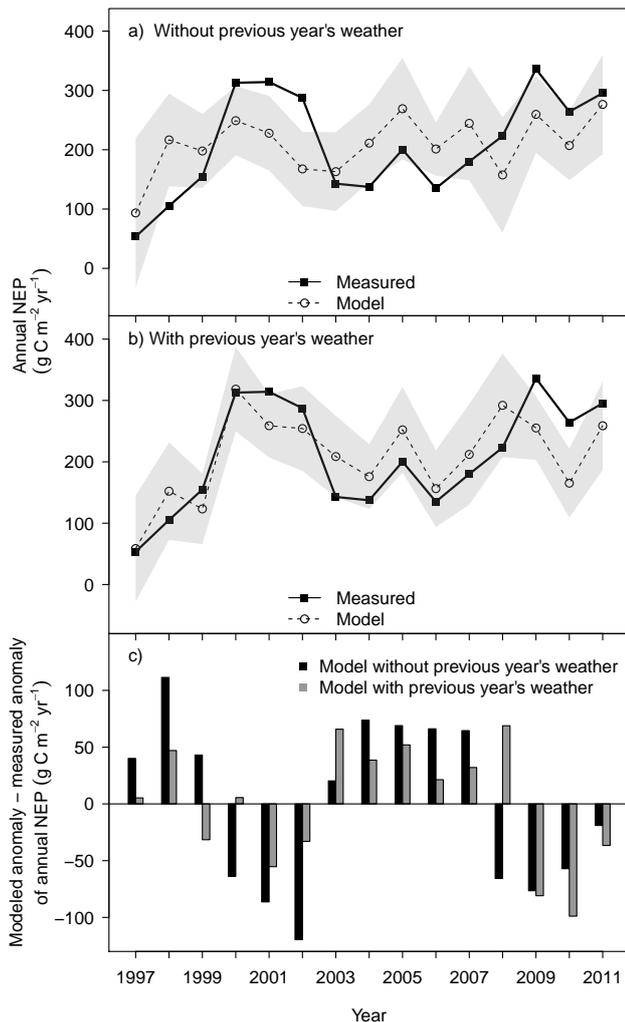


Fig. 5. Measured and modeled annual NEP of the Davos Seehornwald spruce forest for the period 1997–2011 using the best two and three climatic variables from the data subsets with current year's weather only (a) and with both current and previous year's weather (b), respectively. Grey shaded areas indicate 95 % confidence intervals for the modeled annual NEP. Differences between the measured NEP anomalies and modeled NEP anomalies are given as well (c).

only in four years (2003, 2008, 2009, 2010) were the deviations from the measured annual NEP anomalies were larger than $50 \text{ g C m}^{-2} \text{ yr}^{-1}$.

4 Discussion

Our study showed that only when considering previous year's weather we explained interannual variability of NEP well, increasing the explained variance of NEP at the Davos forest from 20 to 53 %. Yet, current year's spring conditions still exerted a continuous influence on NEP, independent of whether or not previous year's weather was included in the analysis.

4.1 Ecosystem carbon sink

The Davos forest was a consistent carbon sink over 15 yr of measurements (1997–2011; Fig. 2), with annual CO_2 sinks ranging from 54 to $336 \text{ g C m}^{-2} \text{ yr}^{-1}$ and no significant trend of increasing CO_2 sink activity with time. Eddy covariance measurements in subalpine forest ecosystems are scarce, and therefore, the possibilities for comparisons of annual NEP with other sites are limited. Zeller and Nikolov (2000) reported a modeled annual C uptake of $196 \text{ g C m}^{-2} \text{ yr}^{-1}$ for the Glacier Lakes Ecosystems Experiment Site (GLEES), a subalpine forest in southern Wyoming, USA, dominated by Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). Long-term CO_2 flux observations at the Niwot Ridge AmeriFlux site, another subalpine coniferous forest (*Abies lasiocarpa*, *Picea engelmannii*, *Pinus contorta*), showed a mean annual uptake of $216 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Desai et al., 2011). These values are in line with the mean annual NEP ($210 \text{ g C m}^{-2} \text{ yr}^{-1}$) at our site in Switzerland. Annual cumulated NEP at the Davos site was controlled by the combination of strongly increasing spring C uptake and consistently low spring C loss, causing NEP to reach 56 % of its annual sum in the three months March, April, and May. Such a strong control of springtime photosynthesis over annual NEP is in accordance with results from a subalpine coniferous forest (*Abies lasiocarpa*, *Picea engelmannii*, *Pinus contorta*) (Niwot Ridge, USA; Monson et al., 2002).

