Climatic and biological drivers of temporal dynamics and feedbacks of the carbon balance of forests

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“Everything will be okay in the end. If it is not okay, it is not the end.”

John Lennon
Abstract

Forest ecosystems, covering a third of the world’s land surface, play a major role in the global carbon (C) cycle due to their ability to take up and store large amounts of atmospheric carbon dioxide (CO$_2$). Thus, accurate and reliable estimates of annual forest C budgets are needed, e.g. for post-Kyoto agreements on national levels. However, the large inter-annual variability and still existing knowledge gaps on drivers and their underlying ecophysiological mechanisms of C exchange processes result in profound difficulties explaining and calculating annual forest C budgets. Uncertainties of these estimates need to be substantially reduced. Hence, this PhD project investigated climatic and biological drivers of temporal and dynamic feedbacks of the C balance of forest ecosystems, including tree growth as its major component.

The aim of this thesis was addressed by analysing data of eddy covariance (EC) measurements of the CO$_2$ exchange as well as dendrometer and tree-ring derived data on tree growth of Swiss, European, and North American forests, covering a broad gradient of climatic conditions and strongly varying site characteristics. First, concentrating on Swiss forests, we showed that the C balance of a subalpine coniferous forest was both strongly and positively driven by current and previous year’s weather conditions in spring (March, April, May). Explained inter-annual variability of the net ecosystem productivity (NEP) rose from 20% to 53%, when the previous year was included into the statistical analysis, indicating delayed responses of forest NEP to previous year’s weather. The relevance of (current year) spring weather was also confirmed by tree-ring analysis of the same subalpine forest as well as by analysis of EC data of a mixed deciduous mountain forest in Switzerland. Air and soil temperature in spring were frequently identified as the driving climate variables of NEP.

By expanding our analysis to the European scale and additionally including two North American forest ecosystems, we could confirm both the single-site results of the influence of the previous year on and the importance of spring for the C balance of strongly differing forests. We quantified that on average (eight out of nine sites), explained inter-annual variability of NEP rose from 49% to 64% when considering both current and previous year’s weather, with weather conditions in current and previous year’s spring being highly influential for forest NEP also on this larger
spatial scale. Yet, the response magnitude to previous year’s weather varied strongly among sites. The strength of this varying response magnitude was determined by exposure to cold climatic conditions and the productivity of the forest, with stronger exposition to low temperatures and lower productivity leading to a more pronounced delayed response. Overall, we provided strong evidence for a consistent delayed response of NEP in boreal and temperate forests and the importance of spring conditions. Also, the compensation of respiratory losses, usually occurring in spring, were shown to be of special importance for year-end NEP of several European forests, explaining on average 70% thereof, and thus, further emphasizing the strong weight of this season on the forest C balance.

However, availability of EC-derived forest NEP data, which is used to determine the forest C budget, is often limited due to the small number of EC sites throughout the world. More widely available data on tree-growth, as measured via tree-ring width or dendrometers, bear large potential to explain NEP, however, linking both information has not been done yet on a larger spatial scale. Thus, we analysed the link between EC derived NEP and tree growth, first using tree-ring data of a Swiss subalpine coniferous forests and in a next step dendrometer data of six highly differing European forests. In the first step, we were able to show a close and positive link between NEP and tree-growth on an annual time scale \((r = 0.661)\). The link was even more profound within the multi-site study, in which we build a simple regression model base on dendrometer data, which was able to explain on average 85% of NEP on a daily basis. The only driver in this model was identified as “time to grow”, defined as the tree-growth amplitude over time.

Our results strongly suggest that including delayed responses of NEP as well as measures integrating over meteorological and biological conditions, such as tree-growth, in forest C budget estimates have great potential to increase their accuracy and reliability as a result of increased process understanding. Moreover, the development of weather conditions in spring under future climate change will be of high importance for the C budget of temperate and boreal forest ecosystems, given the strong determining power of this season as shown in this PhD project.
Zusammenfassung


einzigen Treiber in diesem Modell identifizierten wir als “time to grow”, definiert als die Amplitude des Baumwachstums über die Zeit.


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Chapter 1

General introduction

1.1 Global climate change – the broader context

The climate of the Earth undergoes constant change, however, since the late 19th century this change has become increasingly exceptional. During the last 60 years, combined land and ocean temperature increased by an average of 0.72 °C and the period from 1983 to 2012 was the warmest period during the last 800 years (IPCC, 2013). There is (almost) no doubt (95–100% probability) that this change in climate is caused by human activity. Anthropogenic emissions of carbon dioxide (CO₂), mainly from fossil fuel combustion, are the main driver of this temperature increase due to the modification of the Earth’s energy balance (IPCC, 2013). These emissions resulted in an increase of the CO₂ concentration in the atmosphere from 278 ppm in 1750 to 395.3 ppm in 2013 (Dlugokencky and Tans, 2014). Despite the changes in mean climate, anthropogenic activity also likely changes the frequency and intensity of climate extremes (IPCC, 2012), including extreme temperatures (e.g. Dobrovolný et al., 2010) and precipitation (e.g. Peterson et al., 2008) as well as the lack of the latter leading to drought (e.g. Van der Schrier et al., 2006). It has to be stated here, that, despite global trends, changes of means and extremes may vary strongly on regional scales and uncertainties are usually higher for anticipated changes in extreme events (IPCC, 2012).

Emitted anthropogenic CO₂, the major driver of climate change, enters the global carbon cycle, which includes two major carbon (C) sinks: oceans and terrestrial
1.2 CO₂ EXCHANGE AND FOREST ECOSYSTEMS

Ecosystems. From the annually emitted $9.5 \pm 0.5$ PgC in 2011, $4.1 \pm 0.9$ PgC were taken up by terrestrial biosphere reservoirs via gross primary productivity (GPP) (Le Quéré et al., 2013). Further partitioning of the terrestrial CO₂ sink reveals that forest ecosystems account for almost 60% ($2.4 \pm 0.4$ PgC) of the entire terrestrial C sink strength (Pan et al., 2011). However, both the entire terrestrial as well as the forest C sink strength are obtained by extensive modeling efforts (usually dynamic–global-vegetation–models, DGVM) with accompanied uncertainties (alternatively, the former is calculated simply as the residual flux of all other flux components in the global C cycle). Thus, understanding the climatic and biological drivers as well as mechanisms determining the interaction of the atmosphere and forest ecosystems, the overarching scope of this thesis, are of great global importance for providing high quality C budget estimates of forest ecosystems in the highlight of mitigating climate change as well as under consideration of the need for country-specific C budgets.

1.2 CO₂ exchange and forest ecosystems

Exchange of CO₂ over forests comprises of two oppositional fluxes: uptake of CO₂ from the atmosphere into the biosphere by living plant tissues during the day, that is CO₂ assimilation (photosynthesis), and release of CO₂ from the biosphere through autotrophic and heterotrophic respiration during both day and night. On an ecosystems scale, these two fluxes are usually referred to as gross primary productivity (GPP) and total ecosystem respiration (TER), respectively, and the relatively small difference between these two fluxes is the net ecosystem productivity (NEP). On the one hand, the CO₂ exchange processes of forests ecosystems are driven by climatic (abiotic) drivers, e.g., radiation as well as temperature and moisture content of air and soil. On the other hand, biological processes, such as changes in C storage, stand structure or species composition are assumed to play an increasingly important role at larger time scales (Hui et al., 2003; Richardson et al., 2007; Wu et al., 2012). Both climatic and biological drivers are affected by climate change (IPCC, 2013), and thus, is the ability of forest ecosystems to sequester C. However, the response of the forest C balance to climate change is still unclear, as changes in assimilation and respiration could lead to either an increase, a decrease, or no change of the net C exchange. The unknown changes of these two oppositional fluxes are also coupled to the lack of clarity concerning the relevance of weather conditions in spring versus
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those in fall for the C balance of forests (e.g. Hollinger et al., 2004; Niemand et al., 2005; Sacks et al., 2007; Piao et al., 2008; Richardson et al., 2010; Keenan et al., 2014). Climate change induced alterations of the weather conditions in these seasons could again affect the C balance differently, e.g. due to an earlier start of the growing season, and thus, changes in growing season length or increased respiratory losses in fall due to warmer temperatures late in the year.

Since the 1980s, the eddy covariance (EC) method allows for direct measurements of NEP within the flux footprint at high temporal resolution (20Hz), integrating over the whole ecosystem from hourly to annual time scales (Buchmann and Schulze, 1999; Baldocchi, 2003, 2008). With the establishment of long-term EC measurement sites over forest ecosystems in the early 1990s (e.g. Wofsy et al., 1993; Black et al., 1996; Valentini et al., 1996), scientists are providing CO$_2$ flux data which enable us to study the inter-annual variability of forest NEP as well as its climatic drivers through accompanied micrometeorological measurements. The information gained about drivers of inter-annual variability as well as the data itself in combination with biological process understanding then provide the basis for above mentioned modeling efforts as well as the foundation for model validation. Yet, due to large inter-annual variability in forest NEP as well as knowledge gaps in the understanding of underlying biological processes, explaining as well as modeling this variability has shown to be challenging (Urbanski et al., 2007; Gough et al., 2008). Notably, the inadequate representation of delayed responses of NEP and its determining processes, especially tree-growth, to weather conditions of the previous year(s) is frequently proposed as one possible reason for poor model performance and lack of quality of C budget estimates (Keenan et al., 2012; Babst et al., 2013).

In addition to EC data, measurements on the tree scale, either by tree-ring analysis or by dendrometer measurements, provide valuable insights into the dominating C sink of forest ecosystems, that is tree growth (e.g. Zweifel et al., 2010; Babst et al., 2012; King et al., 2013). Tree-ring width analysis allows for reconstruction of past tree growth over up to several centuries (depending on tree age), yet, is restricted mostly to information on annual time scales. Highly-resolved and continuous dendrometer measurements, although not enabling the look into the past, can depict tree growth at temporal resolutions comparable to the EC method, while providing additional insights into tree-water relations when examining data resolved from minutes to days (Zweifel et al., 2006). Despite their different time resolutions and
information densities, both methods seem to be integrators over the entire ecosystem C balance and consolidate the prevailing meteorological conditions, as shown in a recent single-site study (Zweifel et al., 2010). Thus, combining tree scale measurements with direct forest ecosystem investigations on C exchange via eddy covariance holds great potential to further improve the understanding of forest–atmosphere interactions and their drivers.

1.3 Goals and research questions

Within this Ph.D., we studied temporal dynamics and feedbacks of the C balance of temperate and boreal forests on regional to continental spatial scales and half-hourly to annual time scales. The main goal of this PhD thesis was to substantially increase our so far limited knowledge of climatic and biological drivers of a forest’s C balance as well as identifying the underlying physiological mechanisms responsible for relationships between driver and forest C response. A special emphasis was placed on the relevance and quantification of delayed responses of the C budget of forests to an influence of weather conditions of the previous year. With these goals, we aimed at providing process understanding, leading to reduced uncertainties and increased quality of C budget estimates of forest ecosystems under future climate change. The research questions were:

1. Which climatic drivers influence the (temporal) dynamics of the C balance of forest ecosystems?

2. At what time of the year is the influence of these drivers most important?

3. To what extent do temporal feedback mechanisms, e.g. delayed responses of current year NEP to previous year’s weather, determine the C balance of forest ecosystems? What are the possible implications for C budget estimates?

4. Which climatic and/or biological drivers determine the strength of such feedback mechanisms?

5. How does tree growth relate to the C balance of the entire forest ecosystem and what drivers determine this relationship?
1.4 Approach and outline

To fulfill the goals of this thesis and answer our research questions, we analyzed CO\textsubscript{2} exchange derived from eddy covariance measurements as well as tree growth as given by high-resolution dendrometer measurements and tree-ring width analysis from strongly differing temperate and boreal forests throughout Europe and parts of North America. In combination with site-specific meteorological data and biological information, this approach gave us the opportunity to identify drivers of temporal dynamics and feedbacks of the C balance of forests, quantify their influence and reveal underlying ecophysiological mechanisms relevant at different spatial and temporal scales.

Chapter 2 and Chapter 3 deal with the first three research questions of this thesis by analysing EC-derived CO\textsubscript{2} exchange and meteorological data of Swiss forests. While Chapter 2 focuses on climatic drivers of the inter-annual variability of the C balance as well as the relevance of previous year’s weather for current year C uptake in a subalpine spruce forest, Chapter 3 analyses the influence of a single extreme weather event on the C fluxes of two contrasting forests in Switzerland.

Chapter 4 builds upon the results of Chapter 2, however, expands the analysis of CO\textsubscript{2} exchange to strongly differing European and North American forest ecosystems to validate the findings of the single Swiss forest. By incorporating site-specific climatic and biological information into the analysis, this chapter also tackles the fourth research question on the drivers of differing strengths of feedback mechanisms. This multi-site study then aims at providing ecophysiological insights which hold great potential to increase the precision of annual C budget estimates across different forest ecosystems. This is also true for Chapter 5, which investigates the timing of compensating respiratory C losses of European forests and its ability to predict year-end NEP.

The remaining parts of this thesis, Chapter 6, Appendix A, and Appendix B, address the fifth research question on the relationship between tree growth and the forest ecosystem C balance. Chapter 5 does so by combining tree-ring width analysis with EC measurements of NEP for a Swiss spruce forests. Appendix A and Appendix B, however, relate tree growth derived from highly-resolved dendrometer measurements to EC measurements of NEP. Appendix A provides the methodological basis for
disentangling stem growth from tree water dynamics which then serves as basis for analysing the relationship between tree growth measured by dendrometers and the EC-derived ecosystem C balance for strongly differing forests across Europe (Appendix B).
1.5 References


Chapter 2

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 inter-annual 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 CO$_2$, sequestering $210\pm88$ g C m$^{-2}$ per year on average. Previous year’s weather strongly affected inter-annual 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 CO$_2$ uptake with future climate warming, as long as no other resources become limiting.
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2.1 Introduction

Modeling and explaining inter-annual net ecosystem productivity (NEP) of forests, where NEP is the relatively small difference between gross primary productivity (GPP) and total ecosystem respiration (TER), has been shown to be challenging (Urbanski et al., 2007; Gough et al., 2008), and only weak links (r² < 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 inter-annual NEP may arise from their focus on immediate responses of forest ecosystems to current year 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 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 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 might is yet another process possibly responsible for delayed responses. Therefore, we hypothesize 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 inter-annual variability of forest NEP. Such phenomena have been reported for both non-forest 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 radial tree growth. Until now, however, little attention has been paid to the influence of such relationships on CO$_2$ 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 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 built-up of stored C and the formation of buds might be hampered and thus, affecting current year 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.

2.2 Materials and methods

2.2.1 Site description

We conducted measurements at the Swiss FluxNet site Davos Seehornwald, a subalpine coniferous forest located in the south-eastern 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
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spruce (Picea abies) and shows a patchy understory of shrubs (Vaccinium myrtillus, Vaccinium gaultherioides), mosses (Hylocomium splendes, 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).

2.2.2 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 $r^2 = 0.69; p < 0.001$).

2.2.3 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
2.2. MATERIALS AND METHODS

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 pathlength of the sensor is subject to self-heating effects. The fraction \( \delta \) 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 \( u_\ast \) filter with a threshold of \( u_\ast < 0.2 \text{ m s}^{-1} \).

In addition, we filtered large unrealistic negative nighttime CO\(_2\) fluxes. Therefore, we used a symmetric method, i.e., within a 14 day moving window, both negative and positive nighttime CO\(_2\) fluxes outside the 14 day mean \( \pm 1 \) SD were dismissed.

High-quality data were available during 43\% (2008) to 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 \( \mu\text{mol m}^{-2}\text{s}^{-1} \)).

2.2.4 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 2.1). 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 \textit{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. \textit{SoilTemp.spring}\(-1\). Accordingly, “winter\(-1\)” is the season with the longest time period between itself and current year NEP, including December of the year before the previous year as
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well as January and February of the actual previous year. Current year winter then includes previous year December as well as current year 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 interdependences 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 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 $\geq 1$), 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 $r^2$ ($\text{adj. } r^2$) as selection criterion for the best model and constrained the analysis of climate drivers to models with three variables at the most (see Sect. 2.3.2 for details). By calculating standardized regression coefficients ($\beta$; 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 re-calculate annual NEP.
2.3 Results

2.3.1 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 g C m$^{-2}$ yr$^{-1}$ (1997) to 336 g C m$^{-2}$ yr$^{-1}$ (2009), with a 15 yr average of 210 ± 88 g C m$^{-2}$ yr$^{-1}$ (mean ± 1 SD) (Fig. 2.2) 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 (|TER| > 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. 2.1), photosynthesis 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. 2.1). The temporal pattern of cumulative NEP in 2001 differed substantially from all other years (Fig. 2.2). 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 1981–2010). Consequently, the year 2001 showed the second highest net carbon uptake during the measurement period with an annual NEP of 314 g C m$^{-2}$ 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. 2.3), the time in year when air temperature was well above zero and the snow cover had disappeared (Fig. 2.1). This increase in mean daily NEP from the beginning of spring was mainly 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. 2.3).

### 2.3.2 Climate drivers of net ecosystem productivity

At the Davos site, 20% of inter-annual variability of NEP during 1997–2011 could be explained with two out of a maximum of three climate variables from the current year (Fig. 2.4a). However, also including climate variables from the previous year in the analysis (Fig. 2.4b), and thus accounting for a response of NEP to previous year’s weather, further increased the explained inter-annual variance, reaching 53% (limiting the analysis to three variables, see Sect. 4.2.3). 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 choosen 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. 2.4b, hatched area), yet, strongly overparametrizing the linear models in relation to the dependent variable (i.e., 15 years). Therefore, we limited 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 ($\text{SoilTemp.spring}$) was identified as the most influential driver of NEP (Table 2.2). 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 2.2). When previous year’s weather was included, minimum air temperature of the previous year’s spring ($T2\text{min.spring} - 1$) 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

19
variables, respectively). For both subsets, the third explanatory variable was only of minor importance ($PPFD_{fall} - 1, \beta = -0.30$; Table 2.2) and did not increase the explained inter-annual variability of NEP significantly.

2.3.3 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 2.2) to compare their performance to measured single-year NEP (1997–2011; Fig. 2.5). The model with both current and previous year’s weather was substantially better able to reproduce the inter-annual variability than the one without (current and previous year: $adj. r^2 = 0.53$ vs. current year only: $adj. r^2 = 0.20$, Table 2.2), and also showed smaller confidence intervals (Fig. 2.5a and b). Focusing on single years, the linear model with year’s weather only over- or underestimated measured annual NEP anomalies by more than 50 g C m$^{-2}$ yr$^{-1}$ for 10 of the 15 yr – only in five years (1997, 1999, 2003, 2010, and 2011) this model performed well (Fig. 2.5c). In contrast, the linear model including current and previous year’s weather performed well in 11 out of 15 yr – only in four years (2003, 2008, 2009, 2010) the deviations from the measured annual NEP anomalies were larger than 50 g C m$^{-2}$ yr$^{-1}$.

2.4 Discussion

Our study showed that only when considering previous year’s weather we explained inter-annual 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 were included in the analysis.

2.4.1 Ecosystem carbon sink

The Davos forest was a consistent carbon sink over 15 yr of measurements (1997–2011; Fig. 2.2), with annual CO$_2$ sinks ranging from 54 to 336 g C m$^{-2}$ 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 g C m$^{-2}$ 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 Ameri-Flux site, another sub-alpine coniferous forest (Abies lasiocarpa, Picea engelmannii, Pinus contorta), showed a mean annual uptake of 216 g C m$^{-2}$ yr$^{-1}$ (Desai et al., 2011). These values are in line with the mean annual NEP (210 g C m$^{-2}$ 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).

### 2.4.2 Environmental controls of annual net ecosystem productivity

Considering previous year’s weather substantially increased explained variance of inter-annual variability in NEP from 20% to 53% (Fig. 2.4, Table 2.2), leading to an $\text{adj. } r^2$ 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 ($T_{\text{2min.spring}} - 1$) promoting current year NEP (Table 2.2), 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 non-structural 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
2.4. DISCUSSION

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 2.2). 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 pre-set 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 \((T_{2min\_spring} - 1)\); Table 2.2) 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. 2.5a and b). The incorporation led to more accurate estimates of annual NEP sums, with much smaller deviations between modeled and measured single year NEP (Fig. 2.5c) and reduced uncertainty of modeled NEP (Fig. 2.5b). 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 inter-annual 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 inter-annual variability of NEP unexplained. Unusually extreme weather events occurring at shorter time scales than the seasonal scale used in this study and biotic processes occurring at longer time scales (e.g., changes in stand structure or species composition) were not considered. Biotic processes have been shown to determine 10% of inter-annual 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 time scales (Wu et al., 2012). However, biotic processes are less likely to be responsible for 47% of inter-annual 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 inter-annual variability of NEP when used alone. Higher soil temperatures in spring (March–May) increased annual NEP (Table 2.2), mainly due to GPP increasing earlier and faster in spring than TER (Fig. 2.3). 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. 2.1b) causes soil temperatures to linger at the freezing point (Fig. 2.3). As soon as mean daily soil temperatures rose above 0°C, GPP started to increase (Fig. 2.3), even though air temperatures were still below zero at that time (Fig. 2.1a). 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. 2.3). In contrast, TER started to increase only when soil temperatures values rose above 2°C (Fig. 2.3), which only happened when air temperatures clearly exceeded the freezing point and snow cover had disappeared (Fig. 2.1). 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).