4.2 Environmental controls of annual net ecosystem productivity

Considering previous year's weather substantially increased explained variance of interannual variability in NEP from 20 to 53 % (Fig. 4, Table 2), leading to an adj. r^2 much higher than reported for other studies using only current year's weather (typically, $r^2 < 0.25$ for single climate variables; e.g., Gough et al., 2008). Our analysis highlighted the relevance of favorable previous year's spring conditions ($T2min.spring-1$) promoting current year's NEP (Table 2), e.g., by warm temperatures and/or less frequent occurrence of frost events. Possible reasons for the delayed response of NEP and forest growth to weather of the previous year are manifold and potentially superimposed. It is generally accepted that nonstructural carbohydrates (NSC) stored in the previous year are used to fuel C consuming processes early in the current year, such as for bud break/leaf flush (e.g., Epron et al., 2012) and early wood formation (e.g., Oberhuber et al., 2011), in both deciduous and coniferous trees (Hoch et al., 2003; Schädel et al., 2009). Unfavorable weather during the previous year might lead to a reduction in C allocation to young and readily available NSC, which is primarily used for growth (Richardson et al., 2013), and thus, might affect NEP. Additionally, bud formation in the previous year's late summer and autumn might affect current year's tree growth and thus the ecosystem C balance, as indicated by the

relationship between NEP and previous year's fall radiation ($PPFD_{fall-1}$; Table 2). Weather, and thus GPP and C supply, during the formation process of buds predetermines maximum needle number as well as maximum length of needles and shoots in the following year (Dobbertin, 2005). Hence, closely related variables, such as the maximum LAI and rate of photosynthesis, which build a feedback loop with GPP and tree growth, are partially preset and constrained by previous year's weather (Zweifel et al., 2006).

Furthermore, frost and winter damages to parts of the tree might indirectly play a role in NEP responses to previous year's weather. Warm temperatures and less occurrence of frost events in the previous year's spring ($T2min.spring-1$; Table 2) could be associated with reduced frost damage, e.g., to buds and recently flushed needles, as well as with reduced xylem embolism or fine root mortality (Pederson et al., 2004). Accordingly, less respiratory C losses and an earlier compensation of these C losses by photosynthesis will affect GPP and the ecosystem C balance.

The importance of considering delayed NEP responses, e.g., in SVATs, is clearly shown in the strikingly better fit of the regression models when incorporating previous year's weather (compare Fig. 5a, b). The incorporation led to more accurate estimates of annual NEP sums, with much smaller deviations between modeled and measured single year NEP (Fig. 5c) and reduced uncertainty of modeled NEP (Fig. 5b). Also Babst et al. (2013) emphasized the relevance of lagged climatic effects on radial tree growth, a measure closely related to annual NEP at the Davos site (Zweifel et al., 2010).

Although our models explained 53 % of interannual variability, and thus improved earlier explanations of variance in annual NEP (compare with Urbanski et al., 2007), our models nevertheless focused only on seasonal climatic drivers of NEP, still leaving 47 % (= 100–53 %) of the interannual variability of NEP unexplained. Unusually extreme weather events occurring at shorter timescales than the seasonal scale used in this study and biotic processes occurring at longer timescales (e.g., changes in stand structure or species composition) were not considered. Biotic processes have been shown to determine 10 % of interannual variability of NEP in a coniferous forest (Duke forest, USA; Hui et al., 2003), 55 % in a mixed forest (Howland forest, USA; Richardson et al., 2007), and up to 80 % in a broadleaf forest (Soroe forest, Denmark; Wu et al., 2012), with increasing importance at longer timescales (Wu et al., 2012). However, biotic processes are less likely to be responsible for 47 % of interannual variability of NEP at Davos that remained unexplained, since stand structure and species composition did not change over the 15 yr of EC measurements.