2.5 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 pre-
cise 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.

Acknowledgements

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CHAPTER 2. NEP OF A SWISS SUBALPINE FOREST IS SIGNIFICANTLY DRIVEN NOT ONLY BY CURRENT BUT ALSO BY PREVIOUS YEAR'S WEATHER

2.6 References


CHAPTER 2. NEP OF A SWISS SUBALPINE FOREST IS SIGNIFICANTLY DRIVEN NOT ONLY BY CURRENT BUT ALSO BY PREVIOUS YEAR’S WEATHER


CHAPTER 2. NEP OF A SWISS SUBALPINE FOREST IS SIGNIFICANTLY DRIVEN NOT ONLY BY CURRENT BUT ALSO BY PREVIOUS YEAR’S WEATHER


2.7 Tables and figures

Table 2.1: Abbreviations of the climatic variables used in this study, their descriptions and units.

<table>
<thead>
<tr>
<th>Variable abbreviation</th>
<th>Description</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>T2</td>
<td>Mean air temperature at 2 m height</td>
<td>°C</td>
</tr>
<tr>
<td>T2max</td>
<td>Maximum air temperature at 2 m height</td>
<td>°C</td>
</tr>
<tr>
<td>T2min</td>
<td>Minimum air temperature at 2 m height</td>
<td>°C</td>
</tr>
<tr>
<td>VPD</td>
<td>Vapor pressure deficit</td>
<td>kPa</td>
</tr>
<tr>
<td>Precip</td>
<td>Precipitation</td>
<td>mm</td>
</tr>
<tr>
<td>SoilTemp</td>
<td>Soil temperature 5 cm below-ground</td>
<td>°C</td>
</tr>
<tr>
<td>PPFD</td>
<td>Photosynthetic photon flux density</td>
<td>μmol m⁻² s⁻¹</td>
</tr>
</tbody>
</table>
### Table 2.2: Linear regression coefficients, p values, and $\beta$ 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 adjusted coefficient of determination ($adj. r^2$) and $p$ values for the entire model ($p_{mod}$). Previous year’s weather variables are denoted with “−1”.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Coefficient</th>
<th>$p$</th>
<th>$\beta$</th>
<th>$adj. r^2$</th>
<th>$p_{mod}$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Models with current year’s weather only</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>578.23</td>
<td>0.0139</td>
<td></td>
<td>–</td>
<td></td>
</tr>
<tr>
<td>SoilTemp.spring</td>
<td>49.65</td>
<td>0.0913</td>
<td>0.44</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td>PPFD.winter</td>
<td>−3.12</td>
<td>0.1811</td>
<td>−0.34</td>
<td>0.20</td>
<td>0.1051</td>
</tr>
<tr>
<td><strong>Models with current and previous year’s weather</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>583.93</td>
<td>0.0464</td>
<td></td>
<td>–</td>
<td></td>
</tr>
<tr>
<td>SoilTemp.spring</td>
<td>101.96</td>
<td>0.0022</td>
<td>0.90</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td>T2min.spring−1</td>
<td>75.93</td>
<td>0.0059</td>
<td>0.70</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td>PPFD.fall−1</td>
<td>−1.81</td>
<td>0.1708</td>
<td>−0.30</td>
<td>0.53</td>
<td>0.0094</td>
</tr>
</tbody>
</table>

$p$ and $\beta$ are valid for each independent variable. $adj. r^2$ and $p_{mod}$ are valid for the entire model.
CHAPTER 2. NEP OF A SWISS SUBALPINE FOREST IS SIGNIFICANTLY DRIVEN NOT ONLY BY CURRENT BUT ALSO BY PREVIOUS YEAR’S WEATHER

Figure 2.1: 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.
Figure 2.2: Annual net ecosystem productivity (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).
CHAPTER 2. NEP OF A SWISS SUBALPINE FOREST IS SIGNIFICANTLY DRIVEN NOT ONLY BY CURRENT BUT ALSO BY PREVIOUS YEAR’S WEATHER

Figure 2.3: Smoothed mean daily sums of net ecosystem productivity (NEP), gross primary productivity (GPP) and total ecosystem respiration (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-day and 18-day smoothing window for the fluxes and the soil temperature, respectively. Seasons are defined according to their meteorological definition (winter: DJF; spring: MAM; summer: JJA; fall: SON).
Figure 2.4: Number of predictors used in the models NEP vs. climatic variables (1997–2011) against the adjusted coefficient of determination (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.
CHAPTER 2. NEP OF A SWISS SUBALPINE FOREST IS SIGNIFICANTLY DRIVEN NOT ONLY BY CURRENT BUT ALSO BY PREVIOUS YEAR’S WEATHER

![Figure 2.5](image)

Figure 2.5: Measured and modeled annual net ecosystem productivity (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).
Chapter 3

Contrasting response of grassland versus forest carbon and water fluxes to spring drought in Switzerland

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Abstract

Since the European summer heat wave of 2003, considerable attention has been paid to the impacts of exceptional weather events on terrestrial ecosystems. While our understanding of the effects of summer drought on ecosystem carbon and water vapour fluxes has recently advanced, the effects of spring drought remain unclear. In Switzerland, spring 2011 (March–May) was the warmest and among the driest since the beginning of meteorological measurements. This study synthesizes Swiss FluxNet data from three grassland and two forest ecosystems to investigate the effects of this spring drought. Across all sites, spring phenological development was 11 days earlier in 2011 compared to the mean of 2000–2011. Soil moisture related reductions of gross primary productivity (GPP) were found at the lowland grassland sites, where productivity did not recover following grass cuts. In contrast, spring GPP was enhanced at the montane grassland and both forests (mixed deciduous and evergreen). Evapotranspiration (ET) was reduced in forests, which also substantially increased their water-use efficiency (WUE) during spring drought, but not in grasslands. These contrasting responses to spring drought of grasslands compared to forests reflect different adaptive strategies between vegetation types, highly relevant to biosphere–atmosphere feedbacks in the climate system.
CHAPTER 3. CONTRASTING RESPONSE OF GRASSLAND VERSUS FOREST CARBON AND WATER FLUXES TO SPRING DROUGHT IN SWITZERLAND

3.1 Introduction

Europe has experienced a number of exceptional weather events during the past decades that have attracted the interest of ecologists, such as severe droughts and heatwaves in summer 2003 (Ciais et al., 2005) and 2010 (Barriopedro et al., 2011), flood events in 2002 (Christensen and Christensen, 2003) and 2005 (Schmocker-Fackel and Naef, 2010), and severe storms—such as ‘Lothar’ in 1999 and ‘Gudrun’ in 2005 (Lindroth et al., 2009). These events have claimed lives, caused substantial economic damage in agriculture, forestry and infrastructure, and heavily disturbed the carbon and water balances of terrestrial ecosystems in Europe (Ciais et al., 2005; Reichstein et al., 2007b). With increasing atmospheric greenhouse gas concentrations, regional climate scenarios have predicted more intense and frequent extreme events in Europe for the future (Schär et al., 2004; Frei et al., 2006). In addition, soil moisture feedbacks to the atmosphere might further enhance extreme temperatures on local and regional scales due to reduced evaporative cooling (Granier et al., 2007; Seneviratne et al., 2010). However, our knowledge about the changes in ecosystem carbon and water fluxes in response to such extreme events is still limited, in particular during the transitional seasons of spring and autumn (Richardson et al., 2010; Zhang et al., 2012).

Research has recently focused on summer droughts and heatwaves, e.g. 2003 (Ciais et al., 2005) and 2010 (Barriopedro et al., 2011) in Europe. However, drought events have also occurred during spring, such as in France and south-eastern UK in 2006, in Germany, The Netherlands and Austria in April 2007, and more recently throughout most of central and north-western Europe in spring 2011 (Vogt, 2012; Quesada et al., 2012; Sepulcre-Canto et al., 2012), when historic records of high temperatures were observed (European Drought Observatory, 1976).

In Switzerland, spring 2011 was the warmest (+3.4 °C above average) and the third driest (−47% below average seasonal precipitation) since the beginning of meteorological measurements in 1864 (MeteoSwiss, 2012), following an exceptionally dry winter with below average precipitation and snow accumulation (Pielmeier, 2011). This combination resulted in a pronounced spring drought that affected plant phenology, agricultural production and water supply. Reservoir levels reached record lows, and irrigation measures were required to preserve agricultural production in parts of Switzerland (BAFU, 2009).
The current understanding of drought effects suggests that plant water limitations are less likely in spring than in summer as soil reservoirs should have been recharged by winter precipitation. However, extreme weather events during early season growth could have severe effects on carbon and water fluxes of terrestrial ecosystems.

Only a few studies have investigated the effects of spring drought on ecosystem carbon and water fluxes so far. These studies reported overall reductions in carbon uptake (Zhang et al., 2012; Dong et al., 2011; Kwon et al., 2008; Parton et al., 2012), a small suppression in evapotranspiration (ET) (Dong et al., 2011), and a shift in the environmental controls of net ecosystem exchange (NEE) from vapour pressure deficit (VPD) to soil moisture with progressing drought (Kwon et al., 2008). While the temperature effects are well understood, the effects of moisture limitation during spring on phenology, carbon uptake and water vapour fluxes remain unknown.

The objectives of our study are (1) to synthesize ecosystem carbon dioxide and water vapour fluxes from the national eddy covariance network, Swiss FluxNet, (2) to evaluate the phenological development of vegetation, (3) to investigate carbon–water interactions, and (4) to compare the response of grasslands and forests to the 2011 spring drought in Switzerland.

3.2 Materials and methods

3.2.1 Swiss FluxNet

We synthesized data from the Swiss FluxNet national eddy covariance network (www.swissfluxnet.ch). Swiss FluxNet includes the major land-use types of deciduous and evergreen forests, grassland and cropland along an elevational gradient in Switzerland and currently encompasses eight long-term ecosystem sites. Our synthesis study included five of these sites that provided data for spring 2010 and 2011: Chamaau, Oensingen1, Früebüel (managed grasslands, elevation range from 393 to 982 m a.s.l.), Laegeren (lowland mixed deciduous forest), and Davos (subalpine evergreen forest, table 3.1). All sites have a temperate climate with elevation as a confounding factor, particularly the montane grassland in Früebüel and the subalpine evergreen forest in Davos. Management varied across sites and included 4–6
CHAPTER 3. CONTRASTING RESPONSE OF GRASSLAND VERSUS FOREST CARBON AND WATER FLUXES TO SPRING DROUGHT IN SWITZERLAND

grass cuts per year with subsequent manure or synthetic fertilizer applications in the intensively managed Oensingen1 and Chamau grasslands. At the moderately managed grassland Früebüel, only solid manure was applied once per year and grass cuts were occasionally replaced by cattle grazing. The Laegeren and Davos forest sites had no management events during the time of observations.

3.2.2 Flux measurements and data processing

Flux densities of carbon dioxide, water vapour and energy were measured during 2010 and 2011 using the eddy covariance (EC) method. The micrometeorological measurement setup consisted of open-path infrared gas analysers (Li-7500, LI-COR, Lincoln, USA) and threedimensional sonic anemometers (models Solent R3-50 and HS, Gill Instruments, Lymington, UK). Raw data were recorded at 10 or 20 Hz and processed to half-hourly averages using the eth-flux EC software (Mauder et al., 2008) or a comparable custom-made EC software for Oensingen1 (Ammann et al., 2007). Post-processing included corrections for damping losses (Eugster and Senn, 1995), air density fluctuations (Webb et al., 1980), and data screening for optical sensor contamination, stationarity (Foken and Wichura, 1996), low turbulence conditions (see table 3.1 for site-specific $u^*$-thresholds) and statistical outliers (14 day running mean with ±3 SD range). In addition, negative nighttime fluxes (unreasonable as no photosynthesis occurs at night) and a corresponding amount of positive nighttime fluxes were removed using a trimmed mean approach to avoid a systematic bias of cumulative sums. Standardized gap filling and partitioning of carbon dioxide fluxes was performed using the methodology by Reichstein et al. (2005), i.e., with the marginal distribution sampling (MDS) gap filling algorithm and flux partitioning based on a temperature regression with nighttime fluxes (GPP = −NEE$_{daytime}$ + TER). In addition, we corrected for physiologically unrealistic, negative values of gross primary productivity (GPP) when net ecosystem exchange (NEE) exceeded nighttime derived total ecosystem respiration (TER; e.g., with onset of turbulent mixing or following rainfall), by replacing TER with NEE and setting GPP to zero (Wolf et al., 2011).

Besides flux densities, meteorological variables such as air temperature, relative humidity, precipitation, incoming shortwave radiation ($R_G$) soil temperature and volumetric soil water content (SWC, in %, 5 cm depth; except at Oensingen1: 10 cm)
were measured continuously (half-hourly averages, sums for precipitation) at all sites. SWC was also measured at 15–30 cm depth but showed similar results as for 5 cm depth (not shown). Long-term precipitation data for nearby reference stations (see table 3.2) were provided by MeteoSwiss.

3.2.3 Phenology

Phenological development of vegetation was analysed from species-specific observational data (i.e., dates of phenological phases) provided by MeteoSwiss from the national phenological monitoring network. We used the following nearby stations from this network (including distance and direction from the respective tower site): Chamau–Muri (9.0 km, 317°NW), Oensingen–Wynau (6.6 km, 115°SE), Früebüel–Edlibach (7.5 km, 18°N), Laegeren–Oberehrendingen (5.7 km, 274°W), and Davos–Davos-Dorf (1.4 km, 244°SW). According to the composition of the dominant vegetation at each site (see table 3.1), we used the date of needle emergence of Norway spruce (*Picea abies*) for the Davos site, and averaged the dates of leaf unfolding of European beech (*Fagus sylvatica*) and needle emergence for Norway spruce (*Picea abies*) at the Laegeren site. For all grassland sites, we consistently used the same plant species and averaged the dates of full flowering from cocksfoot grass (*Dactylis glomerata*) and dandelion (*Taraxacum officinale*).

3.2.4 General conventions

We used the R statistics software package, version 2.13.2 (R Development Core Team 2009, www.r-project.org) for data analyses. Daytime data were defined by \( R_G > 10 \text{ W} \text{ m}^{-2} \). The term ‘spring’ refers to the meteorological definition (March, April and May). We use the term ‘drought’ related to precipitation deficits, which can impose (1) plant physiological stress due to soil moisture deficiency and (2) stomatal adjustments in response to high VPD. We compare our data of 2011 relative to 2010, with 2011 being closer to the long-term average precipitation regime for most sites (see table 3.2).
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3.3 Results

3.3.1 Weather conditions during spring 2011

The weather anomaly during spring 2011 resulted in record high temperatures (+3.4°C above average) and substantial below average precipitation (−47%) in Switzerland (MeteoSwiss 2012). March and April were particularly dry and all sites received below average precipitation, ranging from −35 to −85% in March and −42 to −79% in April. The Früebüel montane grassland had the lowest deviations from the long-term mean (−35 and −42%), because of its topographic exposure. Most sites also received below average precipitation during early May 2011, but heavy precipitation events after DOY 131 (May 11) resulted in a substantial monthly surplus at Davos and Früebüel, and a small surplus in Chamau. During spring 2011, all sites except Früebüel had a cumulative precipitation deficit of 34–68% (mean 51%, Früebüel excluded), which was larger than the small deficit of 7% across all sites during spring 2010 (table 3.2). In both years, spring was preceded by similarly dry winters across sites, except at Früebüel (2010: −32%, 2011: −37%).

This precipitation anomaly during spring 2011 was also reflected in the temporal patterns of SWC (figure 3.1), with a substantial decrease from a maximum of 52% (overall mean) on DOY 95 (April 5) to a minimum of 30% on DOY 131 (May 11), which confined the spring drought across all sites between DOY 102–132 (April 12–May 12). Low and increasing SWC at the subalpine Davos site (1639 m) during March was related to frozen soil and associated measurement limitations. During spring 2011, all sites received higher amounts of daily R\textsubscript{G} compared to 2010, in the range of +17% (Davos) to +36% (Früebüel), with a mean of +27% (data not shown). Daily VPD was substantially higher at all sites (overall mean +85%) during spring 2011, particularly at the forest sites (+228% versus +45% at grasslands). Spring was also substantially warmer in 2011 compared to 2010 (see figure 3.5), with mean air temperatures differences of +2.1 to +3.4°C at our sites (overall mean +2.8°C) and the largest increase found at the forest sites (+3.3°C).
3.3. RESULTS

3.3.2 Phenological development

Phenological observations showed that vegetation development started 8–17 days earlier (overall mean −11 days) in 2011 compared to the mean of 2000–2011 (figure 3.2). The opposite pattern was observed in 2010, when vegetation started later at all sites (overall mean +7 days). While sites differed considerably between 2000 and 2009, the late vegetation developments in 2010 and the early vegetation development in 2011 were more consistent across all sites. Compared to 2010, spring phenology developed on average 18 days earlier during spring 2011 at our sites.

3.3.3 Range and magnitude of carbon and water vapour fluxes

We observed large differences in GPP and TER among sites during spring 2011 (figure 3.3, table 3.3). GPP was highest for the grassland sites Chamau (10.2±4.5 g C m⁻² d⁻¹, mean ± standard deviation) and Früebüel (8.8±5.3 g C m⁻² d⁻¹), while lowest GPP was found at the evergreen forest site in Davos (3.4±1.9 g C m⁻² d⁻¹). During the drought period 2011 (DOY 102–132), GPP decreased substantially at Chamau (figure 3.3(a)). Smaller reductions in GPP were observed for the two other grassland sites Oensingen1 and Früebüel at the beginning and towards the end of the drought period (figures 3.3(b) and (c)). We did not find drought related GPP reductions of the forests. However, GPP of the two forest sites was substantially higher in 2011 compared to 2010 (LAE: +54%, DAV: +19%), while the grassland sites did not show a consistent pattern and substantially higher GPP was only found at Früebüel (+38%, table 3.3).

Range and magnitude of TER largely followed the GPP pattern, except for the forest sites Laegeren (3.4±1.2 g C m⁻² d⁻¹) and Davos (1.5±0.5 g C m⁻² d⁻¹), where TER remained low, remarkably stable and decoupled from GPP following the onset of drought conditions in April (figure 3.3). Management of the grassland sites (grass cuts and grazing) resulted in a short-term decoupling of TER from GPP, i.e., reduced GPP along with increased TER (figures 3.3(a)–(c)). Compared to 2010, we observed higher respiratory fluxes for the forest sites (LAE: +23%, DAV: +93%) in spring 2011 (table 3.3). The relative change in GPP versus TER between these years was generally similar or larger for GPP, except at the subalpine site Davos, where higher
soil temperatures in 2011 (i.e., TSoil > 0°C about three weeks earlier) resulted in enhanced TER and substantially larger changes in TER compared to GPP.

Ecosystem ET (i.e., soil and canopy evaporation plus plant transpiration) was highest at the grassland site Früebüel (2.5±1.4 mm m⁻² d⁻¹) and lowest at the evergreen forest in Davos (1.4±0.8 mm m⁻² d⁻¹, figure 3.4). ET was higher in 2011 than 2010 at the Früebüel grassland site (+49%) and lower at the forest sites (LAE: −21%, DAV: −32%; table 3.3).

### 3.3.4 Environmental controls of spring fluxes

In 2011, the main environmental controls of daily spring GPP were RG for Chamau ($R^2 = 0.48$) and Früebüel ($R^2 = 0.67$), soil temperature for Davos ($R^2 = 0.38$), and soil moisture for Oensingen1 ($R^2 = 0.66$) and Laegeren ($R^2 = 0.76$, all $p < 0.001$, linear regression analysis). For Früebüel, soil moisture was a strong residual control of GPP ($R^2 = 0.31$; $p < 0.001$) while no significant control of moisture was detected for Chamau and Davos. Soil temperature and soil moisture were together the main environmental controls of daily spring TER for all sites, but explained a higher variability in TER for the grasslands ($R^2 = 0.54–0.84$; $p < 0.001$) compared to the forest sites ($R^2 = 0.23–0.47$; $p < 0.001$). RG was the main environmental control for daily NEE for all grassland sites ($R^2 = 0.19–0.67$, all $p < 0.001$). In addition, spring NEE of the forest sites was driven by soil moisture at Laegeren ($R^2 = 0.66$) and air temperature at Davos ($R^2 = 0.32$, both $p < 0.001$). Low explanatory power of RG for NEE of the grasslands Chamau ($R^2 = 0.19$) and Oensingen1 ($R^2 = 0.30$) seemed largely related to management effects (grass cuts), while grazing at Früebüel ($R^2 = 0.67$, all $p < 0.001$) had smaller effects on NEE than meteorological variables (figure 3.3(c)). The main driver of ET at the grassland sites was RG, while temperature was the main control at the forest sites ($R^2 = 0.65–0.77$, all $p < 0.001$). VPD was the secondary environmental control of ET at all sites.

### 3.3.5 Carbon uptake and water deficits

We observed net carbon uptake at all sites during spring 2011, ranging from 49 g C m⁻² for Chamau to 282 g C m⁻² for Laegeren (figure 3.5, table 3.3). Unlike the previous year, net carbon uptake (cumulative NEE < 0) in spring 2011
generally started earlier, except for the Oensingen1 grassland. No considerable differences in NEE were found at Chamau, Oensingen1 and Davos between spring 2010 and 2011. Compared to the previous spring, substantially higher net carbon uptake was observed at the sites Früebüel (+123%) and Laegeren (+114%) in 2011.

Spring ET ranged from 12 mm at Davos to 233 mm at Früebüel (mean 187 mm; figure 3.4, table 3.3) during 2011. The difference of precipitation minus ET showed cumulative spring water deficits of −104 and −109 mm for the sites Oensingen1 and Laegeren, respectively (figure 3.6). Only the sites Chamau and Davos recovered from the water deficits accumulated during the drought, mainly due to substantial precipitation in the second half of May 2011. The Früebüel montane grassland had a water surplus of 120 mm at the end of spring 2011. Compared to an overall surplus of 70 mm in spring 2010, the mean water deficit was 17 mm across all sites for spring 2011.

### 3.3.6 Water-use efficiency

During spring 2011, the highest water-use efficiency (WUE, gross carbon uptake per unit water lost) was observed at the Chamau grassland (4.6 g C (kg H\textsubscript{2}O\textsuperscript{−1}), while the forest sites Laegeren (2.3 g C (kg H\textsubscript{2}O\textsuperscript{−1}) and Davos (1.9 g C (kg H\textsubscript{2}O\textsuperscript{−1}) showed overall much lower WUE (figure 3.7). Differences between spring 2011 and 2010 were insignificant at the grassland sites (p > 0.05), whereas WUE of the forest sites significantly increased (Laegeren +109%, Davos +58%, both p < 0.001). A combination of increased GPP along with decreased ET caused the higher WUE of the two forest sites in 2011 (table 3.3).

### 3.4 Discussion

Precipitation deficits during spring 2011 resulted in soil moisture deficiencies similar to those typical during summer months, persisting for an extended period (4–6 weeks) at high temperatures. While a consistently earlier phenological development was found at all sites independent of land-use type or elevation, the response of ecosystem carbon dioxide and water vapour fluxes to these spring drought conditions differed strongly among sites, in particular for water-use efficiency between forests.
and grasslands. Forests adapted to spring drought conditions by increasing water-use efficiency (i.e., reducing transpiration). In contrast, grasslands did not adapt and reductions in productivity of grasslands indicated soil moisture limitations inhibiting regrowth of vegetation after grass cuts during drought conditions in spring.

3.4.1 Phenology

The phenological development in 2011 was the second earliest since 1950 (MeteoSwiss, 2011). It was largely related to temperature and none of our sites showed a delayed development related to drought. While below average precipitation was also observed during early spring 2010 (table 3.2), temperatures were considerably lower in 2010 (−2.7 °C), and closer to the long-term average as compared to 2011 (MeteoSwiss, 2011). These differences and regression analysis (phenological development versus temperature) showed that temperature was the main control for spring phenology at our sites during both years ($R^2 = 0.74$; $p < 0.001$), along with photoperiod and chilling (Körner and Basler, 2010), and that soil moisture limitations during spring did not inhibit the onset of leaf activity, despite strong effects on ecosystem fluxes.

3.4.2 Carbon uptake and gross primary productivity

In contrast to other studies that found largely reduced carbon uptake during spring drought in steppe ecosystems (Dong et al., 2011; Parton et al., 2012; Kwon et al., 2008), we observed only small reductions in net carbon uptake (NEE) for some of our sites. Instead, we found substantially increased net carbon uptake of a montane grassland (Früebüel), similar to Gilgen and Buchmann (2009), and lowland mixed deciduous forest (Laegeren) in response to drought—similar to findings by Black et al. (2000) for boreal deciduous forest in years with a warm spring. Overall, these results indicated that spring drought resulted in smaller carbon losses, which are in contrast to the substantial carbon losses that were observed during the severe summer drought in 2003 (Ciais et al., 2005).

GPP reductions for most sites at the beginning of the drought period (DOY 102–107) were related to incoming cold air masses from the arctic (MeteoSwiss, 2011)
that affected in particular the higher elevation sites Früebüel and Davos, where mean temperatures dropped below 5 °C and close to freezing, respectively (figure 3.5). This temperature drop also reduced TER at all sites, with larger reductions observed for the grassland compared to the forest sites (figure 3.3).

Soil moisture related reductions in GPP were found at the lowland grassland sites, where productivity did not recover following grass cuts in Chamau mid-April (DOY 109, figure 3.3(a)) and Oensingen1 in early May (DOY 124, figure 3.3(b)). At Chamau, GPP only recovered following the next major rainfall (DOY 123). Similar reductions in grassland productivity in response to drought were found by Gilgen and Buchmann (2009) for the Chamau grassland, and by Craine et al. (2012) for grasslands in north-eastern Kansas. In addition, the smaller net carbon uptake of Chamau seemed related to higher manure inputs compared to the Oensingen1 grassland zeeman:2010, which resulted in higher TER relative to GPP (ratio of 0.95 versus 0.68, table 3.3).

For both forest sites, cumulative annual net carbon uptake (not shown) started earlier in 2011 compared to 2010, 16 days at Laegeren and 13 days at Davos. These differences were similar to the results from phenological observations, which showed differences of 16 and 12 days for both forest sites between years (figure 3.2). The findings for Laegeren confirmed Ahrends et al. (2009) and Etzold et al. (2011), who reported enhanced productivity and net carbon uptake in a year (2007), when bud break at Laegeren occurred 10 days earlier compared to the two previous years (Ahrends et al., 2009). In contrast to our two forests, we could not find a similar relation of phenological observations and NEE for the grasslands due to management at these sites, i.e., grass cuts being performed before flowering to prevent reduced biomass production after flowering.

GPP increases from 2010 to 2011 were smaller in Davos compared to Laegeren (table 3.3), suggesting that productivity in evergreen needleleaf forest is less sensitive to seasonal climate anomalies compared to deciduous broadleaf forest (Richardson et al., 2010). In contrast, the opposite pattern was found for TER between both years: during spring 2011, TER was increased only marginally in Laegeren but largely enhanced in Davos (related to higher temperatures), where TER substantially exceeded the increase in GPP (table 3.3). This indicated limitations for higher net carbon uptake in subalpine forest ecosystems during years with above average
CHAPTER 3. CONTRASTING RESPONSE OF GRASSLAND VERSUS FOREST CARBON AND WATER FLUXES TO SPRING DROUGHT IN SWITZERLAND

spring temperatures—an important implication when considering the projected temperature increases for Switzerland for all seasons CH (2011).

3.4.3 Evapotranspiration and water-use efficiency

Evapotranspiration of both forests was substantially reduced in spring 2011 compared to 2010, a clear signal of stomatal regulation (i.e., reduction of leaf transpiration) as an early response to drought (see also Jarvis and McNaughton, 1986). Such regulation in forests was also shown by Teuling et al. (2010) during a summer heatwave that was enhanced by drought: unlike grasslands, forests employ water saving strategies and reduce their ET early on, thereby reducing evaporative cooling of the atmosphere. In contrast, grasslands maintain their ET as long as soil moisture is available. In our study, grasslands did not reduce ET during spring drought either, suggesting a consistent behaviour of grassland vegetation to spring and summer droughts. The Früebüel grassland even increased ET, probably due to more available energy from clear skies during spring 2011.

In addition, both our forest sites significantly increased their WUE in response to spring drought, while no such effect was observed for the grassland sites in Switzerland. This increase in WUE is in accordance with the expected response of WUE at the leaf level, to reduce water stress while keeping foliar assimilation high (see Bacon, 2004; Schulze et al., 2005). However, such response at the leaf level does not necessarily translate to the ecosystem scale (Jarvis and McNaughton, 1986), which additionally includes soil evaporation, and in fact, only few ecosystem-scale studies reported increased WUE during drought (e.g. Krishnan et al., 2006). Nonetheless, Beer et al. (2009) concluded from a global synthesis study of 43 flux tower sites that changes in WUE (or inherent WUE) indicate the adjustment of ecophysiology at stand level and thus enable the transfer of the WUE concept from the leaf to the ecosystem level.

The stronger increase of WUE at Laegeren (broadleaved) compared to Davos (coniferous) can be explained by stronger stomatal regulation of leaves versus needles (Schulze et al., 2005), supporting results from Granier et al. (2007) in response to the 2003 summer drought in Europe. For the same drought event, however, decreased WUE was also reported by Reichstein et al. (2007a) for mostly forest ecosystems and
Hussain et al. (2011) for a grassland. Ponce-Campos et al. (2013) recently added further evidence for higher WUE across biomes during drier years that increased with drought intensity. Therefore, further research with large observational datasets (e.g. FLUXNET) is needed to comprehensively distinguish the WUE response to drought between forests and grasslands—in general and also evaluating potential differences between spring and summer drought.

The observed water deficits (negative $P-\text{ET}$) or minor surplus at the end of spring could have important implications for the vegetation during summer, as spring is typically a period of water recharge for soil and groundwater reservoirs. A combination of spring and summer droughts in the same year could substantially increase the impact of summer drought, e.g. with larger reductions in productivity, enhanced temperature feedbacks amplifying heatwaves, and severe deficits in water supply for agriculture and society. In 2011, however, carry-over effects into the following season were prevented by heavy precipitation during early summer that counteracted the potential risk of extreme summer temperatures (Quesada et al., 2012).

Overall, we conclude that forests adapt to spring drought by increasing WUE much stronger than grasslands, which could be due to an evolutionary strategy to secure carbon investments during harsh conditions (Schulze et al., 2005).

### 3.5 Conclusions

Grasslands and forests responded very differently to spring drought in terms of ecosystem carbon dioxide and water vapour fluxes: while forests adapted and reduced their WUE significantly, grasslands did not show this behaviour, or maybe would only after a prolonged drought. These contrasting responses to drought will not only affect the feedback to the atmosphere via ET, but also indicate different susceptibilities of grasslands versus forests to future drought events, predicted to increase in frequency and severity. Our results further suggest that understanding the response of different land-use types to drought is highly relevant to predict impacts of climate change.
Acknowledgements

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Author contribution

SW conceived the study with inspiration from NB. WE, CA, MH, SZ, RH, JS and DI provided data. SW, WE and CA post-processed the data. SW performed the analyses and wrote the first draft of the manuscript. All authors contributed to data interpretation and the final manuscript.


Granier, A., Reichstein, M., Bréda, N., Janssens, I., Falge, E., Ciais, P., Grünwald, T., Aubinet, M., Berbigier, P., Bernhofer, C., Buchmann, N., Facini, O., Grassi,


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3.6. REFERENCES


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3.7 Tables and figures
Table 3.1: Swiss FluxNet sites used in this synthesis study. Abbreviations denote the International Geosphere-Biosphere Programme (IGBP) mean annual temperature (MAT), mean annual precipitation (MAP), and friction velocity (\(u_\tau\))—a measure for turbulence conditions. Data were compiled from published literature except MAP, which was derived from long-term data provided by MeteoSwiss (see table 3.2).

<table>
<thead>
<tr>
<th>Site</th>
<th>Chamau</th>
<th>Oensingen1</th>
<th>Fruebtiel</th>
<th>Laegeren</th>
<th>Davos</th>
</tr>
</thead>
<tbody>
<tr>
<td>IGBP land use, Abbreviation</td>
<td>Grasslands, GRA (intensively managed)</td>
<td>Grasslands, GRA (intensively managed)</td>
<td>Grasslands, GRA (moderately managed)</td>
<td>Mixed Forest, MF (deciduous dominated)</td>
<td>Evergreen Needleleaf Forest, ENF</td>
</tr>
<tr>
<td>Dominant species</td>
<td>Italian ryegrass (Lolium multil.)</td>
<td>English ryegrass (Lolium perenne)</td>
<td>Meadow foxtail (Alopecurus prat.)</td>
<td>Cockfoot grass (Dactylis glomerata)</td>
<td>European beech (Fagus sylvatica)</td>
</tr>
<tr>
<td></td>
<td>White clover (Trifolium repens)</td>
<td>Meadow foxtail (Alopecurus prat.)</td>
<td>Dandelion (Taraxacum offic.)</td>
<td>Buttercup (Ranunculus sp.)</td>
<td>Sycamore maple (Acer pseudoplat.)</td>
</tr>
<tr>
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<td>47°17′08.1″N</td>
<td>47°06′17.0″N</td>
<td>47°28′42.0″N</td>
<td>46°48′55.2″N</td>
</tr>
<tr>
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<td>7°43′55.9″E</td>
<td>8°32′16.0″E</td>
<td>8°21′51.1″E</td>
<td>9°31′21.3″E</td>
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<td>452 m</td>
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<td>682 m</td>
<td>1639 m</td>
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<td>9.5°C</td>
<td>7.5°C⁰a</td>
<td>7.4°C</td>
<td>3.4°C</td>
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<td>1184 mm</td>
<td>1516 mm</td>
<td>1070 mm</td>
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<td>0.20</td>
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<td></td>
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<td></td>
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<td>Etzold et al (2011)</td>
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</table>

\(^{a}\) Mean from 2006 to 2007 (Zeeman et al., 2010)
Table 3.2: Precipitation sums and relative deviations from the long-term means (1981–2010) for the year 2011. Deviations for 2010 are reported comparisons. Long-term data were derived from nearby reference stations by MeteoSwiss while data for 2010 and 2011 were measured directly at the sites.

<table>
<thead>
<tr>
<th>Site</th>
<th>Chamau</th>
<th>Oensingen</th>
<th>Früebiol</th>
<th>Laegeren</th>
<th>Davos</th>
</tr>
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<tbody>
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<td>Reference station</td>
<td>Cham</td>
<td>Wynau</td>
<td>Zugerberg</td>
<td>Dietikon</td>
<td>Davos</td>
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<tr>
<td>Mean ± SD (mm)</td>
<td>180 ± 70</td>
<td>251 ± 82</td>
<td>215 ± 100</td>
<td>238 ± 71</td>
<td>185 ± 82</td>
</tr>
<tr>
<td>Winter (DJF)</td>
<td>274 ± 85</td>
<td>264 ± 100</td>
<td>353 ± 111</td>
<td>279 ± 102</td>
<td>204 ± 56</td>
</tr>
<tr>
<td>Annual</td>
<td>1112 ± 162</td>
<td>1129 ± 201</td>
<td>1457 ± 272</td>
<td>1110 ± 164</td>
<td>1035 ± 156</td>
</tr>
<tr>
<td>2011 (mm)</td>
<td>165</td>
<td>173</td>
<td>245</td>
<td>132</td>
<td>66</td>
</tr>
<tr>
<td>Winter (DJF)</td>
<td>182</td>
<td>93</td>
<td>353</td>
<td>89</td>
<td>133</td>
</tr>
<tr>
<td>Annual</td>
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<td>995</td>
<td>869</td>
<td>624</td>
<td>776</td>
</tr>
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<td>-45</td>
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<td>-35</td>
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<td>-25</td>
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<tr>
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<td>+23</td>
<td>-43</td>
<td>-56</td>
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</tbody>
</table>
Table 3.3: Cumulative gross primary productivity (GPP), total ecosystem respiration (TER), net ecosystem exchange (NEE), and evapotranspiration (ET) during spring (MAM) 2011. Relative deviations are reported for spring 2011 compared to 2010.

<table>
<thead>
<tr>
<th>Site</th>
<th>Chamau</th>
<th>Oensingen</th>
<th>Fruebuel</th>
<th>Laegeren</th>
<th>Davos</th>
</tr>
</thead>
<tbody>
<tr>
<td>GPP (g C m⁻²)</td>
<td>940</td>
<td>586</td>
<td>809</td>
<td>598</td>
<td>324</td>
</tr>
<tr>
<td>TER (g C m⁻²)</td>
<td>891</td>
<td>401</td>
<td>536</td>
<td>316</td>
<td>137</td>
</tr>
<tr>
<td>NEE (g C m⁻²)</td>
<td>-49</td>
<td>-185</td>
<td>-273</td>
<td>-282</td>
<td>-187</td>
</tr>
<tr>
<td>ET (mm)</td>
<td>181</td>
<td>196</td>
<td>233</td>
<td>198</td>
<td>125</td>
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Deviations 2011 versus 2010 (%)

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<tr>
<td>GPP</td>
<td>3</td>
<td>-20</td>
<td>38</td>
<td>54</td>
<td>19</td>
<td>19</td>
<td>3</td>
<td>-20</td>
<td>38</td>
<td>54</td>
</tr>
<tr>
<td>TER</td>
<td>4</td>
<td>-20</td>
<td>15</td>
<td>23</td>
<td>93</td>
<td>93</td>
<td>4</td>
<td>-20</td>
<td>15</td>
<td>23</td>
</tr>
<tr>
<td>NEE</td>
<td>-14</td>
<td>-21</td>
<td>123</td>
<td>114</td>
<td>-7</td>
<td>-7</td>
<td>-14</td>
<td>-21</td>
<td>123</td>
<td>114</td>
</tr>
<tr>
<td>ET</td>
<td>-4</td>
<td>1</td>
<td>49</td>
<td>-21</td>
<td>-32</td>
<td>-32</td>
<td>-4</td>
<td>1</td>
<td>49</td>
<td>-21</td>
</tr>
</tbody>
</table>
Figure 3.1: Daily mean volumetric soil water content (SWC) at 5 cm depth (Oensingen1: 10 cm depth) at five Swiss FluxNet sites for the full year (a) and for spring 2011 (b). For comparison, the overall mean SWC across all sites is also shown for 2010. The dashed box in (b) confines the period of spring drought across all sites (DOY 102–132).
Figure 3.2: Site-specific phenological development compared to 2000–2011 mean of each site. Grasslands are denoted by dotted and forests by striped fill patterns. Sites are ordered according to land-use type (grassland, forest) and their respective elevational gradient from left (lowest) to right (highest). The bold black line shows the mean across all sites. Negative deviations indicate earlier, positive deviations later than average phenological development in spring. Species-specific observational data were provided by MeteoSwiss for nearby sites from the national phenological monitoring network: Davos–Norway spruce (needle emergence), Laegeren–European beech and Norway spruce (leaf unfolding needle emergence), Früebüel, Chama, Oensingen–Cocksfoot grass and Dandelion (full flowering). Data availability for Früebüel was limited to the years 2008–2011.
Figure 3.3: Daily total gross primary productivity (GPP), total ecosystem respiration (TER) and net ecosystem exchange (NEE; full shading indicates periods of carbon sink, striped shading of carbon sources) during spring 2011. Lines and shading are 7 day running means. The bars at the bottom of each panel show daily precipitation totals. Arrows indicate management at grassland sites, i.e. grass cuts (a), (b) and begin of grazing (c). The dashed lines confine the period of spring drought across all sites (DOY 102–132). Abbreviations in titles indicate the IGBP land-use class with grasslands (GRA), mixed forest (MF) and evergreen needleleaf forest (ENF). The grassland sites in the top panels are ordered according to their elevational gradient from left (lowest) to right (highest), and similarly the forest sites in the bottom panels.
CHAPTER 3. CONTRASTING RESPONSE OF GRASSLAND VERSUS FOREST CARBON AND WATER FLUXES TO SPRING DROUGHT IN SWITZERLAND

Figure 3.4: Daily total ecosystem evapotranspiration (ET) during spring 2010 and 2011. Lines are 7 day running means and numbers following years show total spring ET. Arrows indicate management at grassland sites, i.e. grass cuts (a), (b) and start of grazing (c). The dashed lines confine the period of spring drought across all sites (DOY 102–132). Abbreviations in titles indicate the IGBP land-use class with grasslands (GRA), mixed forest (MF) and evergreen needleleaf forest (ENF).
Figure 3.5: Cumulative net ecosystem exchange (NEE, solid lines) and air temperature (dashed lines, 7 day running mean) during spring 2010 (grey) and 2011 (black). The numbers following the years show total spring NEE. Arrows indicate management at grassland sites, i.e. grass cuts (a), (b) and start of grazing (c). The vertical dashed lines confine the period of spring drought across all sites (DOY 102–132). Abbreviations in titles indicate the IGBP land-use class with grasslands (GRA), mixed forest (MF and evergreen needleleaf forest (ENF)).
Figure 3.6: Cumulative daily precipitation (P) minus evapotranspiration (ET) during spring 2011. For comparison, the ensemble mean of all sites is also shown for 2010. The numbers in brackets show spring totals. The vertical dashed lines confine the period of spring drought across all sites (DOY 102–132).
Figure 3.7: Water-use efficiency (WUE), i.e. the ratio of gross primary productivity (GPP) and ecosystem evapotranspiration (ET), in spring 2011 compared to 2010. Significant differences in WUE (slopes) were detected at the forest sites Laegeren (d) and Davos (e), both $p < 0.001$. Abbreviations in titles indicate the IGBP land-use class with grasslands (GRA), mixed forest (MF) and evergreen needleleaf forest (ENF).
Chapter 4

Relevance of previous year’s weather for forest NEP increases with cold temperatures and at low productive sites

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This chapter is intended for submission to New Phytologist
• Delayed responses of forest carbon (C) exchange with the atmosphere to weather conditions during the previous year are a commonly observed phenomenon. However, a general understanding of the relevance of previous year’s weather on forest net ecosystem productivity (NEP) is still lacking.

• We quantified the influence of current and previous year’s weather on the inter-annual variability of NEP for nine European and North American forest sites. Multiple linear regression models between NEP and meteorological variables including both the current and the previous year’s weather were used to investigate the respective relevance.