Despite the impact of previous year's weather on NEP, current year's weather in spring had a consistent and strong influence on annual NEP of our subalpine spruce forest over 15 yr, although current year's weather only explained 20 % of the interannual variability of NEP when used alone. Higher soil temperatures in spring (March–May) increased annual

NEP (Table 2), mainly due to GPP increasing earlier and faster in spring than TER (Fig. 3). This asynchrony of GPP and TER seems to be related to different temperature responses. During winter, the thermal insulation of a full snow cover (Fig. 1b) causes soil temperatures to linger at the freezing point (Fig. 3). As soon as mean daily soil temperatures rose above 0 °C, GPP started to increase (Fig. 3), even though air temperatures were still below zero at that time (Fig. 1a). Thawing of the upper soil layer, and thus mediating water availability, has been shown to control annual NEP (Monson et al., 2002; Sacks et al., 2007), trigger photosynthesis (Jarvis and Linder, 2000; Bergh and Linder, 2001), and radial tree growth (Vaganov et al., 1999) in forests of cold climates, such as the Davos Seehornwald forest. Suni et al. (2003) showed that photosynthetic C uptake was possible even with soil temperatures at the freezing point, supporting our results of needle C uptake throughout the whole winter (Fig. 3). In contrast, TER started to increase only when soil temperatures values rose above 2 °C (Fig. 3), which only happened when air temperatures clearly exceeded the freezing point and snow cover had disappeared (Fig. 1). Such a response to temperatures well above the freezing point was also shown for soil respiration, the major component of TER at the Davos site (Etzold et al., 2011).

5 Conclusions

Based on this long-term, 15 yr dataset we strongly recommend considering the influence of previous year's weather on NEP modeled SVATs to allow for more precise estimates of annual C budgets in forest ecosystems. With this addition to a SVAT we expect the greatest improvements in modeled NEP of forest ecosystems in cold climates, as shown here for the subalpine Davos forest. Moreover, assuming a continuing trend of increasing spring temperatures in Europe under future climate warming, we expect that the carbon sequestration potential of the Davos forest will further increase, unless other resources become limiting.