• On average, explained inter-annual variability of NEP increased by 30% for eight of the nine sites when delayed responses were accounted for. Forests experiencing cold temperatures as well as low productive and old forests responded strongest to previous year’s weather.

• These drivers of the relevance of previous year’s weather most likely reflect among-site differences in (1) respiratory C losses due to repair processes of frost induced damage, (2) utilization of new assimilates versus stored C, and (3) differences in timing of leaf flush and cambial activity between young and old forests. These insights may substantially increase the reliability of annual C budget models for forests under future changing climate.
CHAPTER 4. RELEVANCE OF PREVIOUS YEAR’S WEATHER FOR FOREST NEP INCREASES WITH COLD TEMPERATURES AND AT LOW PRODUCTIVE SITES

4.1 Introduction

Forest ecosystems across the globe store on average 1.2 Pg carbon (C) per year (Pan et al., 2011), and account for 45% of the entire terrestrial biosphere C storage. Climate driven inter-annual variability of this sink strength is high (Reichstein et al., 2007; Pan et al., 2011), making estimates of C uptake in forest ecosystems difficult (Urbanski et al., 2007; Gough et al., 2008). Increasing the quality of these estimates and revealing potential drivers of the inter-annual variability in NEP is thus of great importance for reliable estimates of annual forest C budgets.

Terrestrial biosphere models are frequently used to assess the effect of climate and its variability on the net ecosystem productivity (NEP) of forest ecosystems (Ciais et al., 2005; Phillips et al., 2009), which is the difference between gross primary productivity (GPP) and total ecosystem respiration (TER). Such models were developed to calculate present forest NEP and to predict its development under a changing climate (Beer et al., 2010), highly relevant for post-Kyoto agreements or forest management strategies. However, various analyses and model comparison studies have shown that the performance of models declined with increasing temporal integration intervals from daily (Braswell et al., 2005) to annual and inter-annual resolutions (Hanson et al., 2004; Urbanski et al., 2007), mainly due to an increase in complexity of the biological processes involved (Braswell et al., 2005). Keenan et al. (2012) identified missing representation of lagged effects in the models as one of the major culprits responsible for poor model performance at larger time scales by comparing 16 terrestrial biosphere models in their ability to reproduce inter-annual variability of carbon dioxide (CO$_2$) fluxes. Such lagged effects are here defined as the response of current year’s forest NEP to weather of the previous year.

Delayed responses of CO$_2$ fluxes to previous year’s weather were already shown for different ecosystems. For example, Rocha and Goulden (2010) reported a decreased GPP for subsequent year(s) as a consequence of drought in a freshwater marsh, and a similar response to drought was shown for NEP of grassland ecosystems (Arnone III et al., 2008). Recently, we could show that the general consideration of previous year’s weather, and thus not only extreme events, increased the explained inter-annual variability of NEP in a coniferous subalpine forest (Zielis et al., 2014). Moreover, delayed responses for GPP (Urbanski et al., 2007) and net primary productivity (NPP) (Gough et al., 2008) have been reported in single-site studies for
mixed and deciduous forests, respectively. However, despite frequent observations, delayed responses of CO₂ flux processes of forests to previous year’s weather are to our knowledge not adequately represented in terrestrial biosphere models, possibly due to a lack of understanding of the underlying ecophysiological mechanisms.

Although it is not clear up to what degree NEP of forest ecosystems is generally affected by previous year’s weather, possible ecophysiological mechanisms driving the dependence were already proposed in earlier studies, such as the recovery from events/disturbances influencing the C cycle of a tree, e.g. harsh winters with strong frost events (Zielis et al., 2014), and alterations of non-structural carbohydrate (NSC) pools due to weather in the previous year (Gough et al., 2009; Richardson et al., 2013). Consequently, the diversity of these mechanisms suggest a wide-spread existence of a dependency, however, we do not expect all forest ecosystems to respond to previous year’s weather to the same extent. For example, differences in the exposure to harsh weather conditions or size and accessibility of stored C pools might lead to varying response magnitudes among sites.

This multi-site study evaluates the influence of previous year’s weather on the NEP of temperate and boreal forests, using long-term (≥10 years) eddy-covariance (EC) net CO₂ flux measurements from nine sites in Europe and North America. The studied forest ecosystems vary substantially in their climate conditions and site characteristics. We hypothesized: (1) Forest ecosystems show in general a significant response to previous year’s weather, however, the magnitude of the response to previous year’s weather is expect to vary with forest ecosystems. (2) Forest ecosystems exposed to harsh climate conditions, especially in terms of low temperatures, and those with small NSC pools are responding more strongly to previous year’s weather due to consequences of frost damages and shortage of stored C supply for NEP carried-over from one year to the next year.

4.2 Materials and methods

4.2.1 Study sites

We analysed seven European and two North American forest FLUXNET sites, including evergreen needleleaf forests (ENF), broadleaf deciduous forests (DBF), and
CHAPTER 4. RELEVANCE OF PREVIOUS YEAR’S WEATHER FOR FOREST NEP INCREASES WITH COLD TEMPERATURES AND AT LOW PRODUCTIVE SITES

a mixed forest (MF). For a site to be included in this study, a minimum of ten consecutive years of NEP measurements of sufficient quality (see below) as well as meteorological data had to be available. Furthermore, a site should not have experienced any major disturbance, e.g., logging, windthrow, or insect outbreaks within the measurement period, since this would have strongly influenced CO₂ exchange. Thus, we chose the following nine sites, which fulfilled these criteria: Campbell River, Canada (CA1), Davos Seehornwald, Switzerland (DAV), Fyodorovskoye, Russia (FYO), Hyytälä, Finland (HYY), Loobos, Netherlands (LOO), Niwot Ridge, USA (NR1), Soroe, Denmark (SOE), Tharandt, Germany (THA), and Vielsalm, Belgium (VIE) (Table 1).

4.2.2 Data sources and data handling

Eddy covariance CO₂ flux measurements and meteorological data used in this study were freely available data either downloaded from the European Fluxes Database Cluster (http://www.gaia.agraria.unitus.it/home), data servers of the Ameriflux (ftp://cdiac.ornl.gov/pub/ameriflux/) and Fluxnet Canada network (ftp://daac.ornl.gov/data/fluxnet/fluxnet_canada/) or, in the case of meteorological variables, were received in exceptional cases from the site PIs directly. Downloaded and received data fulfilled Level2 criteria of the respective data base, i.e., the general plausibility of the CO₂ fluxes was checked by the site PIs. Data filtering and gap-filling was done for all sites in an uniformly procedure as follows:

Half-hourly CO₂ flux raw data were filtered for unrealistically high or low values (outside the range of ± 50 µmol m⁻² s⁻¹), and particularly for low negative nighttime fluxes using a symmetric filter. This filter removes an equal amount of the most positive fluxes for each record with a negative flux that was discarded. In detail, we dismissed negative and positive nighttime CO₂ fluxes outside the range given by ±1 SD around the 14 day mean CO₂ flux. Furthermore, we accounted for conditions considered problematic for the EC method, i.e., during low turbulence conditions, using a u* filter with a threshold of u* < 0.2 m s⁻¹. Gap-filling and partitioning of the CO₂ fluxes into GPP and TER were done using the marginal distribution sampling (MDS) method by Reichstein et al. (2005).

We cross-referenced annual NEP derived from flux data filtered and gapfilled ac-
4.2. MATERIALS AND METHODS

cording to the method described above with annual NEP derived from filtered and
gapfilled data by the site PIs, when available. We accepted some deviations due
to methodological differences in data handling, but excluded sites, for which no
comparable and plausible values could be obtained. Thus, certain sites, providing
long-term data sets otherwise suitable for this study, were not considered here.

Gaps in the meteorological data were filled using the online MDI meteo gap-filling
tool (http://www.bgc-jena.mpg.de/ MDIwork/meteo/), which relates the local me-
teorological site conditions to the gridded spatial data from the ERA-Interim re-
analysis by the European Centre for Medium-Range Weather Forecasts (ECMWF).
Gaps in soil temperature, which cannot be calculated by the online tool, were filled
by inference from air temperature via a linear regression between the two variables.
The site LOO showed a continuous gap in soil temperature over two years and in-
ference from air temperature produced only a weak linear relationship. Thus, soil
temperature was excluded from the statistical analysis for this site.

4.2.3 Data analysis

All statistical analyses were performed using the R statistical software, version 3.0.3
(R Core Team, 2012). To identify climatic drivers of NEP and to determine at
what time of the year they exerted the greatest influence, we used seasonal climate
variables, with seasons defined according to the meteorological definition (winter:
DJF; spring: MAM; summer: JJA; fall: SON). Climate variable denominations used
in this study were composed of the abbreviation of the meteorological variable and
the season, with an additional “−1” indicating previous year’s variables.

We assessed the influence of previous year’s weather on inter-annual variability of
NEP by fitting linear models to NEP, first with current year weather only and then
with weather of both the current and the previous year. Hereafter, models which
only contain current year variables are named Type A models, while those contain-
ing current and previous year’s variables are named Type B models. At first, both
data sets of weather variables were corrected for collinearity using a correlation-
based method according to Dormann et al. (2012). When the correlation coefficient
between two climate variables exceeded a site-specific threshold (|r| = 0.4–0.6), we
kept the climate variable with the higher explanatory power for NEP based on the
Akaike Information Criterion (Quinn and Keough, 2001). Then, we selected the best linear regression models with up to three independent variables according to the adjusted $r^2$ ($adj. \ r^2$). Although the $adj. \ r^2$ of the linear models explaining inter-annual variability of NEP tend to further rise at some sites when more than three independent variables were chosen, we neglected these results due to emerging over-parameterization related to the dependent variable (i.e., 12–15 site-years). Model performance was tested by re-calculating annual NEP using the obtained multiple linear regressions and comparing modeled NEP with measured NEP.

Subsequently, we evaluated which climate variables, both of the current and the previous year, and seasons were most important for determining the inter-annual variability of NEP. This was done by calculating the respective frequency of variables in all Type B models with one up to three variables, when both current and previous year’s weather were included. The frequency of seasons was obtained by splitting the climate variable denominations into the meteorological variable and its seasons, and counting only the season of the variables used in Type B models, ignoring the meteorological variable itself.

Finally, we determined the relevance of previous year’s weather for explaining the inter-annual variability of NEP as a function of site characteristics. Here, we used given site characteristics (cf. Table 1) as well as the following derived variables and characteristics: annual minimum, maximum, and range of air temperature ($T_{mean}$, $T_{min}$, $T_{max}$, $T_{range}$), the number of days with a minimum air temperature below $-5 \ °C$ ($DegDays-5$), the above-ground biomass ($BiomassAbove$), the biodiversity of the tree species expressed as the Shannon-Wiener-Index ($Biodiv$) as well as net ecosystem productivity (NEP), gross primary productivity (GPP), and total ecosystem respiration (TER). Then, we calculated simple linear regressions of selected site characteristics (cf. Appendix Table A.1) against the percent increase of $adj. \ r^2$ from Type A models to Type B models. Both the independent and the dependent variables ($y$) were log-transformed to account for skewness in the data using a log($y+c$) transformation, where $c$ is the 2.5%-quantile allowing the inclusion of zero values. To account for a probable inflation of the alpha level due to this multiple testing approach, we corrected the $p-values$ of the linear regressions by using the Holms adjustment method (Aickin and Gensler, 1996). We then used a principal component analysis (PCA) to infer the interdependence among significant site characteristics, and thus, to possibly combine site characteristics containing similar information into
4.3. RESULTS

4.3 Results

4.3.1 Influence of previous year’s weather on current year NEP

Explained inter-annual variability of NEP increased on average by 30% for eight of the nine sites (eight sites; rise of adj. $r^2$ from 0.49 to 0.64) when previous year’s weather variables were included (Type B models) and not only current year weather variables (Type A models) (Table 2). The most substantial increases were found for the evergreen coniferous sites DAV (+30%), NR1 (+76%), and FYO (+218%). Moreover, the NEP models for these three sites were significant only when previous year’s weather was included. The ENF site CA1 experienced only a marginal increase in explained NEP by including previous year’s weather (+3%), while for the remaining four sites (ENF, DBF, and MF) increases ranged between 9% and 17% (Table 2). The Finish site Hyytälä (HYY) was the only site for which the explained inter-annual variability of NEP did not further increase with the inclusion of previous year’s weather (Table 2).

We evaluated the performance of the linear regression Type A and Type B models by re-calculating annual NEP as well as assessing the confidence intervals of these models and compared them to measured NEP. As examples, the comparisons of measured and modeled NEP for three sites (FYO, THA, and CA1) with a high (+218%), a medium (+17%), and a low (+3%) increase in explained inter-annual variability are shown here (Fig. 1; see Appendix Fig. A.1 and A.2 for the remaining six sites). At the site FYO, annual NEP calculated by Type B models almost perfectly matched measured NEP for the whole measurement period, and model uncertainty was strongly reduced compared to Type A models (Fig. 1a,b). In contrast, at the THA site, the uncertainty of Type A and Type B models remained unaltered, but Type B models clearly outperformed Type A models in calculating annual NEP, especially in the period 1998–2004, where the latter only captured the decreasing trend, yet no inter-annual variability of NEP (Fig. 1c,d). For the site
CHAPTER 4. RELEVANCE OF PREVIOUS YEAR’S WEATHER FOR FOREST NEP INCREASES WITH COLD TEMPERATURES AND AT LOW PRODUCTIVE SITES

CA1, differences between Type A and Type B models were low, and both models also showed similar uncertainties (Fig. 1e,f).

4.3.2 Current and previous year’s environmental drivers of NEP

Maximum air temperature in spring of the current year ($T_{2\text{max.spring}}$) was the variable that was most frequently included in Type B models to predict NEP across all nine sites (Fig. 2a), followed by the current year variables maximum air and mean soil temperature in summer ($T_{2\text{max.summer}}, \text{SoilTemp.summer}$). The most frequent variables of the previous year were vapor pressure deficit in spring ($\text{VPD.spring}$), photosynthetic photon flux density in fall ($\text{PPFD.fall}$), and precipitation in winter ($\text{Precip.winter}$; Fig. 2a). $T_{2\text{max.spring}}, \text{SoilTemp.summer}$, and $\text{Precip.winter}$ altered annual NEP at all sites positively, while $T_{2\text{max.summer}}$ and $\text{PPFD.fall}$ affected annual NEP always negatively. On the contrary, $\text{VPD.spring}$ had both positive and negative effects on current year NEP, depending on the site. Focusing solely on seasons in Type B models and leaving the specific meteorological variable aside, current year’s weather in spring affected annual NEP the most, followed by weather in current year’s summer. The most influential season of the previous year was spring (Fig. 2b).

4.3.3 Site characteristics determining the relevance of previous year’s weather

We assessed differences in relevance of previous year’s weather for NEP among sites by examining the relationship between percent increases in $adj. r^2$ from Type A models to Type B models and selected site characteristics. From the 18 site characteristics analyzed (Appendix Table A.1), annual minimum air temperature ($T_{\text{min}}$) explained most of the variation of NEP and was negatively related to the relevance of previous year’s weather ($r^2 = 0.87, p < 0.01$; Fig. 3a). Furthermore, the number of days with a daily mean temperature below $-5\degree\text{C}$ ($\text{DegDays}-5$), the range of annual air temperature ($\text{Trange}$), NEP and GPP as well as stand age (Age) showed also significant relationships with the relevance of previous year’s weather (Fig. 3b–
4.4 DISCUSSION

However, all relationships were only significant when the ENF site Hyytälä, the site with no quantifiable delayed response of NEP to previous year’s weather (cf. Table 2), was excluded from the analysis except for the relationship with stand age (Fig. 3f). Analysis of interdependence via a PCA of the five significant site characteristics revealed the expected close and positive relationship between GPP and NEP due to their ecophysiological interdependence, with higher NEP being associated with higher GPP (Fig. 4). We also found a close, yet, negative relationship between $T_{min}$ on the one hand and $DegDays-5$ as well as $Trange$ on the other hand. A higher minimum air temperature was, not surprisingly, directly coupled with a smaller number of days with a minimum air temperature below $-5 \, ^{\circ}C$. The annual temperature range was related to $T_{min}$, since the investigated sites did not show large differences in summer temperatures (data not shown), so that existing differences in winter temperatures strongly determined the range of annual temperatures. Moreover, productivity of the sites increased with increasing temperatures, here displayed as the relationships of NEP and the temperature variables (Fig. 4). Stand age was the only variable unrelated to the other site characteristics (Fig. 4). Thus, we could reduce the significant site characteristics for the relevance of previous year’s weather on NEP to three variables – the occurrence of low temperatures and frosts, productivity as well as stand age.

4.4 Discussion

Weather of the previous year was important for determining inter-annual NEP more accurately for eight out of nine sites investigated (Tab. 2), substantially increasing the performance of linear regression models and reducing their uncertainty (Fig. 1, A.1, A.2). Thus, based on this multi-site analysis, we were able to provide strong evidence for a consistent and wide-spread occurrence of a dependency of forests’ annual C budgets not only on current, but also on previous year’s weather. This was true for a wide range of forests with substantial differences in climate conditions and site characteristics. Although to our knowledge only shown for a single site before (Zielis et al., 2014), a consistent dependence of NEP was expected. Current year tree growth, the dominating C sink in forest ecosystems, relies on ecophysiological processes influenced by the previous year, such as the formation of buds (Gordon et al., 2006) and shoots (Remphrey and Davidson, 1994) as well as the build-up of
non-structural carbohydrates (NSC) (e.g., Epron et al., 2012) in fall of the previous year. Also, dendrochronological studies repeatedly reported effects of past weather conditions on current year tree growth via tree-ring width analysis (e.g., Skomarkova et al., 2006), yet, focusing mostly on the multi-year effects of extreme events (e.g., Johnson et al., 1988; Bigler et al., 2007), neglecting the influence of “normal” and non-extreme weather variability as studied here.

We identified low temperatures and frosts, ecosystem productivity as well as stand age as the most influential site characteristics, determining the relevance of previous year’s weather for current year’s NEP (Fig. 3, Table 2). Low temperatures and more frequent occurrences of frost events could affect current year’s NEP in two ways. First, severe frost events in the previous year’s spring, fall, or winter, as indicated by the frequent occurrence of these seasons in our models (Fig. 2b), can harm buds and needles, and increase fine root mortality (Pederson et al., 2004). Higher respiratory C losses due to repair or replacement processes as a consequence of these damages will reduce current year forest NEP. This mechanism is supported by the positive influence of previous year’s winter precipitation, i.e., snow at most of the sites, especially at DAV and NR1. The snow cover prevents soil temperatures to drop well below zero due to its insulating effect, and thus reduces the risk of frost damage of fine roots (Tierney et al., 2001; Monson et al., 2005; Schaberg et al., 2008).

Second, the period of respiratory C losses, starting usually in (late) fall, is longer in colder climates with low minimum air temperatures and frequent frost events due to an earlier end as well as a late start of the growing season (Keenan et al., 2014). The recovery from these C losses therefore might also result in decreased current year’s forest NEP. Conversely, a short or even non-existing dormancy between two growing seasons would thus reduce an influence of the previous year’s weather on current year NEP.

Moreover, NEP of highly productive forests was less dependent on previous year’s weather than forests with a lower productivity (Fig. 3c,d), with different explanations for this finding being possible. (1) A recent study by Carbone et al. (2013) showed that faster growing deciduous trees in the Harvard Forest, USA, had higher concentrations of non-structural carbohydrates (NSC), i.e., stored C in the stemwood in fall compared to slower growing trees. Assuming a generally close link between tree growth and productivity of the entire forest ecosystem, as shown earlier (e.g., Rocha et al., 2006; Zweifel et al., 2010; Churakova et al., 2013), we expect fast grow-
ing, and thus highly productive forests to have large C reserves in stemwood and also in branches. For example, Hoch et al. (2003) showed that a highly productive mixed forest in Switzerland stored enormous amounts of C in stems and branches, which can be up to a decade old (Richardson et al., 2013). Therefore, highly productive forests could be able to buffer variations in C allocation to storage pools better than forests with a lower productivity, since an already large storage pool in highly productive forests (built up over several years) is less sensitive to short-term environmental changes such as previous year’s weather. In contrast, for a low productive forest with accordingly smaller C reserves, unfavorable weather conditions late in the previous year could lead to only a small refill of C storage pools, and thus to a smaller forest NEP in the current year.

(2) Carbone et al. (2013) also showed that the C pool of vigorous trees has a faster turnover and includes considerable amounts of new assimilates. Although disentangling the contribution of new and old C for tree growth remains challenging (Rocha, 2013), these findings could also imply a lower importance of C reserves for growth of vigorous trees due to the use of large quantities of newly assimilated C, despite their large NSC pool size. Any alteration of this NSC pool by unfavorable weather conditions of the previous year would therefore have little or even no effect on the current year productivity of highly productive forests, diminishing the relevance of the past conditions. Low productive forests, on the other hand, might thus rely less on new assimilates and relevance of past conditions is increased.

Also, stand age showed a significant relationship with the relevance of previous year’s weather, which increased with increasing age (Fig. 3f). Yet, our findings do not necessarily imply that older forests are simply more sensitive to weather of the past. In fact, we propose instead that older forests have a generally lower sensitivity to weather anomalies, or in other words, a greater ability to buffer current year’s weather than younger forests, which leads to a predominating influence of previous year’s weather, and vice versa for younger forests. The reason behind might be an earlier onset of leaf flush in younger compared to older trees. For example, Seiwa (1999) showed that the timing of leaf emergence of deciduous broadleaf trees (Acer mono) was earliest for youngest and latest for oldest trees, resulting in differences of leaf flush timing of up to almost two month. This earlier onset of leaf flush, as part of an evolutionary strategy, might allow younger trees growing within a structured forest stand to increase light reception, and thus photosynthesis and growth com-
pared to older trees. However, this competitive advantage comes with an increased vulnerability towards late frost events in spring, and hence the risk of a complete loss of newly grown foliage. Besides leaf flush, cambial activity also starts earlier in younger than in older trees (Rossi et al., 2008) and the hydraulic conductivity of stem, branches and leaves tends to decrease with increasing age (Mencuccini and Grace, 1996; Hubbard et al., 1999; McDowell et al., 2002). Earlier onset of xylogenesis as well as earlier and faster transport of water and nutrients into the crown in spring could result in a similar trade-off of a competitive advantage against an increased risk in spring (see above). Conversely, the overall effect of current year’s weather on NEP of old forests is reduced relative to the effect of previous year’s weather when spring conditions are less important due to late leaf flush or late cambial activity. This explanation is supported by our findings concerning the positive influence of high air temperatures in spring (Fig. 2a) and the overall relevance of spring conditions on annual forest NEP (Fig. 2b). Additionally, stand age had no influence on productivity (Fig. 4), confirming the findings concerning the ability of old forests to continuously sequester C and their importance for climate change mitigation (Luyssaert et al., 2008).

In conclusion, our multi-site study provides strong evidence of a consistent dependence of temperate and boreal forests on previous year’s weather, particularly strongly expressed at sites with low temperatures and at low productive and old sites. Gaining further insights into the mechanisms of inter-annual variability of NEP has the great potential to lead to more reliable estimates of forest C budgets under future environmental conditions. However, whether climate warming leads to a smaller dependency on previous year’s weather or whether this effect is counteracted by more frequent drought events, and thus water and nutrients limiting productivity, in turn leading to a larger dependency on previous year’s weather, remains to be investigated.

Acknowledgments

We thank all site PIs for their provision of publicly available data used in this study as well as for further site-specific information and support. The study was funded by the Swiss National Science Foundation (grant PDFMP3_132562) and the State
Secretariat for Education, Research and Innovation (COST SBF Nr. C10.0101), and contributes to COST Action FP 0903 "Climate Change and Forest Mitigation and Adaption in a Polluted Environment" (MAFor).
CHAPTER 4. RELEVANCE OF PREVIOUS YEAR’S WEATHER FOR FOREST NEP INCREASES WITH COLD TEMPERATURES AND AT LOW PRODUCTIVE SITES

4.5 References


CHAPTER 4. RELEVANCE OF PREVIOUS YEAR’S WEATHER FOR FOREST NEP INCREASES WITH COLD TEMPERATURES AND AT LOW PRODUCTIVE SITES


4.5. REFERENCES


CHAPTER 4. RELEVANCE OF PREVIOUS YEAR’S WEATHER FOR FOREST NEP INCREASES WITH COLD TEMPERATURES AND AT LOW PRODUCTIVE SITES

4.6 Tables and figures
Table 4.1: Site characteristics of the nine FLUXNET sites used. ENF = Evergreen needleleaf forest; DBF = Deciduous broadleaf forest; MF = Mixed forest. Data refers to the eddy covariance (EC) years used. Sunhours are mean hours per year with global radiation > 120 W m\(^{-2}\).

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<th>Type</th>
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<th>Lat.</th>
<th>Long.</th>
<th>Elevation m a.s.l.</th>
<th>T(_{a,\text{avg}}) °C</th>
<th>Precip. mm</th>
<th>Sunhours h yr(^{-1})</th>
<th>Age yrs</th>
<th>Height m</th>
<th>LAI m(^2) m(^{-2})</th>
<th>N(_{\text{dep}}) kg N ha(^{-1}) yr(^{-1})</th>
<th>Soil type</th>
<th>FAO classification</th>
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na: not available
CHAPTER 4. RELEVANCE OF PREVIOUS YEAR’S WEATHER FOR FOREST NEP INCREASES WITH COLD TEMPERATURES AND AT LOW PRODUCTIVE SITES

Table 4.2: Climatic variables, $p$ and $\beta$ values of each climatic variable, $p$ values of the intercept ($p_{\text{Intercept}}$) and the entire model ($p_{\text{mod}}$) as well as model adjusted $r^2$ (adj. $r^2$) for the three-variables models with current year’s weather (Type A models) and both current and previous year’s weather (Type B models).

### Type A models (Models with current year’s weather)

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<th>HYY</th>
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<th>NRI</th>
<th>SOR</th>
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<td>T2max.winter</td>
<td>T2max.spring</td>
<td>T2max.winter</td>
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<td>0.061</td>
<td>0.064</td>
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<td>adj. $r^2$</td>
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### Type B models (Models with both current and previous year’s weather)

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<th>HYY</th>
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<th>NRI</th>
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<td>T2max.winter</td>
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<td>T2max.winter</td>
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<td>0.007</td>
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<tr>
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<tr>
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<tr>
<td>$\beta_3$</td>
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<td>&lt;0.001</td>
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<td>&lt;0.001</td>
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<td>0.039</td>
<td>0.003</td>
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<td>0.002</td>
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<tr>
<td>adj. $r^2$</td>
<td>0.74</td>
<td>0.39</td>
<td>0.70</td>
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<td>0.82</td>
<td>0.72</td>
<td>0.62</td>
<td>0.46</td>
<td>0.09</td>
</tr>
</tbody>
</table>
Figure 4.1: Measured and modeled annual net ecosystem productivity for three selected sites with high (Fyodorovskoye, FYO; increase of \( \text{adj. } r^2 \) from 0.22 to 0.70), medium (Tharandt, THA; increase of \( \text{adj. } r^2 \) from 0.40 to 0.46), and low (Campbell River, CA1; increase of \( \text{adj. } r^2 \) from 0.71 to 0.74) increase in explained inter-annual variability when using current year’s weather (Type A models; a,c,e) or both current and previous year’s weather (Type B models; b,d,f). Grey shaded areas indicate 95% confidence intervals for the modeled NEP.
CHAPTER 4. RELEVANCE OF PREVIOUS YEAR’S WEATHER FOR FOREST NEP INCREASES WITH COLD TEMPERATURES AND AT LOW PRODUCTIVE SITES

Figure 4.2: Frequency (%) of variables (A) and seasons (B) used in the models linking NEP to climate variables for all Type B models with both current and previous year’s weather (from one up to three variables, i.e., overall 27 models with 54 variables). Light and dark grey parts of the bars in A indicate the frequency of the variables/seasons having a positive or negative relationship with NEP, respectively, based on the $\beta$ values in Table 2.
Figure 4.3: Log-log regressions of annual minimum air temperature (Tmin; a), number of days with a daily mean temperature below $-5 \, ^\circ C$ (DegDays$-5$; b), range of annual air temperature (Trange; c), net ecosystem productivity (NEP; d), gross primary productivity (GPP; e), and stand age (Age; f) against the relevance of previous year’s weather expressed as percent increase of the explained variance of inter-annual variability in NEP from Type A models vs. Type B models. Open circles in a–e represent the site HYY. Adj. $r^2$ values are given for relationships with and without HYY, since the site often did not follow the otherwise clear pattern (a–e). Log-log regression lines in a–f are shown for the significant regressions. Asterisks in a–f give the statistical significance of the corrected $p$-values of the linear regressions according to the Holms adjustment procedure, with * and ** indicating $p \leq 0.05$ and $p \leq 0.01$, respectively.
CHAPTER 4. RELEVANCE OF PREVIOUS YEAR’S WEATHER FOR FOREST NEP INCREASES WITH COLD TEMPERATURES AND AT LOW PRODUCTIVE SITES

Figure 4.4: Biplot for a principal component analysis of annual minimum air temperature (Tmin), number of days with a daily mean temperature below $-5^\circ$C (DegDays$-5$), range of annual air temperature (Trange), net ecosystem productivity (NEP), gross primary productivity (GPP), and stand age (Age).
4.7 Appendix
CHAPTER 4. RELEVANCE OF PREVIOUS YEAR’S WEATHER FOR FOREST NEP INCREASES WITH COLD TEMPERATURES AND AT LOW PRODUCTIVE SITES

Table 4.A.1: Summary of the 18 site characteristics and climate variables used for assessing the relevance of previous year’s weather for the nine sites analyzed. Air temperatures ($T_{\text{mean}}$, $T_{\text{min}}$, $T_{\text{max}}$, $T_{\text{range}}$) are annual values, DegDays$-5$ are number of days with a daily mean temperature below $-5 \, ^{\circ}\text{C}$, Sunhours are mean hours per year with global radiation $> 120 \, \text{Wm}^{-2}$, and Biodiv is the biodiversity (tree species only) expressed as Shannon-Wiener index.

<table>
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<th>Site</th>
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<th>Temp. °C</th>
<th>Min. K</th>
<th>Max. K</th>
<th>Range K</th>
<th>DegDays$-5$</th>
<th>Precip. mm</th>
<th>Sunhours h yr$^{-1}$</th>
<th>Age yrs</th>
<th>Height m</th>
<th>LAI $\text{m}^2 , \text{m}^{-2}$</th>
<th>BiomassAbove g C m$^{-2}$</th>
<th>Biodiv</th>
<th>NEP g C m$^{-2}$ yr$^{-1}$</th>
<th>GPP g C m$^{-2}$ yr$^{-1}$</th>
<th>TER g C m$^{-2}$ yr$^{-1}$</th>
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<td>12</td>
<td>4.2</td>
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<td>1.07</td>
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na: not available
Figure 4.A.1: Measured and modeled annual net ecosystem productivity for sites Davos (DAV; increase of \( \text{adj. } r^2 \) from 0.30 to 0.39), Hyytiälä (HYY; no change of \( \text{adj. } r^2 \)), and Loobos (LOO; increase of \( \text{adj. } r^2 \) from 0.73 to 0.82) when using current year’s weather (Type A models; A, C, E) or both current and previous year’s weather (Type B models; B, D, F). Grey shaded areas indicate 95% confidence intervals for the modeled NEP.
CHAPTER 4. RELEVANCE OF PREVIOUS YEAR’S WEATHER FOR FOREST NEP INCREASES WITH COLD TEMPERATURES AND AT LOW PRODUCTIVE SITES

Figure 4.A.2: Measured and modeled annual net ecosystem productivity for sites Niwot Ridge (NR1; increase of adj. $r^2$ from 0.41 to 0.72), Soroe (SOR; increase of adj. $r^2$ from 0.57 to 0.62), and Vielsalm (VIE; increase of adj. $r^2$ from 0.59 to 0.69) when using current year’s weather (Type A models; G, I, K) or both current and previous year’s weather (Type B models; H, J, L). Grey shaded areas indicate 95% confidence intervals for the modeled NEP.
Chapter 5

Timing of respiratory carbon loss compensation drives annual net ecosystem productivity in European forests

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Abstract

Accurate predictions of carbon dioxide (CO₂) uptake by forest ecosystems are fundamental for policy-relevant reporting on forest carbon (C) uptake for many national forest growth and greenhouse gas inventories, not only for the Kyoto Protocol. After analysing the timing of the day of year (DOY\textsubscript{Comp}) when respiratory losses during the dormancy period are fully compensated by the onset of spring assimilation, we determined to what extent DOY\textsubscript{Comp} can predict annual C uptake (cumulative net ecosystem productivity, NEP\textsubscript{c}, measured by the eddy covariance method) of eleven forest ecosystems within continental Europe. In addition, we compared different static and dynamic integration methods for annual NEP\textsubscript{c}. DOY\textsubscript{Comp} ranged from Jan 3 to Jul 24, with a mean of Apr 18. Vegetation type was the main driver for DOY\textsubscript{Comp}, mainly due to the differences between deciduous and broadleaved forest in onset of assimilation. In addition, mean annual temperature was an relevant driver for DOY\textsubscript{Comp}, probably due to the dormancy period and the start of the growing season. For the prediction of NEP\textsubscript{c}, the later the date of DOY\textsubscript{Comp}, the lower the annual NEP, probably due to the dormancy period and the start of the growing season. In general, DOY\textsubscript{Comp} was highly indicative for inter-annual variability of NEP\textsubscript{c} with cooler and older forest sites showing stronger relationships, explaining on average 70% of NEP\textsubscript{c} variability. While all three integration methods gave very similar NEP\textsubscript{c} magnitudes, we found that the dynamic integration of NEP\textsubscript{c} greatly improved the prediction of NEP\textsubscript{c} by DOY\textsubscript{Comp} compared to the classical calendar year integration (from 51% to 70% = 37% improvement), most likely by much better capturing the real ‘ecological year’ (in contrast to the calendar year) and thus...
5.1 Introduction

Accurate predictions of carbon dioxide (CO$_2$) uptake by forest ecosystems are fundamental for policy-relevant estimates of annual carbon (C) budgets. Considerable research in the past decades focused on improving these predictions, especially on annual time scales. Analysing intra-annual variability has also shown to be very promising, e.g. in relation to extreme events (e.g. Baldocchi and Wilson, 2001; Ciais et al., 2005; Richardson et al., 2009; Wu et al., 2013; Wolf et al., 2013). Focusing on either the intra-annual or inter-annual time scales alone has its limits, and therefore, it is crucial that more attention is paid to linking both time scales. Thus, this study builds on the current understanding that distinct periods within the year drive the annual and inter-annual variabilities of C uptake within European forests.

Dendro-chronologists have analysed individual tree rings at medium- to long-term time scales and the reconstruction of past climatic conditions has much changed our view on climate change and corresponding ecosystem responses (cf. Cook and Kairiukstis, 1990; Douglass, 1941; Schweingruber et al., 1988; Babst et al., 2013). However, extracting intra-annual information from these annual data is still difficult, but here a different technique can help, i.e., the use of automated dendrometers (Zweifel et al., 2010). These continuous measurements of stem radius changes at high temporal resolutions capture both actual tree water-relations and long-term tree growth and responses to microclimate (Zweifel et al., 2006). This knowledge fundamentally improved our understanding of both water and C related processes within a forest. Yet, continuous and long-term dendrometer data at a high temporal resolution are still scarce in forest ecosystems around the world. Nevertheless, a recent study has proven a close link between stem radius changes and annual net ecosystem CO$_2$ uptake (integrated/cumulative net ecosystem productivity NEP = NEP$_c$) as measured by the eddy covariance (EC) technique (Zweifel et al., 2010). EC is an established and widely-used method to measure and integrate C exchange between biosphere and atmosphere, resulting in continuous and long-term time series (cf. Baldocchi et al., 2001; Baldocchi, 2003; Aubinet et al., 2012). Therefore, we explore the possibility to transfer the methodological concept from the stem radius measurements to the EC measured at forest ecosystem level.

Traditionally, NEP$_c$ (= negative net ecosystem exchange, -NEE) has been integrated over a time period of calendar years, although respiratory losses do not statically
start on January 1 (Fig. 5.1), and in general, forest ecosystems do not follow the man-
made calendar year. Thus, this classical integration method ignores the dynamics of
a complex ecosystem to a large extent, while considering a more suitable integration
period might increase the accuracy of estimating C uptake of forests as well as
the certainty with which predictions can be made. In line with these thoughts,
Urbanski et al. (2007) have introduced a method integrating NEP$_c$ from October
28 to October 27 of the following year, thus starting integration earlier, but over a
static time period (Harvard forest).

Here, we propose a dynamic and hence more ecological integration method integrat-
ing the NEP fluxes from the cumulated fall maximum point reached in the previous
year ($\text{Fall}_{\text{Max}}$) to the next $\text{Fall}_{\text{Max}}$ of the next year (Fig. 5.1). In addition, we define
the day of compensation ($\text{DOY}_{\text{Comp}}$) as the day in the year when respiratory losses
during the last months are compensated by beginning net assimilation, equivalent to
an economic break-even point (Fig. 5.1). This mean, $\text{DOY}_{\text{Comp}}$ represents the day
when respiratory losses during the dormancy period, i.e., the period after the fall
maximum point ($\text{Fall}_{\text{Max}}$) until the minimum in the NEP$_c$ curve ($\text{Winter}_{\text{Min}}$) are
compensated by the beginning of canopy assimilation. Clearly, canopy assimilation
considerably influences annual forest C uptake (cf. Aurela et al., 2004; Richardson
et al., 2009; Etzold et al., 2011; Wu et al., 2013), but it is not clear how best to use
this information to predict NEP$_c$.

In this study, we used forest sites throughout Europe to address four specific objec-
tives: (1) to quantify $\text{DOY}_{\text{Comp}}$; (2) to identify drivers of $\text{DOY}_{\text{Comp}}$; (3) to evaluate
the usefulness of of $\text{DOY}_{\text{Comp}}$ to predict NEP$_c$; and (4) to compare three different
temporal integration methods for NEP$_c$.

5.2 Materials and methods

5.2.1 Study site selection

The study is based on carbon dioxide (CO$_2$) flux data from 115 site years from
eleven eddy covariance (EC) forest sites within Europe (Tab. 5.1, Fig. 5.2): Bily
Laegeren (2004–2012), Loobos (1997–2011), Soroe (1997–2010) and Tuczno (2008–2011). The selected sites are characterized by: (1) availability of continuous and complete data sets from EC measurements from at least four consecutive years; (2) data either downloadable from the European Fluxes Database in Level 4 or reliable Level 2 quality (European Fluxes Database Cluster, 2013), or directly receivable from the Principle Investigators (PIs) in high quality; (3) availability of site level meteorological data; (4) no relevant disturbances during the time period of data analysed, and (5) being a carbon (C) sink and not a C source. The vegetation is classified as six evergreen needle leaf forests (ENF), three deciduous broad leaf forests (DBF), one evergreen broad leaf forest (EBF), and one mixed forest (MF).

5.2.2 CO₂ flux measurements

Half-hourly CO₂ flux data (net ecosystem productivity, NEP, processed data), derived by EC measurements, were post-processed for all sites by first filtering out unrealistically high values (±50 µmol m⁻² s⁻¹) and unfavorable atmospheric conditions such as snow, heavy rain and/or dust (window dirtiness > 70%, open-path IRGA fluxes). Insufficient turbulent mixing of the atmosphere was accounted for via a u*-filter with a threshold of u* < 0.2 m s⁻¹, which corresponds to what the online EC gap-filling and flux partitioning tool provided with standardized methods (Reichstein et al., 2005; Reichstein and Menzer, 2013). After gap-filling, we filtered out large (positive) night time CO₂ fluxes, which by definition indicate CO₂ uptake, and thus are physiologically unrealistic when there is absolutely no light. Within a 14-day moving window, both negative and positive night time CO₂ fluxes (symmetric filtering) outside the range of ±3 standard deviations of the 14-day mean were dismissed. CO₂ is converted to units of C in NEP in g m⁻² s⁻¹. Positive NEP indicates net C uptake, while negative NEP indicates net C release (Aubinet et al., 1999). NEPₖ is defined as the integrated sum of NEP, yielding net C flux between the atmosphere and the forest. Positive year-end NEPₖ indicates that the forest is a C sink, while negative NEPₖ reflect a C source.
5.2. MATERIALS AND METHODS

5.2.3 CO₂ flux integration (ΣNEP = NEPₖ)

Classically, NEPₖ is the cumulated (= integrated) sum of NEPₖ over time, from January 1 to December 31 (Fig. 5.1). However, a calendar year does not capture biological or climatic variations on an ecological chronology and this is the reason why we also compared the classical integration method two other methods. First, the ‘Urbanski’ integration method, where NEPₖ is integrated always from October 28 to October 27 one year later (Urbanski et al., 2007). Second, a dynamic, ecological method, where we integrate from the NEPₖ maximum peak point (typically in fall; FallₖMax) from previous year to the next year.

**Period definitions**

We departed from the classical definition of winter and spring by calendar months and use the direction of fluxes as determinants. The respiratory loss period starting after the NEPₖ fall maximum peak (FallₖMax) leading to a NEPₖ local minimum point (particularly in winter, hence WinterₖMin) was the so-called dormancy period (Fig. 5.1). The time period after the WinterₖMin, leading up to the day of compensation (DOYₖComp), marked the so-called compensation period.