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References

- Babst, F., Carrer, M., Poulter, B., Urbinati, C., Neuwirth, B., and Frank, D.: 500 years of regional forest growth variability and links to climatic extreme events in Europe, *Environ. Res. Lett.*, 7, 045705, doi:10.1088/1748-9326/7/4/045705, 2012.
- Babst, F., Poulter, B., Trouet, V., Tan, K., Neuwirth, B., Wilson, R., Carrer, M., Grabner, M., Tegel, W., Levanic, T., Panayotov, M., Urbinati, C., Bouriaud, O., Ciais, P., and Frank, D.: Site- and species-specific responses of forest growth to climate across the European continent, *Global Ecol. Biogeogr.*, 22, 706–717, 2013.
- Bergh, J. and Linder, S.: Effects of soil warming during spring on photosynthetic recovery in boreal Norway spruce stands, *Glob. Change Biol.*, 5, 245–253, 2001.
- Bonan, G. B.: Forests and climate change: forcings, feedbacks, and the climate benefits of forests, *Science*, 320, 1444–1449, 2008.
- Burba, G. G., McDermitt, D. K., Grelle, A., Anderson, D. J., and Xu, L.: Addressing the influence of instrument surface heat exchange on the measurements of CO₂ flux from open-path gas analyzers, *Glob. Change Biol.*, 14, 1854–1876, 2008.
- Carbone, M. S., Czimczik, C. I., Keenan, T. F., Murakami, P. F., Pederson, N., Schaberg, P. G., Xu, X., and Richardson, A. D.: Age, allocation and availability of nonstructural carbon in mature red maple trees, *New Phytol.*, 187, 819–830, 2013.
- Desai, A. R., Moore, D. J., Ahue, W. K., Wilkes, P. T., De Wekker, S. F., Brooks, B. G., Campos, T. L., Stephens, B. B., Monson, R. K., Burns, S. P., Quaife, T., Aulenbach, S. M., and Schimel, D. S.: Seasonal pattern of regional carbon balance in the central Rocky Mountains from surface and airborne measurements, *J. Geophys. Res.-Biogeo.*, 116, G04009, doi:10.1029/2011JG001655, 2011.
- Dobbertin, M.: Tree growth as indicator of tree vitality and of tree reaction to environmental stress: a review, *Eur. J. Forest Res.*, 124, 319–333, 2005.
- Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D., and Lautenbach, S.: Collinearity: a review of methods to deal with it and a simulation study evaluating their performance, *Ecography*, 36, 27–46, 2012.
- Elith, J., Graham, C. H., Anderson, R. P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R. J., Huettmann, F., Leathwick, J. R., Lehmann, A., Li, J., Lohmann, L. G., Loiselle, B. A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J. McC., Townsend Peterson, A., Phillips, S. J., Richardson, K., Scachetti-Pereira, R., Schapire, R. E., Soberón, J., Williams, S., Wisz, M. S., and Zimmermann, N. E.: Novel methods improve prediction of species' distributions from occurrence data, *Ecography*, 29, 129–151, 2006.
- Epron, D., Bahn, M., Derrien, D., Lattanzi, F. A., Pumpanen, J., Gessler, A., Hogberg, P., Maillard, P., Dannoura, M., Gerant, D., and Buchmann, N.: Pulse-labelling trees to study carbon allocation dynamics: a review of methods, current knowledge and future prospects, *Tree Physiol.*, 23, 776–798, 2012.
- Etzold, S., Ruehr, N. K., Zweifel, R., Dobbertin, M., Zingg, A., Pluess, P., Häslér, R., Eugster, W., and Buchmann, N.: The carbon balance of two contrasting mountain forest ecosystems in Switzerland: similar annual trends, but seasonal differences, *Ecosystems*, 14, 1289–1309, 2011.