**Statistical analyses**

Statistical analyses were performed using dynamic scripts with R statistical software, version 3.0.3 (R Core Team, 2012). All regression models were based on linear relationships and adjusted R² (adjR²). In order to determine the drivers of DOYₖComp and to evaluate the prediction of annual NEPₖ based on DOYₖComp, we conducted stepwise multiple regression models based on the inclusion of explaining variables in a stepwise manner. Forest type was parametrized with numbers (DBF = 1, MF = 2, ENF = 3, EBF = 4). β-coefficients, so-called standardized regression coefficients, were used to determine the relative importances of variables within the models, ranging between −1 as the highest negative and +1 as the highest positive correlative importance (Quinn and Keough, 2001). A β-coefficient of zero indicates that the variable does not add anything to the model.
5.3 Results

5.3.1 Compensation of respiratory losses

Median $\text{DOY}_{\text{Comp}}$ (day in the year when respiratory losses from the proceeding dormancy period are compensated) differed strongly across sites and somewhat less on integration methods (i.e., ‘classical’, ‘Urbanski’ and ‘ecological’) for integrated net ecosystem productivity ($\text{NEP}_c$; Tab. 5.2, Fig. 5.3). $\text{DOY}_{\text{Comp}}$ occurred during a period of more than half a year, from January (Espirra, Jan 3) to July (Soroe, Jul 24) with a mean of Apr 28 (overall integration methods). $\text{DOY}_{\text{Comp}}$ of the classical integration method were on average almost a month earlier than the ones obtained with the Urbanski and the ecological integration methods. The start of the respective integration years ($\text{Fall}_{\text{Max}}$ of the previous years) were two months earlier with the Urbanski method and on average three months earlier with the ecological method compared to the classical method starting on January 1 (Fig. 5.3, Tab. 5.2). The standard deviation of $\text{DOY}_{\text{Comp}}$ for individual sites ranged from four days (Hainich, all methods) to more than 47 days (Loobos, ecological method). When looking at the median of the $\text{DOY}_{\text{Comp}}$ of all three methods, only five of the eleven sites (Loobos, Bily Kriz, Laegeren, Davos, Hyytiälä) compensated their respiratory losses in the traditionally defined spring calendar months March, April and May. Three sites (Espirra, El Saler, Tuczno) compensated before these spring months, while three (Collelongo, Hainich, Soroe) compensated after May. All integration methods showed on average a relatively similar standard deviation of $\text{DOY}_{\text{Comp}}$, ranging from 54 days (classical) to 57 days (ecological).

5.3.2 Drivers of $\text{DOY}_{\text{Comp}}$

$\text{DOY}_{\text{Comp}}$ was mainly explicable by forest type and temperature. Forest type alone explained $\text{DOY}_{\text{Comp}}$ with an adj$R^2$ of 0.64 (Tab. 5.3). The Mediterranean evergreen broad leaf forest (Espirra, EBF) had the earliest $\text{DOY}_{\text{Comp}}$, followed by the evergreen needle leaf, the mixed, and the deciduous broad leaf forests. A stepwise multiple regression model, including variables one-by-one, led to temperature as the second most important driving factor (Tab. 5.3). With the inclusion of temperature, we
achieved a significant adjR$^2$ of 0.78 (Tab. 5.3). Temperature explained 78% and 80% of the variation of the timing of DOY$_{\text{Comp}}$ (both significant) for evergreen needle leaf and deciduous forests, respectively, the two main vegetation types investigated (see order of sites in Fig. 5.3). Although the highest adjR$^2$ of 0.92 (explaining 92% of the variation of the timing of DOY$_{\text{Comp}}$) was achieved when including six variables (forest type, temperature, canopy height, longitude, latitude and tree age). This over-parametrized the multiple regression in relation to the dependent variable (only eleven sites). In addition, there was a strong interdependency of some of these variables, e.g., temperature depended strongly on latitude. Throughout all models and forest types, temperature was negatively correlated to DOY$_{\text{Comp}}$, i.e., the cooler the site was, the later DOY$_{\text{Comp}}$ occurred.

5.3.3 Annually integrated NEP$_c$ as function of the integration method

In contrast to the date of DOY$_{\text{Comp}}$, which strongly depended on the integration method, integrated net ecosystem productivity (NEP$_c$) showed only a small variability among the different integration methods (Tab. 5.2). However, variability of NEP$_c$ among sites was large. The forest with on average the smallest C uptake was Soroe with 160 g C m$^{-2}$ yr$^{-1}$ (ecological integration). Largest C uptake occurred at Bily Kriz (ecological integration) with 866 g C m$^{-2}$ yr$^{-1}$, almost 5.5 times larger than the smallest C uptake (Soroe). For all sites, standard deviations of NEP$_c$ did not exceed annual NEP$_c$. Both the classical and the Urbanski integration methods of NEP$_c$ yielded years with 365 days (by definition). Using the ecological method, the periods were in a range from 290 days (ten months) to 444 days (15 months; supplemental Fig. 5.5). The length of these integration periods did not have a significant influence on the differences of NEP$_c$ among the classical, Urbanski and ecological integration methods (data not shown).

5.3.4 Estimating NEP$_c$ from DOY$_{\text{Comp}}$

The relationships between DOY$_{\text{Comp}}$ and NEP$_c$ showed good agreements, with the ecological method being in most cases the best integration method (explaining 53% to 85% of the NEP$_c$ variance) to estimate NEP$_c$ from DOY$_{\text{Comp}}$ (Tab. 5.2, Fig. 5.4).
Independent of the integration method, NEP$_c$ of three sites (Espirra, Hainich and Tuczno) could not be predicted from DOY$_{Comp}$ at all. DOY$_{Comp}$ in Espirra and Tuczno did not occur every year, due to very small net C losses during winter-time. DOY$_{Comp}$ in Hainich were consistent, however, the range of DOY$_{Comp}$ timing was so small that no relationship between DOY$_{Comp}$ and NEP$_c$ was found (more facts see below). For the classical integration method, five out of the remaining eight sites showed a significant relationship, with adjR$^2$ ranging between 0.41 and 0.80, and an average adjR$^2$ of 0.63 (Tab. 5.2). With the Urbanski integration method, seven out of the eight sites showed a significant relationship, with a range of adjR$^2$ between 0.46 and 0.82 and an average of 0.63 (Tab. 5.2). The ecological integration method led to significant relationships between DOY$_{Comp}$ and NEP$_c$, with adjR$^2$ ranging from 0.53 (El Saler) to 0.85 (Davos), resulting in a high average value of 0.70 (Tab. 5.4). For one site (Collelongo), the Urbanski integration method was the best integration method, while for two sites, the classical integration method showed the best relationship between DOY$_{Comp}$ and NEP$_c$ (Tab. 5.4). For five of the eight sites, adjR$^2$ using the ecological integration method was 23% (+0.13 absolute) higher than that of the Urbanski method and 37% (+0.19 absolute) higher than that of the classical method.

5.3.5 Prediction quality of NEP$_c$ from DOY$_{Comp}$

The quality of DOY$_{Comp}$ as a predictor for NEP$_c$ (adjR$^2$ between DOY$_{Comp}$ and NEP$_c$) was found to depend on distinct site characteristics (Tab. 5.4). Tree age and temperature explained the goodness of fit consistently and significantly ($\beta$-coefficients $> \text{absolute 0.46}$, for models with up to three variables). When looking at the one-variable model alone, it included forest type, which explained most of the prediction quality ($= 0.56$; Tab. 5.4). When introducing tree age and temperature into the model, the importance of forest type, however, vanished almost completely ($\beta$-coefficient of almost zero), leaving tree age and temperature as the two most relevant variables ($\beta$-coefficients: 0.51 for tree age and -0.46 for temperature). In terms of tree age, the older the forest, the better the predictability of NEP$_c$ based on DOY$_{Comp}$ (Tab. 5.4). Furthermore, the lower the mean annual temperature, the better the predictability of NEP$_c$ based on DOY$_{Comp}$ (Tab. 5.4).
5.4 Discussion

Seasonal anomalies, such as deviations from long-term temperature averages or climatic extreme events, have shown to be of importance to understand EC-based integrated net ecosystem productivity (NEP$_c$, Baldocchi and Wilson, 2001; Ciais et al., 2005; Richardson et al., 2009; Wu et al., 2013; Wolf et al., 2013). A better understanding of potential NEP$_c$ drivers thus needs a focus on highly temporal resolved time series below inter-annual time scales (cf. Zweifel et al., 2006). Recent studies have also shown that a considerable proportion of the inter-annual variability of NEP$_c$ cannot be explained by the current year’s climatic variability alone (cf. Zielis et al., 2014). In order to catch the intra-annual variability of NEP$_c$ and its drivers, we introduced the day of compensation (DOY$_{Comp}$), which marks the day of the year — typically in spring — when respiratory losses during dormancy are compensated by spring and early summer assimilation (Fig. 5.1). Comparing the variability of DOY$_{Comp}$ with the one of NEP$_c$ at eight of eleven forest ecosystems throughout Europe revealed an intriguingly close relationship between DOY$_{Comp}$ and NEP$_c$ (Fig. 5.4). Thus, we conclude that DOY$_{Comp}$ incorporates much of the seasonal characteristics of temperate forests driving NEP$_c$, being an excellent predictor of annual variability of NEP$_c$ in most cases. The predictions worked the better, the older and the cooler the forest sites were (Tab. 5.4), indicating the importance of the dormancy period for upcoming C sink processes in these forest ecosystems.

5.4.1 Environmental drivers of DOY$_{Comp}$

The loss of C during the dormancy and the respective compensation of this C loss was found to depend on forest type and temperature, while structural forest characteristics (e.g., tree height and LAI) did not play a role for the timing of DOY$_{Comp}$ (Tab. 5.3, Fig. 5.3). In general, the coniferous forests showed earlier DOY$_{Comp}$, while the deciduous forests compensated their respiratory losses later in the year, clearly reflecting foliage phenology and the ability of an earlier onset of assimilation in evergreen than in deciduous forests (Richardson et al., 2010), since photosynthetic capacity of needles can be attained after only a few days upon exposure to optimal environmental conditions (Ottander and Öquist, 1991; Ottander et al., 1995; Suni et al., 2003). In contrast, deciduous forests need more time in spring for bud burst,
leaf flushing and the onset of photosynthetic activity (Epron et al., 1996; Jurik, 1986; Koike, 1990; Reich et al., 1991). Besides forest type, also temperature significantly influenced the timing of the DOY\textsubscript{Comp}. However, this was found to be consistently for a given vegetation type and not across different vegetation types (Tab. 5.3). Low temperatures not only determine the length of the dormancy period, but in general drive and also limit metabolic processes (Richardson et al., 2010). In general, the cooler the site, the later DOY\textsubscript{Comp} (Fig. 5.3). It has been shown, especially for boreal forests, that the rate of recovery at the beginning of the growing period strongly depends upon ambient air temperatures (Lundmark et al., 1988; Koike, 1990; Suni et al., 2003). For example, some studies showed that the sum of temperature was the main determinant of the recovery of photosynthetic capacity after winter (Häkkinen et al., 1998; Hannerz, 1999; Linkosalo, 2000; Sarvas et al., 1972; Suni et al., 2003), while others have stressed the role of soil temperature and/or soil thawing (De Lucia et al., 1991; Sarvas et al., 1972). Also, melting of snow, as a consequence of rising temperatures in spring, has been suggested (Monson et al., 2011). The start of the dormancy period (\text{Fall}_{\text{Max}}) is the result of the processes from that year, while \text{Winter}_{\text{Min}} is partly the result of previous year’s weather and of the next year’s weather (Zielis et al., 2014). Time lag effects, due to processes which happened in the previous year, but influence a forest in the following year, have been proposed. These, however, are up to now inadequately included in ecosystem carbon models (Keenan et al., 2012; Zielis et al., 2014). Zielis et al. (2014) showed that at a subalpine forest in Switzerland (DAV, also included in this study), soil temperature in the current year’s spring played the major role controlling annual NEP\textsubscript{c}, mainly by influencing when and at what rate assimilation started early in the year. Although process understanding seems still limited, DOY\textsubscript{Comp} seems to capture these temperature-driven processes very well, and reflecting the ecological variability along the gradient of eleven forest ecosystems throughout Europe.

5.4.2 Strengths and limitations of DOY\textsubscript{Comp} for NEP\textsubscript{c} prediction

The value of DOY\textsubscript{Comp} as a predictor of NEP\textsubscript{c} was found to be very high (adjR\textsuperscript{2} > 0.53). In addition, DOY\textsubscript{Comp} explained NEP\textsubscript{c} consistently better the older and the cooler the forest ecosystems were (Tab. 5.4). Mechanisms explaining
our observation might be an earlier photosynthetic activity in younger forests and a higher susceptibility to frost events in early springs affecting C investments into tissue repair (see above). Besides age, lower annual air temperatures furthermore increased the explanatory power of DOY\textsubscript{Comp} for NEP\textsubscript{c}. This highlights the importance of the dormancy period, e.g., its length affected by the timing of the snow melt (Aurela et al., 2004; Monson et al., 2011). Recent studies have been contradictory on how generally higher temperatures and earlier growing periods influence annual NEP\textsubscript{c}. Sacks et al. (2007) revealed that annual NEP\textsubscript{c} of a subalpine conifer forest decreased in years with an early spring, due to the melting of a shallow snowpack (but compare to Monson et al., 2011), which resulted in reduced soil water contents, and ultimately water limitations, later in the growing season.

The determination of DOY\textsubscript{Comp} requires that a forest shows a strong seasonality of C loss and C uptake. If this is not the case, e.g., at warmer sites (Espirra, El Saler) or very productive sites (Tuczno), this approach cannot be used (Tab. 5.2, Fig. 5.3). This limits the DOY\textsubscript{Comp} concept to mainly temperate forests only.

The beech forest Hainich was in several aspects a startling case, with the amazingly small inter-annual time window of DOY\textsubscript{Comp} with ±4 days (in eight years). Hainich was the only site, where a linear regression between DOY\textsubscript{Comp} and NEP\textsubscript{c} could not be found, considering enough converging DOY\textsubscript{Comp} (Tab. 5.2, Fig. 5.4). Other beech forests (Soroe, Collelongo and Laegeren) did not have such narrow windows of DOY\textsubscript{Comp}, although climate variation was not smaller at Hainich than at the other sites (Tab. 5.2, Fig. 5.4). Of all of the deciduous and mixed forests, Hainich had the highest LAI (6 m\textsuperscript{2} m\textsuperscript{-2} in comparison to 5, 3.6 and 4.8 m\textsuperscript{2} m\textsuperscript{-2} for Collelongo, Laegeren and Soroe, respectively). No relationship, however, was found between the timing of the window of DOY\textsubscript{Comp} and LAI (data not shown). Of the deciduous and mixed forests, Hainich also yielded the smallest standard deviations of annual NEP\textsubscript{c}, with 67 g C m\textsuperscript{-2} yr\textsuperscript{-1} in comparison with 202, 129 and 110 g C m\textsuperscript{-2} yr\textsuperscript{-1} for Collelongo, Laegeren and Soroe, respectively (Tab. 5.2). A highly significant relationship was found for the standard deviation of annual productivity (NEP\textsubscript{c}) influencing the timing window of DOY\textsubscript{Comp} (adjR\textsuperscript{2} = 0.78***, supplemental Fig. 5.6). Therefore, we assume that for Hainich, the relatively small variability of NEP\textsubscript{c} itself also led to very low power of DOY\textsubscript{Comp} to predict NEP\textsubscript{c}. 

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5.4.3 Why integrating NEP$_c$ with a dynamic method?

The ecological integration method of NEP$_c$, which runs from the previous year’s peak of NEP$_c$ (Fall$_{Max}$) to the current year’s peak (Fall$_{Max}$), resulted in distinctly better fits (higher adjR$^2$) for predicting NEP$_c$ from DOY$_{Comp}$ among all three methods (Tab. 5.2). Although the integration method strongly affected the timing of DOY$_{Comp}$, it had only little influence on the magnitude of NEP$_c$. The annual sum of NEP$_c$ is classically summed up over a calendar year and although this is an easy thing to do, it neglects seasonal variation of ecological processes and carry-over effects in temperate forests (e.g., Keenan et al., 2012; Urbanski et al., 2007; Zweifel et al., 2010; Zielis et al., 2014). The ‘Urbanski’ method (Urbanski et al., 2007), used at Harvard forest, shifted away from this calendar-based year and integrated from fall to fall, however, statically from October 28 to October 27 of the following year (Fig. 5.1). Although this method provided better results to predict NEP$_c$ than the classical method, it did not achieve the quality of prediction as the ecological integration method proposed here, across many European forests, from Portugal to Finland. The reasons for the improved prediction quality of the ecological method may originate from the dynamic — instead of static — consideration of biological processes (Zweifel et al., 2010) and potential time lag effects (Zielis et al., 2014). The NEP$_c$ peak used to determine the integration period reflects the end of the ‘ecological year’, in the sense of net C accumulation of a forest stand until the next year. Beyond this point in time, forest ecosystems are not able to compensate their respiratory losses by assimilation any longer, growth and therefore C sequestration stopped. NEP$_c$ peak (Fall$_{Max}$) therefore also determines the start of the dormancy period. Since Fall$_{Max}$ is not only determined by the tree species, but also by environmental factors at the site, and these factors vary temporally, we believe that this dynamic behaviour of the environment is much better captured by a dynamic than a static method, thus, explaining the higher prediction quality of the ecological integration method.

5.5 Acknowledgements

The authors are grateful for the funding from both the Swiss National Science Foundation (grant PDFMP3_132562) and the State Secretariat for Education, Research
and Innovation (COST SBFI Nr. C10.0101), and is part of COST Action FP0903 ‘Climate Change and Forest Mitigation and Adaptation in a Polluted Environment’ (MAFor). We acknowledge furthermore the funding for two COST Short Term Scientific Missions (Action FP0903) in Sweden (Prof. Anders Lindroth, Dr. Fredrik Lagergren and Dr. Meelis Mölder) and in Poland (Prof. Janusz Olejnik and Dr. Marek Urbaniak). In addition, we are grateful for the statistical consulting (Mark Hannay) at the Seminar for Statistic, ETH Zürich.
5.6 References


CHAPTER 5. TIMING OF RESPIRATORY CARBON LOSS COMPENSATION DRIVES ANNUAL NET ECOSYSTEM PRODUCTIVITY IN EUROPEAN FORESTS


5.7 Tables and figures
### Table 5.1: Detailed description of the selected sites used in this study (Fig. 5.2, European Fluxes Database Cluster 2013).

Sites are abbreviated with the original three letter FLUXNET codes, not including the country code. Forest types: DBF = deciduous broad leaf forests, ENF = evergreen needle leaf forests, MF = mixed forests, and EBF = evergreen broad leaf forests. Species = dominant species in the forest. Latitude and longitude positive, when North or East respectively. Years used are the years received. Precipitation = mean annual sum. Annual air temperature = mean annual temperature at the top of the eddy towers. Winter temperature = mean temperature of the months of December, January and February. Age = average age of the mature trees in the stand. Height = maximum of the canopy height above ground. LAI = leaf area index. N deposition = mean annual value. Data access = either download from the European Database Cluster in mostly Level 4 (highest) quality, or receipt directly from the PIs.

<table>
<thead>
<tr>
<th>Site FLUXNET</th>
<th>Forest Type</th>
<th>Dominant Species</th>
<th>Lat</th>
<th>Long</th>
<th>Years</th>
<th>Precip</th>
<th>Annual Temp</th>
<th>Winter Temp</th>
<th>Altitude</th>
<th>Age</th>
<th>Height</th>
<th>LAI</th>
<th>N deposition</th>
<th>Data Access</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bily Kriz, CZ</td>
<td>ENF</td>
<td>Picea abies</td>
<td>49.51</td>
<td>18.54</td>
<td>2000-2010</td>
<td>1100</td>
<td>4.9</td>
<td>-2.2</td>
<td>898</td>
<td>30</td>
<td>10</td>
<td>7.5</td>
<td>28.0</td>
<td>download, L4 post-processed</td>
</tr>
<tr>
<td>Collelongo, IT</td>
<td>DBF</td>
<td>Fagus sylvatica</td>
<td>41.85</td>
<td>13.59</td>
<td>1996-2011</td>
<td>1180</td>
<td>6.3</td>
<td>-0.2</td>
<td>1550</td>
<td>105</td>
<td>25</td>
<td>5.0</td>
<td>10.0</td>
<td>download, L4 post-processed</td>
</tr>
<tr>
<td>Davos, CH</td>
<td>ENF</td>
<td>Picea abies</td>
<td>46.81</td>
<td>9.86</td>
<td>1997-2011</td>
<td>1000</td>
<td>3.4</td>
<td>-3.3</td>
<td>1639</td>
<td>240</td>
<td>25</td>
<td>3.9</td>
<td>1.5</td>
<td>own site own processing</td>
</tr>
<tr>
<td>El Saler, ES</td>
<td>ENF</td>
<td>Pinus halepensis</td>
<td>39.35</td>
<td>-0.32</td>
<td>2000-2008</td>
<td>445</td>
<td>17.1</td>
<td>11.1</td>
<td>5</td>
<td>100</td>
<td>10</td>
<td>3.5</td>
<td>6.0</td>
<td>download, L4 post-processed</td>
</tr>
<tr>
<td>Espirra, PT</td>
<td>EBF</td>
<td>Eucalyptus globulus</td>
<td>38.64</td>
<td>-8.60</td>
<td>2002-2008</td>
<td>665</td>
<td>15.4</td>
<td>10.3</td>
<td>85</td>
<td>12</td>
<td>20</td>
<td>3.1</td>
<td>14.0</td>
<td>download, L4 post-processed</td>
</tr>
<tr>
<td>Hainich, DE</td>
<td>DBF</td>
<td>Fagus sylvatica</td>
<td>51.08</td>
<td>10.45</td>
<td>2000-2007</td>
<td>750</td>
<td>7.0</td>
<td>0.1</td>
<td>445</td>
<td>125</td>
<td>33</td>
<td>6.0</td>
<td>11.0</td>
<td>download, L4 post-processed</td>
</tr>
<tr>
<td>Hyytiala, FI</td>
<td>ENF</td>
<td>Pinus sylvestris</td>
<td>61.85</td>
<td>24.30</td>
<td>1997-2012</td>
<td>650</td>
<td>3.5</td>
<td>-5.7</td>
<td>170</td>
<td>40</td>
<td>14</td>
<td>2.5</td>
<td>4.0</td>
<td>direct download post-processed</td>
</tr>
<tr>
<td>Laegeren, CH</td>
<td>MF</td>
<td>Mixed</td>
<td>47.48</td>
<td>8.37</td>
<td>2004-2012</td>
<td>1000</td>
<td>7.4</td>
<td>-0.8</td>
<td>682</td>
<td>140</td>
<td>31</td>
<td>3.6</td>
<td>26.1</td>
<td>own site own processing</td>
</tr>
<tr>
<td>Loobos, NL</td>
<td>ENF</td>
<td>Pinus sylvestris</td>
<td>52.17</td>
<td>5.74</td>
<td>1997-2011</td>
<td>966</td>
<td>10.0</td>
<td>3.2</td>
<td>25</td>
<td>90</td>
<td>18</td>
<td>1.9</td>
<td>40.0</td>
<td>download, L2 post-processed</td>
</tr>
<tr>
<td>Soroe, DK</td>
<td>DBF</td>
<td>Fagus sylvatica</td>
<td>55.49</td>
<td>11.65</td>
<td>1997-2010</td>
<td>510</td>
<td>8.1</td>
<td>1.3</td>
<td>35</td>
<td>100</td>
<td>35</td>
<td>4.8</td>
<td>23.0</td>
<td>download, L4 post-processed</td>
</tr>
<tr>
<td>Tuczno, PL</td>
<td>ENF</td>
<td>Pinus sylvestris</td>
<td>53.21</td>
<td>16.10</td>
<td>2008-2011</td>
<td>625</td>
<td>7.8</td>
<td>0.3</td>
<td>105</td>
<td>54</td>
<td>20</td>
<td>1.1</td>
<td>8.5</td>
<td>direct post-processed</td>
</tr>
</tbody>
</table>

El Saler was dismantled in the beginning of 2009.
Table 5.2: Overview of main results: Compensation days ($DOY_{Comp}$), integrated net ecosystem productivity ($NEP_c$), and the adjusted R-squared ($adjR^2$) of the relationship between $DOY_{Comp}$ and $NEP_c$ for each site: $DOY_{Comp}$ in days of year ($DOY$), ± one standard deviation range and date (Fig. 5.4). Integrated $NEP_c$ in g C m$^{-2}$ yr$^{-1}$. $adjR^2$ = linear model fit between $DOY_{Comp}$ and $NEP_c$. The differences between the time integration methods are that the classical method integrates half hourly $NEP_c$ values from January 1 to December 31, the Urbanski method from October 28 to October 27, and the ecological method from previous year’s maximum peak within the integrated $NEP_c$ curve (typically in fall) to the next year. Best fit indicates which method yielded the highest $adjR^2$, considering enough years with a distinct compensation of respiratory losses.

<table>
<thead>
<tr>
<th>Site</th>
<th>Vegetation</th>
<th>$DOY_{Comp}$</th>
<th>$NEP_c$</th>
<th>$adjR^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>[doy ± 1sd days (date)]</td>
<td>[g C m$^{-2}$ yr$^{-1}$]</td>
<td>[0...1]</td>
</tr>
<tr>
<td></td>
<td>classical</td>
<td>ecological</td>
<td>classical</td>
<td>ecological</td>
</tr>
<tr>
<td>BK1</td>
<td>ENF</td>
<td>94 ±3 (Apr 03)</td>
<td>98 ±10 (Apr 08)</td>
<td>102 ±10 (Apr 11)</td>
</tr>
<tr>
<td>COL</td>
<td>ENF</td>
<td>142 ±25 (May 21)</td>
<td>157 ±16 (Jun 07)</td>
<td>157 ±22 (Jun 06)</td>
</tr>
<tr>
<td>DAV</td>
<td>ENF</td>
<td>134 ±21 (May 14)</td>
<td>130 ±30 (Jun 09)</td>
<td>163 ±42 (Jun 12)</td>
</tr>
<tr>
<td>ESI</td>
<td>ENF</td>
<td>13 ±17 (Jan 13)</td>
<td>25 ±27 (Jan 25)</td>
<td>39 ±34 (Feb 07)</td>
</tr>
<tr>
<td>ESP</td>
<td>ENF</td>
<td>3 ±4 (Jun 05)</td>
<td>11 ±14 (Jun 11)</td>
<td>25 ±20 (Jun 24)</td>
</tr>
<tr>
<td>HAI</td>
<td>ENF</td>
<td>164 ±4 (Jun 13)</td>
<td>160 ±14 (Jun 28)</td>
<td>182 ±4 (Jun 30)</td>
</tr>
<tr>
<td>HYY</td>
<td>ENF</td>
<td>132 ±9 (May 11)</td>
<td>152 ±10 (May 31)</td>
<td>157 ±10 (Jun 06)</td>
</tr>
<tr>
<td>LAE</td>
<td>MF</td>
<td>115 ±18 (Apr 24)</td>
<td>134 ±14 (May 13)</td>
<td>136 ±13 (May 16)</td>
</tr>
<tr>
<td>LOO</td>
<td>ENF</td>
<td>64 ±36 (Mar 04)</td>
<td>82 ±47 (Mar 22)</td>
<td>89 ±47 (Mar 29)</td>
</tr>
<tr>
<td>SOR</td>
<td>ENF</td>
<td>164 ±14 (Jun 13)</td>
<td>193 ±21 (Jul 12)</td>
<td>205 ±25 (Jul 24)</td>
</tr>
<tr>
<td>TUC</td>
<td>ENF</td>
<td>18 ±24 (Jan 17)</td>
<td>26 ±NA (Jan 26)</td>
<td>69 ±10 (Mar 10)</td>
</tr>
</tbody>
</table>

*p<0.05; **p<0.01; ***p<0.001
Table 5.3: Drivers of the compensation day (DOY\textsubscript{Comp}) in stepwise multiple linear regression models. The variables (vars) are included one-by-one in the models. The β-coefficients (β-coefs) — indicating the relative importance of the variable, ranging from −1 (highest importance, negative correlation) to +1 (highest importance, positive correlation). † = the linear significance for forest type — as parametrized with DBF=1, MF=2, ENF=3 and EBF=4 — was not calculated.

<table>
<thead>
<tr>
<th>Drivers of DOY\textsubscript{Comp}</th>
<th>adjR\textsuperscript{2}</th>
<th>Stepwise multiple regression models (β-coefs)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>alone</td>
<td>1 var</td>
</tr>
<tr>
<td>forest type</td>
<td>0.64†</td>
<td>1.00</td>
</tr>
<tr>
<td>temperature</td>
<td>0.53*</td>
<td>−</td>
</tr>
<tr>
<td>canopy height</td>
<td>0.45*</td>
<td>−</td>
</tr>
<tr>
<td>longitude</td>
<td>0.33</td>
<td>−</td>
</tr>
<tr>
<td>latitude</td>
<td>0.28</td>
<td>−</td>
</tr>
<tr>
<td>tree age</td>
<td>0.23</td>
<td>−</td>
</tr>
<tr>
<td>LAI</td>
<td>0.16</td>
<td>−</td>
</tr>
<tr>
<td>altitude</td>
<td>0.15</td>
<td>−</td>
</tr>
<tr>
<td>precipitation</td>
<td>0.05</td>
<td>−</td>
</tr>
<tr>
<td>N deposition</td>
<td>0.00</td>
<td>−</td>
</tr>
<tr>
<td><strong>Total adjR\textsuperscript{2}</strong></td>
<td>−</td>
<td>0.64†</td>
</tr>
</tbody>
</table>

*: \(p<0.05\), **: \(p<0.01\), ***: \(p<0.001\)
Table 5.4: Quality of prediction (adjR²) of net ecosystem productivity (NEP<sub>c</sub>) based on the timing of compensation days (DOY<sub>Comp</sub>) in stepwise multiple linear regression models based on characteristics from each site (Tab. 5.1). The variables (vars) are included one-by-one in the models. The β-coefficients (β-coefs) — as the determinants of the relative importance of the variable — ranging from values from –1 (highest importance, negative correlation) to +1 (highest importance, positive correlation). † = the linear significance for forest type — as parametrized with DBF=1, MF=2, ENF=3 and EBF=4 — was not calculated.

<table>
<thead>
<tr>
<th>Quality of prediction</th>
<th>adjR²</th>
<th>Stepwise mult. regr. mod. (β–coefs)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>alone</td>
<td>1 var</td>
</tr>
<tr>
<td>forest type</td>
<td>0.56†</td>
<td>1.00</td>
</tr>
<tr>
<td>tree age</td>
<td>0.50*</td>
<td>-</td>
</tr>
<tr>
<td>temperature</td>
<td>0.46*</td>
<td>-</td>
</tr>
<tr>
<td>latitude</td>
<td>0.27</td>
<td>-</td>
</tr>
<tr>
<td>longitude</td>
<td>0.26</td>
<td>-</td>
</tr>
<tr>
<td>altitude</td>
<td>0.15</td>
<td>-</td>
</tr>
<tr>
<td>precipitation</td>
<td>0.15</td>
<td>-</td>
</tr>
<tr>
<td>canopy height</td>
<td>0.12</td>
<td>-</td>
</tr>
<tr>
<td>N deposition</td>
<td>0.05</td>
<td>-</td>
</tr>
<tr>
<td>LAI</td>
<td>0.00</td>
<td>-</td>
</tr>
<tr>
<td>Total adjR²</td>
<td></td>
<td>0.56†</td>
</tr>
</tbody>
</table>

*: p<0.05, **: p<0.01, ***: p<0.001
Figure 5.1: Three different methods of integrating net ecosystem productivity (NEP$_c$) over time: ‘Classical’ integration (=c) runs from Jan 1 to Dec 31 of every individual year; ‘Urbanski’ integration (=U) from Oct 28 of the previous year to Oct 27 of the actual year; ‘Ecological’ integration (=e) runs dynamically for every site and for every year from the previous year’s NEP$_c$ maximum (Fall$_{Max}$) to the current year’s NEP$_c$ maximum (Fall$_{Max}$), e.g. 2008 may run from Sep 25, 2007 to Sep 13, 2008. Respiratory losses occur between the maximum peak of NEP$_c$ of the previous year (typically in fall, hence Fall$_{Max}$) and the minimum peak of NEP$_c$ of the current year (particularly in winter, hence ). This period is here defined as the ‘dormancy period’. The compensation period is the interval between and the day of compensation (DOY$_{Comp}$).
Figure 5.2: Spatial distribution of the eleven sites included in this study. The original three letter FLUXNET abbreviations are used as identifiers (see Tab. 5.1).
Figure 5.3: Occurrence of the compensation days (DOY_{Comp}) for all three integration methods ('classical', 'Urbanski' and 'ecological') for all sites. The sites (abbreviated according to Tab. 5.1 and Fig. 5.2) are sorted by forest type and mean annual air temperature (the two consistent drivers of the timing of the DOY_{Comp}, Tab. 5.3). The dashed vertical lines depict the calendaric spring (months March, April and May). The linear regression lines are depicted for coniferous and deciduous forests only, as the relationship between DOY_{Comp} and mean annual air temperature with adjusted R^2 (adjR^2) of high significance (p<0.001).
Figure 5.4: Linear regression models for each method and site between the compensation days (DOY\textsubscript{Comp}) and integrated annual net ecosystem productivity (NEP\textsubscript{c}) (Tab. 5.2). For each site and method (□: classical, △: Urbanski and ○: ecological), the adjusted \( R^2 \) (adj\( R^2 \)) values are derived from the linear model of the relationship between DOY\textsubscript{Comp} and NEP\textsubscript{c}. A regression line is only depicted, when the relationship is significant.
5.8 Supplemental material
Supplemental Table 5.1: Comparison of the quality predicting integrated net ecosystem productivity (NEP<sub>c</sub>) based on three indicator days (maximum peak within the previous year’s NEP<sub>c</sub> curve = Fall<sub>Max</sub>, minimum peak in the current year = , compensation day = DOY<sub>Comp</sub>, Fig. 5.1).

<table>
<thead>
<tr>
<th>Site</th>
<th>Fall&lt;sub&gt;Max&lt;/sub&gt; adjR²</th>
<th>Winter&lt;sub&gt;Min&lt;/sub&gt; adjR²</th>
<th>DOY&lt;sub&gt;Comp&lt;/sub&gt; adjR²</th>
<th>best indicator</th>
</tr>
</thead>
<tbody>
<tr>
<td>BK1</td>
<td>0.09</td>
<td>0.06</td>
<td>0.68**</td>
<td>DOY&lt;sub&gt;Comp&lt;/sub&gt;</td>
</tr>
<tr>
<td>COL</td>
<td>0.08</td>
<td>0.19</td>
<td>0.60***</td>
<td>DOY&lt;sub&gt;Comp&lt;/sub&gt;</td>
</tr>
<tr>
<td>DAV</td>
<td>0.04</td>
<td>0.68***</td>
<td>0.89***</td>
<td>DOY&lt;sub&gt;Comp&lt;/sub&gt;</td>
</tr>
<tr>
<td>ES1</td>
<td>0.16</td>
<td>0.98***</td>
<td>0.53*</td>
<td>Winter&lt;sub&gt;Min&lt;/sub&gt;</td>
</tr>
<tr>
<td>ESP</td>
<td>0.84*</td>
<td>0.42</td>
<td>0.35</td>
<td>Fall&lt;sub&gt;Max&lt;/sub&gt;</td>
</tr>
<tr>
<td>HAI</td>
<td>0.20</td>
<td>0.16</td>
<td>0.03</td>
<td>no regressions</td>
</tr>
<tr>
<td>HYY</td>
<td>0.32*</td>
<td>0.06</td>
<td>0.64***</td>
<td>DOY&lt;sub&gt;Comp&lt;/sub&gt;</td>
</tr>
<tr>
<td>LAE</td>
<td>0.16</td>
<td>0.08</td>
<td>0.73**</td>
<td>DOY&lt;sub&gt;Comp&lt;/sub&gt;</td>
</tr>
<tr>
<td>LOO</td>
<td>0.54**</td>
<td>0.52**</td>
<td>0.78***</td>
<td>DOY&lt;sub&gt;Comp&lt;/sub&gt;</td>
</tr>
<tr>
<td>SOR</td>
<td>0.25*</td>
<td>0.02</td>
<td>0.74***</td>
<td>DOY&lt;sub&gt;Comp&lt;/sub&gt;</td>
</tr>
<tr>
<td>TUC</td>
<td>0.83</td>
<td>0.71</td>
<td>n=1</td>
<td>insufficient years</td>
</tr>
</tbody>
</table>

*: p<0.05, **: p<0.01, ***: p<0.001
Supplemental Figure 5.5: Length of integrated periods in days for the ecological integration method (of net ecosystem productivity, NEP$_c$) (see Fig. 5.1). The integration periods vary in a range from less than 290 days (ten months) to more than 444 days (15 months). However, the average length is with 364.0 days very close to an actual calendar year (classical method). Site years included: 115.
Supplemental Figure 5.6: Window size of day of compensation (DOY\textsubscript{Comp}) (difference between first and last date of DOY\textsubscript{Comp}) in relation to the absolute standard deviation of net ecosystem productivity (NEP\textsubscript{c}, in g C m\textsuperscript{-2} yr\textsuperscript{-1}) for mixed and deciduous forests only. The linear relationship is highly significant with an adjusted R-squared (adjR\textsuperscript{2}) of 0.78 (p<0.001).
Chapter 6

Increasing relevance of spring temperatures for Norway spruce trees in Davos, Switzerland, after the 1950s

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Abstract

We investigated long-term (over 100 years) tree-ring width (TRW) variabilities as well as short-term (10 years) variations in net ecosystem productivity (NEP) in response to climate to assess the driving factors for stem growth of Norway spruce in a subalpine forest at Davos in Switzerland. A tree-ring width index (TRWi) chronology for the period from 1750 to 2006 was constructed and linked with climate data from 1876 to 2006, and with NEP available for the period from 1997 to 2006. Based on TRWi, we found that only two out of the 257 years exhibited extreme negative TRWi, compared to 29 years with extreme positive anomalies, observed mainly in recent decades. Annual temperature, annual precipitation, as well as autumn and winter temperature signals were well preserved in the TRWi chronology over the last 130 years. Spring temperatures became increasingly relevant for TRWi, explaining less than 1% of the variation in TRWi for the period from 1876 to 2006, but 8% for the period from 1950 to 2006 \((p = 0.032)\), and even 47% for 1997–2006 \((p = 0.028)\). We also observed a strong positive relationship between annual TRWi and annual NEP \((r = 0.661; p = 0.037)\), both strongly related to spring temperatures \((r = 0.687\) and \(r = 0.678\) for TRWi and NEP, respectively; \(p = 0.028; p = 0.032)\). Moreover, we found strong links between monthly NEP of March and annual TRWi \((r = 0.912; p = 0.0001)\), both related to March temperatures \((r = 0.767, p = 0.010\) and \(r = 0.724, p = 0.018\), respectively). Thus, under future climate warming, we expect stem growth of these subalpine trees and also ecosystem carbon (C) sequestration to increase, as long as water does not become a limiting factor.
6.1 Introduction

Annual changes in the environment are well recorded in tree-ring widths (TRW), since tree rings integrate physiological responses of trees to climatic and environmental changes (Schweingruber et al., 1988; Spiecker, 2002). Therefore, tree rings are often used as archives of climate change (Fritts, 1976; Kozlowski et al., 1991; Schweingruber et al., 1996; Vaganov et al., 2006), in particular because instrumental records of climatic conditions for the Northern Hemisphere older than 100 years are rare. Several dendrochronological studies have shown increases in radial stem growth related to warming in subalpine regions throughout the world during the last century (e.g. Neumann and Schadauer, 1995; Bolli et al., 2007), most pronounced during the last decade (Rolland et al., 1998; Paulsen et al., 2000). However, changes in the environmental conditions that trees experience do not only originate from climatic changes, but also from changes in forest stand structure due to natural disturbances or management. Thus, studies of tree-ring chronologies for the last two centuries, characterized by pronounced changes in forest, are best supplemented with historical data on forest management.

In Switzerland, temperature and water regimes have already been changing over the last decades (CH, 2012). For the near future, drought is expected to increase, with unknown consequences on forest ecosystems. The relatively high mortality rate of Scots pine during the last 30 years in Valais, Southern Switzerland, and the increasing crown dieback and mortality rates of European larch during recent years have been discussed with respect to climate change (e.g. Eilmann and Rigling, 2012). Thus, it is crucial to increase our understanding of how and to what degree trees—which are considered significant carbon sinks—respond to such changes.

Moreover, tree rings can be used to deduce stem biomass increments over long periods (Landsberg et al., 2005; Spiecker, 2002), providing archived information on the carbon accumulation in a forest. On the other hand, measurements of the exchange of carbon dioxide between biosphere and atmosphere using the eddy-covariance technique allow the quantification of net ecosystem productivity (NEP). Carbon accumulation in tree stems is reported to have a strong weight on NEP (Rocha et al., 2006; Gough et al., 2009; Grant et al., 2009; Ohtsuka et al., 2009; Stoy et al., 2009; Mund et al., 2010; Goulden et al., 2011; Metsaranta and Kurz, 2012), although the link between tree-ring growth and net ecosystem CO₂ fluxes is
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not yet fully understood, and studies often show contradicting results: Rocha et al. (2006) reported tight relationships between TRW and net ecosystem CO$_2$ exchange ($r^2 = 0.85$). Similarly, Grant et al. (2009) found positive relationships between both approaches. However, other studies only mentioned similar orders of magnitude for both estimates (Mund et al., 2010; Metsaranta and Kurz, 2012). Nevertheless, combining eddy-covariance measurements with tree-ring analyses seems very promising, using the benefits of both methods: information on high temporal resolution net ecosystem CO$_2$ fluxes and their drivers at the ecosystem scale with the long-term information on stem growth at the tree scale (Williams et al., 2005; Girardin et al., 2011). However, complementary data of these two independent data streams for forest sites are scarce, constraining the ability to generalize the coupling between TRW and NEP.

Here, we present results from the Davos Seehornwald forest, Switzerland, where information from different approaches is available: tree-ring width index (TRWi) chronology since 1750, instrumental climate records since 1876, and eddy-covariance measurements of forest net CO$_2$ exchange since 1997. Based on these data, we addressed the following questions:

1. Which climate drivers influenced Norway spruce treering growth most strongly over the last 130 years?

2. To what degree is TRW—as a proxy for stem increment—related to NEP, representing a close link between TRW at the tree scale and NEP at the ecosystem scale?

3. Is there a common driver linking TRW and NEP?

6.2 Materials and methods

6.2.1 Study site

The study site is located in the subalpine zone of Switzerland in the Davos Seehornwald forest (46°48′N and 9°51′E, 1639 m a.s.l.), where detailed ecophysiological measurements have been carried out since 1987 (Herzog et al., 1995), complemented by ecosystem CO$_2$ flux measurements since 1997 (Zweifel et al., 2010). Monthly tem-
perature and precipitation data are available since 1876 (MeteoSwiss site at Davos; 46°49' N, 9°51' E, 1594 m a.s.l.). These data were homogenized and corrected for dislocation of the Davos station in the early period of the measurements by MeteoSwiss using the homogenization procedure of Begert et al. (2005), which is divided into two main steps: the detection of inhomogeneities and the calculation of the adjustments. The annual mean temperature for the period from 1876 to 2006 is 3.14 °C, and the average annual precipitation is 997 mm. The typical growing season length according to Davos weather station data, when temperatures rise above 5 °C (see Fritts, 1976; Schweingruber et al., 1988, 1996), is around 5 months, starting in May and ending in September. Snow cover usually starts in early November and can last until May.