- Gough, C. M., Vogel, C. S., Schmid, H. P., Su, H. B., and Curtis, P. S.: Multi-year convergence of biometric and meteorological estimates of forest carbon storage, *Agr. Forest Meteorol.*, 148, 158–170, 2008.
- Hanson, P., Amthor, J., Wullschleger, S., Wilson, K., Grant, R., Hartley, A., Hui, D., Hunt, E., Johnson, D., Kimball, J., King, A., Luo, Y., McNulty, S., Sun, G., Thornton, P., Wang, S., Williams, M., Baldocchi, D., and Cushman, R.: Oak forest carbon and water simulations – model intercomparison and evaluation against independent data, *Ecol. Monogr.*, 74, 443–489, 2004.
- Hoch, G., Richter, A., and Körner, C.: Non-structural carbon compounds in temperate forest trees, *Plant Cell Environ.*, 26, 1067–1081, 2003.
- Hui, D., Luo, Y., and Katul, G.: Partitioning interannual variability in net ecosystem exchange between climatic variability and functional change, *Tree Physiol.*, 23, 433–442, 2003.
- Järvi, L., Mammarella, I., Eugster, W., Ibrom, A., Siivola, E., Dellwik, E., Keronen, P., Burba, G., and Vesala, T.: Comparison of net CO₂ fluxes measured with open- and closed-path IRGA in an urban complex environment, *Boreal Environ. Res.*, 14, 499–514, 2009.
- Jarvis, P. and Linder, S.: Botany: constraints to growth of boreal forests, *Nature*, 405, 904–905, 2000.
- Jörg, S.: Böden im Seehornwald bei Davos und deren Vorrat an Kohlenstoff und Stickstoff, diploma thesis, Zürcher Hochschule für Angewandte Wissenschaften ZHAW, 2008.
- Katul, G., Lai, C.-T., Schäfer, K., Vidakovic, B., Albertson, J., Ellsworth, D., and Oren, R.: Multiscale analysis of vegetation surface fluxes – from seconds to years, *Adv. Water Resour.*, 24, 1019–1032, 2001.
- Mauder, M., Foken, T., Clement, R., Elbers, J. A., Eugster, W., Grünwald, T., Heusinkveld, B., and Kolle, O.: Quality control of CarboEurope flux data – Part 2: Inter-comparison of eddy-covariance software, *Biogeosciences*, 5, 451–462, doi:10.5194/bg-5-451-2008, 2008.
- Monson, R., Turnipseed, A., Sparks, J., Harley, P., Scott-Denton, L., Sparks, K., and Huxman, T.: Carbon sequestration in a high-elevation, subalpine forest, *Glob. Change Biol.*, 8, 459–478, 2002.
- Oberhuber, W., Swidrak, I., Pirkebner, D., and Gruber, A.: Temporal dynamics of nonstructural carbohydrates and xylem growth in *Pinus sylvestris* exposed to drought, *Can. J. Forest Res.*, 41, 1590–1597, 2011.
- Pederson, N., Cook, E. R., Jacoby, G. C., Peteet, D. M., and Griffin, K. L.: The influence of winter temperatures on the annual radial growth of six northern range margin tree species, *Dendrochronologia*, 22, 7–29, 2004.
- Pichler, P. and Oberhuber, W.: Radial growth response of coniferous forest trees in an inner Alpine environment to heat-wave in 2003, *Forest Ecol. Manag.*, 242, 688–699, 2007.
- Quinn, G. and Keough, M.: *Experimental Design and Data Analysis for Biologists*, Cambridge University Press, 2001.
- R Core Team: *R: A Language and Environment for Statistical Computing*, R Foundation for Statistical Computing, Vienna, Austria, available at: <http://www.R-project.org/>, 2012.
- Rawlings, J. O., Pantula, S. G., and Dickey, D. A.: *Applied Regression Analysis: a Research Tool*, Springer, 1998.
- Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Aubinet, M., Berbigier, P., Bernhofer, C., Buchmann, N., Gilmanov, T.,

- Granier, A., Grünwald, T., Havráňková, K., Ilvesniemi, H., Janous, D., Knohl, A., Laurila, T., Lohila, A., Loustau, D., Matteucci, G., Meyers, T., Miglietta, F., Ourcival, J.-M., Pumpanen, J., Rambal, S., Rotenberg, E., Sanz, M., Tenhunen, J., Seufert, G., Vaccari, F., Vesala, T., Yakir, D., and Valentini, R.: On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm, *Glob. Change Biol.*, 11, 1424–1439, 2005.
- Richardson, A. D., Hollinger, D. Y., Aber, J. D., Ollinger, S. V., and Braswell, B. H.: Environmental variation is directly responsible for short- but not long-term variation in forest-atmosphere carbon exchange, *Glob. Change Biol.*, 13, 788–803, 2007.
- Richardson, A. D., Carbone, M. S., Keenan, T. F., Czimczik, C. I., Hollinger, D. Y., Murakami, P., Schaberg, P. G., and Xu, X.: Seasonal dynamics and age of stemwood nonstructural carbohydrates in temperate forest trees, *New Phytol.*, 197, 850–861, 2013.
- Rocha, A. V. and Goulden, M. L.: Drought legacies influence the long-term carbon balance of a freshwater marsh, *J. Geophys. Res.*, 115, G00H02, doi:10.1029/2009JG001215, 2010.
- Rocha, A. V., Goulden, M. L., Dunn, A. L., and Wofsy, S. C.: On linking interannual tree ring variability with observations of whole-forest CO₂ flux, *Glob. Change Biol.*, 12, 1378–1389, 2006.
- Sacks, W. J., Schimel, D. S., and Monson, R. K.: Coupling between carbon cycling and climate in a high-elevation, subalpine forest: a model-data fusion analysis, *Oecologia*, 151, 54–68, 2007.
- Schädel, C., Blöchl, A., Richter, A., and Hoch, G.: Short-term dynamics of nonstructural carbohydrates and hemicelluloses in young branches of temperate forest trees during bud break, *Tree Physiol.*, 29, 901–911, 2009.
- Stoy, P. C., Richardson, A. D., Baldocchi, D. D., Katul, G. G., Stanovick, J., Mahecha, M. D., Reichstein, M., Detto, M., Law, B. E., Wohlfahrt, G., Arriga, N., Campos, J., McCaughey, J. H., Montagnani, L., Paw U, K. T., Sevanto, S., and Williams, M.: Biosphere-atmosphere exchange of CO₂ in relation to climate: a cross-biome analysis across multiple time scales, *Biogeosciences*, 6, 2297–2312, doi:10.5194/bg-6-2297-2009, 2009.
- Suni, T., Berninger, F., Vesala, T., Markkanen, T., Hari, P., Mäkelä, A., Ilvesniemi, H., Hänninen, H., Nikinmaa, E., Huttula, T., Laurila, T., Aurela, M., Grelle, A., Lindroth, A., Arneeth, A., Shibistova, O., and Lloyd, J.: Air temperature triggers the recovery of evergreen boreal forest photosynthesis in spring, *Glob. Change Biol.*, 9, 1410–1426, 2003.
- Suzuki, N., Olson, D. H., and Reilly, E. C.: Developing landscape habitat models for rare amphibians with small geographic ranges: a case study of Siskiyou Mountains salamanders in the western USA, *Biodivers. Conserv.*, 17, 2197–2218, 2008.
- Urbanski, S., Barford, C., Wofsy, S., Kucharik, C., Pyle, E., Budney, J., McKain, K., Fitzjarrald, D., Czikowsky, M., and Munger, J. W.: Factors controlling CO₂ exchange on timescales from hourly to decadal at Harvard Forest, *J. Geophys. Res.*, 112, G02020, doi:10.1029/2006JG000293, 2007.
- Vaganov, E., Hughes, M., Kirilyanov, A., Schweingruber, F., and Silkin, P.: Influence of snowfall and melt timing on tree growth in subarctic Eurasia, *Nature*, 400, 149–151, 1999.
- Webb, E. K., Pearman, G. I., and Leuning, R.: Correction of flux measurements for density effects due to heat and water vapour transfer, *Q. J. Roy. Meteor. Soc.*, 106, 85–100, 1980.
- Wu, J., van der Linden, L., Lasslop, G., Carvalhais, N., Pilegaard, K., Beier, C., and Ibrom, A.: Effects of climate variability and functional changes on the interannual variation of the carbon balance in a temperate deciduous forest, *Biogeosciences*, 9, 13–28, doi:10.5194/bg-9-13-2012, 2012.
- Zeller, K. and Nikolov, N.: Quantifying simultaneous fluxes of ozone, carbon dioxide and water vapor above a subalpine forest ecosystem, *Environ. Pollut.*, 107, 1–20, 2000.
- Zweifel, R., Zimmerman, L., Zeugin, F., and Newbery, D.: Intra-annual radial growth and water relations of trees: implications towards a growth mechanism, *J. Exp. Bot.*, 57, 1445–1459, 2006.
- Zweifel, R., Eugster, W., Etzold, S., Dobbertin, M., Buchmann, N., and Häsler, R.: Link between continuous stem radius changes and net ecosystem productivity of a subalpine Norway spruce forest in the Swiss Alps, *New Phytol.*, 187, 819–830, 2010.