The dominant tree species growing in the Davos Seehornwald forest is Norway spruce (Picea abies (L.) Karst.). The vegetation has a maximum canopy height of 27 m (mean height around 18 m), and is considered to be moderately productive in the regional context at this altitude (Zweifel et al., 2010). The mean age of the co-dominant and dominant spruce trees is around 240 years, ranging between 200 and up to 450 years (Etzold et al., 2011). The understory vegetation is rather patchy, covering roughly 50% of the ground, and is mainly composed of dwarf shrubs, primarily Vaccinium myrtillus L. and Vaccinium gaultherioides Bigelow as well as mosses. The remaining 50% of the soil surface is covered by spruce litter without vegetation cover.

### 6.2.2 Dendrochronological analysis

Cross sections were taken from nine dominant living spruce trees at around 20 cm from the ground in autumn 2006, during a thinning event within regular forest management. Due to economical constraints, no tree cores at breast height (1.3 m height) could be taken. Nevertheless, it has been shown that tree-ring samples taken at lower heights yield similar results to those taken at breast height (Schweingruber et al., 1988; Cherubini et al., 2002). Stem discs were dried and sanded, allowing a clear identification of individual tree rings. TRW were measured using semiautomatic devices (LINTAB measuring table) with 0.01 mm precision combined with the program TSAP (Rinntech, Heidelberg, Germany) for the period from 1750 to 2006. To avoid the influence of compression wood on TRW measurements, two to
four different radii on each disc were measured and averaged. Mean tree diameter was $44 \pm 15$ cm (mean ± SD), ranging from 18 to 59 cm, taking into account growth patterns of different diameter classes, to avoid sampling biases (Cherubini et al., 1998; Brienen et al., 2012).

The TRW time-series were visually cross-dated and dating quality was verified using the program COFECHA (Holmes, 2001). The mean age of the dominant trees sampled was 230 years. The age trend in the individual (raw) TRW chronologies was removed according to the standard procedures (method of standardization) provided by the ARSTAN Software program (Cook and Krusic, 2008a) by selecting a negative exponential curve ($k > 0$) or a linear regression. Standardized TRWi chronology based on the average of nine trees was used for further analysis. Then, TRWi chronology was normalized to calculate TRW anomalies, with an average of zero for the whole analyzed period and to reveal so-called pointer years (i.e., extreme cold and warm years: ± 1.5 $\sigma$).

To define a threshold level of common signals among tree-ring series, the Expressed Population Signal (EPS) was calculated based on the average correlation among trees. An EPS value higher or equal 0.85 is considered to be reliable along the entire time-series (Wigley et al., 1984). In addition, the running robust average inter-series correlation (RBAR), which is independent of sample size, was used as an indicator of common variance among tree-ring series (Wigley et al., 1984; Cook and Kairiukstis, 1990). EPS and RBAR were calculated among all samples using the ARS41d_xp.exe software, with a 10-year running RBAR window with a 5-year overlap (Cook and Krusic, 2008a). Hamming smoothing (Blackman et al., 1959) with an 11-year window was used to test for long-term trends of TRWi and climate data chronologies.

### 6.2.3 Net ecosystem productivity (NEP)

CO$_2$ exchange rates between the atmosphere and the biosphere for the years 1997–2006 were measured by the eddy-covariance technique, consisting of a triaxial ultrasonic anemometer (Solent R2 ultrasonic anemometerthermometer; since 2006: Solent R3-50, Gill Instruments Ltd., Lymington, UK) and an infrared gas analyser (closedpath Licor 6262; since September 2005: open-path Licor 7500, Licor, Lincoln,
USA), mounted on a horizontal boom attached to the top platform of a 35 m high tower, 17 m above the mean canopy height. The eddy-covariance data were measured at 20 Hz resolution, from which 30 min averages were computed according to the European standard methodology (Aubinet et al., 2012).

In addition, a correction for temperature fluctuations (Webb–Pearman–Leuning correction; (Webb et al., 1980)) and self-heating of the LI-7500 instrument surface was applied to the flux measurements in 2006. For the latter correction, the procedure exactly followed the one described in Rogiers et al. (2008) and validated by Järvi et al. (2009). Then, fluxes were filtered for unrealistically high values (±50 µmol m⁻² 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 $u_* < 0.2$ m s⁻¹. Gaps in the data set, due to malfunction of instruments or filtering (as described above), were filled according to gap length. Small gaps (2 h) were linearly interpolated. Larger daytime and nighttime gaps were filled with modeled data utilizing light (Moffat, 2010) and temperature response functions (Lloyd and Taylor, 1994), respectively, with a moving window of variable size. Remaining gaps were filled with a running mean approach.

In this study, we calculated NEP for every month, for the four standard climatological seasons, and for each calendar year by summing up the 30 min CO₂ flux averages over the respective periods to link it with TRWi and climate data. Positive values of NEP indicate net uptake of carbon (ecosystem acting as a C sink), while negative values represent net respiratory losses of C (ecosystem acting as a C source).

### 6.2.4 Forest management

Information on forest management was taken from earlier reports on Swiss forestry (Petitmermet, 1950), studies on forest development within the Davos region (Cook and Krusic, 2008b; Günther, 1984) as well as from a compilation for our forest site (Tschopp, 2012). General management information dates back to the end of the nineteenth century.
6.3 Results

The mean TRW from a set of nine cross-dated individual TRW chronologies was 0.94 mm for the period 1750–2006 (Fig. 6.1a). Based on strong relationships among individual trees (RBAR of 0.68; EPS of 0.94), the individual TRW and the normalized average TRWi chronologies (Fig. 6.1b, c) were constructed. Persistently large annual width increments were observed after the 1950s.

While precipitation did not show a clear trend with time between 1876 and 2006, air temperatures have increased during these 130 years (Fig. 6.2b, c; Table 6.1). Both factors significantly influenced the TRWi of Norway spruce, in addition to winter and autumn temperatures (Fig. 6.2a, e, f; Table 6.1). Highest correlation coefficients with TRWi (unsmoothed values) were found for winter air temperatures (December to February; \(r = 0.354; p = 0.001\)) and annual mean air temperatures \((r = 0.297; p = 0.001)\), while correlations were lower but still significant for annual precipitation \((r = 0.214; p = 0.014)\) and autumn air temperatures (September to November; \(r = 0.191; p = 0.029\)). Spring (March to May) or summer (June to August) temperatures did not have any significant effects on the TRWi record over the 130-year period.

However, after the 1950s, among annual temperatures \((r = 0.299; p = 0.024)\), spring temperatures became a significant climate factor \((r = 0.285; p = 0.032)\) (Table 6.1). This relevance for tree-ring growth further increased when only considering the last 10 years of the long-term record. During these 10 years (1997–2006), spring temperatures showed a very tight link with TRWi \((r = 0.687; p = 0.028)\), together with summer precipitation \((r = 0.792; p = 0.006)\). Both climate factors, spring temperatures and summer precipitation, did increase by 0.6 °C and by 53 mm at the Davos weather station for the period from 1997 to 2006 compared to the period from 1876 to 1996, respectively.

Annual TRWi and annual NEP for the period from 1997 to 2006 were significantly correlated \((r = 0.661; p = 0.037)\) (Fig. 6.3a), indicating a large contribution of stem growth to ecosystem C sequestration. In turn, both TRWi and NEP were significantly related to spring temperatures \((r = 0.687 \text{ and } r = 0.678; p = 0.028 \text{ and } p = 0.032 \text{ for TRWi and NEP, respectively; 1997 to 2006; Table 6.1})\). Furthermore, high correlations were found between TRWi and monthly NEP of February \((r = 0.729; p = 0.017)\) (data not shown) and monthly NEP of March \((r = 0.912;\)
for the last 10 years (Fig. 6.3a). At the same time, strong positive responses of both TRWi and NEP to March air temperatures were observed ($r = 0.767$, $p = 0.010$ and $r = 0.724$, $p = 0.018$, respectively).

### 6.4 Discussion

#### 6.4.1 Long-term tree-ring and climate chronologies

Only few years before 1950 were classified as extreme years, i.e., falling outside the ±1.5σ range around the overall mean (Fig. 6.1c, horizontal dashed lines). Of these extreme years, only two showed negative growth anomalies, i.e., 1820 and 1821, which is in close agreement with the Alpine climate reconstruction by Frank and Esper (2005), who identified 1821 as the year with the lowest summer (June to August) temperatures during the period 1600 to 2000. All other pointer years showed positive growth anomalies, larger than average long-term growth, i.e., in the 1860s (1863, 1866, 1867, 1869), most of the 1950s (1952–1961), 1968, 1969, and during 12 out of 20 years between 1983 and 2002 (1983, 1985, 1988–1990, 1992–1996, 2000, 2001). Such positive growth anomalies since the 1950s as in our study have also been reported by Rolland et al. (1998) for *Picea abies*, *Larix decidua*, *Pinus cembra* and *Pinus uncinata* near the alpine timberline and by Paulsen et al. (2000) studying tree rings along elevational transects at and below the upper treeline in the European Alps.

While some years with negative growth anomalies clearly showed the response to climatic anomalies (namely in 1948 or during the period of the Little Ice Age from 1750 to 1837 which includes very cold years such as 1821), others rather showed the response to severe weather events (see also Babst et al., 2012). For example, low treering growth in 1980 was probably due to the exceptionally high snow loads in September 1979, reported by Cook and Krusic (2008b).

#### 6.4.2 The influence of climate on TRWi

Focusing on the period between 1920 and 1970, Babst et al. (2013) also found higher correlations of TRWi with temperatures than with precipitation for the Alpine
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region, and a clear dominance of temperature on TRWi for Norway spruce in this time window. While annual temperature and precipitation are known to affect plant growth (Larcher, 1995), high autumn (September to November) and mild winter temperatures (December to February) at this subalpine site might have two effects; (1) less frost damage, when winter and spring average temperatures are close to their norm temperatures and not anomalies and (2) less intensive frost hardening and therefore earlier and larger tree-ring growth. (1) Milder winters with less severe frost periods will reduce the risk of frost damage. This means that the water-conducting xylem vessels are less likely to be destroyed (Larcher, 1995), and hence stem dehydration and embolism will become less severe (Sperry and Sullivan, 1992; Mayr et al., 2002). Also impacts on phloem cells in the bark (Zweifel and Häsler, 2000) and cell death in general will become less likely during mild winter conditions. Thus, frost-related cell repair will be less C consuming and consequently growth and biomass production can start earlier in the following spring. Thus, mild temperatures during the winter season are clearly advantageous for tree-ring growth. (2) Furthermore, frost hardening might have been impacted by increasing temperatures over the last decades. Once plants are frost hardened, their metabolic activities are highly reduced and cell division is shut down (Sakai, 1970; Sakai et al., 1987), and literature therein). The lower the temperatures and the longer the cold winter periods, the more intensive is the frost hardening and its persistence, with negative consequences for spring metabolic activities. With increasing winter temperatures, frost hardening will not be as intensive and the de-hardening process can start earlier in spring (Sakai, 1970), also contributing to increased tree-ring growth.

6.4.3 Changes in management recorded in tree rings between 1876 and 2006

In general, forest management in Switzerland has been obliged to adopt the sustainability concept, since the Swiss Federal Forestry Law entered into force in 1876, thus forest use should not have exceeded tree growth, although reinforcement did not start until some decades later (Petitmermet, 1950). Until mid-twentieth century, forest use in Switzerland consisted of tree harvests for multiple purposes (e.g., timber, fencewood, firewood, litter); in addition, forest grazing by cattle, sheep, and
goats was common (Günther, 1984; Cook and Krusic, 2008b). However, both litter raking and forest grazing strongly decreased until the 1950s (Cook and Krusic, 2008b). During and after World War II, tree harvests in Swiss forests, particularly during the period from 1940 to 1946, were higher than usual, with about double the harvest amounts as compared with previous years (Petitmermet, 1950). Forest harvests (carried out in winters) only resumed to “normal” magnitudes in winter 1946/1947. Overall, Swiss forests during the last two centuries were rather overexploited until sustainable management was reinforced around 1900 (Günther, 1984; Cook and Krusic, 2008b; Tschopp, 2012); they were strongly impacted by wood demand during the two world wars (Petitmermet, 1950), and are currently rather underused, with increasing wood stocks accumulating in Swiss forests (Brändli, 2012; Tschopp, 2012).

For the Davos forests, Tschopp (2012) reported an average harvest rate of 1.9 m$^{-3}$ ha$^{-1}$ year$^{-1}$ during the period from 1924 to 1964, which drastically decreased to an average 0.8 m$^{-3}$ ha$^{-1}$ year$^{-1}$ thereafter from 1964 to 1983. However, our TRWi data clearly show a very fast transition from average annual growth rates to increased stem biomass production (positive TRWi anomalies) in the early 1950s, which suggests that this transition in management intensities occurred already a decade earlier in the Davos Seehornwald forest compared to forests in the larger Davos region. Moreover, Tschopp (2012) analyzed aerial photographs from this period and found evidence of increasing density of the forest canopy already in the period from 1954 to 1985.

### 6.4.4 Tree-ring growth, net ecosystem productivity and climate variability

Based on mean monthly flux rates, highest net CO$_2$ uptake of the Davos Seehornwald forest was found in April and May compared to the rest of the year (for the years 1997–2009) (Etzold et al., 2011). Similarly, Metsaranta and Kurz (2012) reported warm spring temperatures increasing net primary production (NPP) of boreal forests, pointing to the high relevance of spring conditions on tree growth and thus carbon sequestration in forests. Furthermore, the tight positive relationship between tree-ring growth and NEP found at the Davos Seehornwald forest site (Fig. 6.3) is supported by high-resolution point-dendrometer measurements (Zweifel...
et al., 2010), showing a strong link between radial diameter increments and NEP. Similar patterns were also reported by Rocha et al. (2006) who showed a highly significant relationship between TRWi and NEP for an old black spruce stand in Canada (about 150 years old), and by Jassal et al. (2010) who reported increased TRWi and simultaneously net ecosystem exchange (NEE) for three relatively young Douglas fir stands in the Pacific Northwest after 2 years of fertilization (7, 19 and 59 years old). Since no management interventions had taken place during the period from 1997 to 2006 at our site, we can exclude respective influences on such a spring-driven link.

6.5 Conclusions

In this study, we have been able to identify the high relevance of increment growth and its contribution to ecosystem C sequestration based on the combination of different approaches and data streams, i.e., long-term tree-ring growth chronology, forest management information, instrumental climate records, and high temporal resolution net ecosystem CO$_2$ fluxes, which would not have been possible with one approach alone. The increasing relevance of spring temperatures over time on stem growth suggests that C sequestration in woody biomass in our subalpine Davos forest might increase substantially under future climatic warming, as long as soil moisture does not become a growth-limiting factor in spring. Potential mechanisms for increased stem growth might be a combination of less frost damage and reduced frost hardening. Nevertheless, information on the long-term soil C sequestration is needed to predict the fate of the total C sequestration of this subalpine forest under future climate conditions.

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6.6 References


6.6. REFERENCES


6.7 Tables and figures
Table 6.1: Correlation coefficients between climate data and annual (unsmoothed) tree-ring width index (TRWi) and net ecosystem productivity (NEP) for the periods from 1876 to 2006, 1950 to 2006, and 1997 to 2006

<table>
<thead>
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<th>Period</th>
<th>Parameter</th>
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<th>Precipitation</th>
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<td>Annual</td>
<td>Spring</td>
<td>Summer</td>
<td>Autumn</td>
<td>Winter</td>
<td>Annual</td>
<td>Spring</td>
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<tr>
<td>1876–2006</td>
<td>TRWi</td>
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<td>0.019</td>
<td>-0.005</td>
<td>0.191</td>
<td><strong>0.354</strong></td>
<td>0.214</td>
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<td><strong>p = 0.960</strong></td>
<td><strong>p = 0.029</strong></td>
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<td>TRWi</td>
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<td>0.285</td>
<td>0.176</td>
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<td><strong>p = 0.619</strong></td>
<td><strong>p = 0.253</strong></td>
<td><strong>p = 0.522</strong></td>
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<td>1997–2006</td>
<td>TRWi</td>
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<td>-0.025</td>
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<td><strong>p = 0.511</strong></td>
<td><strong>p = 0.028</strong></td>
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<td><strong>p = 0.107</strong></td>
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<td></td>
<td>NEP</td>
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<td>0.678</td>
<td>-0.061</td>
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<td>-0.042</td>
<td>0.366</td>
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<td>0.254</td>
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<td><strong>p = 0.939</strong></td>
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<td><strong>p = 0.987</strong></td>
<td><strong>p = 0.615</strong></td>
<td><strong>p = 0.908</strong></td>
<td><strong>p = 0.298</strong></td>
<td><strong>p = 0.950</strong></td>
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Significant values are in bold
Figure 6.1: Individual tree-tring width chronologies of nine trees (a), tree-ring width index (TRWi) and number of trees (b), and normalized average chronology with extreme pointer years defined as years outside the mean ± 1.5σ (dashed lines) (c) for the period from 1750 to 2006
Figure 6.2: Tree-ring width index (TRWi) (a), annual precipitation (b), annual temperature (c) as well as spring (d), autumn (e), and winter (f) air temperatures for the period 1876 to 2006. The bold black curves are smoothed by a 11-year Hamming window.
Figure 6.3: Time courses of tree-ring width index (TRWi), annual net ecosystem productivity (NEP) and net ecosystem productivity of March (a) as well as annual average temperature, average spring and average March air temperature (b) for the period 1997 to 2006
Chapter 7

General conclusion

This Ph.D. thesis aimed at increasing the understanding of driving mechanisms determining the forest C balance, which is of utmost importance for more precise C budget estimates under future climate change. Besides this general aim, this thesis focused especially on delayed responses of forest net ecosystems productivity (NEP) to weather of the previous year. To reach this goal, we analysed data of the C balance of forests and/or components thereof derived by eddy-covariance (EC), dendrometer, and tree ring measurements of boreal and temperate forests on temporal scales ranging from half-hours to years. Based on our initial research questions, this Ph.D. project comprises three main findings, which will be briefly concluded in this chapter: (1) the influence of spring weather on the C balance of forests; (2) delayed responses of forest ecosystems to previous year’s weather; and (3) the link between tree growth and forest NEP.

7.1 Influence of spring weather on forest C balance

Our various analyses of climatic drivers and the time of the year, when these drivers most strongly influence the C balance of forests and its components, strikingly highlight the importance of spring (March, April, May) conditions for the studied temperate and boreal forest ecosystems. With only the exception of TER, we show that NEP, gross primary productivity (GPP), and tree-growth as the major component of the forest C balance, of two Swiss forests are strongly influenced by weather
conditions in spring (Chapters 2, 3, and 6). Mostly, air and soil temperature in spring were identified as the main drivers, showing a positive relationship with forest NEP, even if these temperatures were classified as extremes (cf. Chapter 3). These findings indicate that the studied Swiss forest ecosystems bear potential to further increase their ability to take up CO₂ with increasing temperatures in the future (CH, 2012), and thus, further strengthen their already important role in mitigating climate change (Pan et al., 2011), if no other resources become limiting.

Also on a large spatial scale our findings on the importance of weather conditions in spring held true. Across a wide range of different forest ecosystems, both current and previous year’s weather in spring were most important for forest NEP (Chapter 4). Moreover, we showed that the compensation date of respiratory C losses (DOY\textsubscript{comp}, day of year of compensation) is of great use to predict the annual forest C budget, with an earlier compensation date leading to higher annual NEP. The DOY\textsubscript{comp} explained on average 70% of the annual NEP for a wide range of European forests (Chapter 5). For almost half of the investigated sites, this compensation occurred in spring. Thus, we were providing more insights into the debate whether climate change and its consequence for changes in spring or fall weather conditions affect the C balance of forest ecosystems positively or negatively and which of these two seasons determines the C balance more strongly (e.g. Hollinger et al., 2004; Niemand et al., 2005; Sacks et al., 2007; Piao et al., 2008; Richardson et al., 2010; Keenan et al., 2014). Our results strengthen the position of a positive and stronger determination of the C balance by weather conditions in spring across a wide range of temperate and boreal forests.

7.2 Delayed responses of forest ecosystems

In Chapter 2 of this thesis we addressed the task of providing evidence for significant delayed feedback mechanisms between forest ecosystems and climatic drivers. In more detail, we quantified the influence of previous year’s weather on current year annual NEP in a subalpine Norway spruce forest. Such delayed responses of C exchange processes are repetitively proposed as a possible cause for poor model performance due to the underrepresentation of such temporal feedback mechanisms (if represented at all). This underrepresentation is potentially responsible for the so
far challenging efforts to explain inter-annual variability of NEP (Urbanski et al., 2007; Gough et al., 2008) and might lead to imprecise C budget estimates (Keenan et al., 2012; Babst et al., 2013). We showed that NEP of the subalpine forest Davos Seehornwald had a significantly response to previous year’s weather. We quantified this delayed response as a drastically increase in explained inter-annual variability of NEP with the \( \text{adj. } r^2 \) raising from 0.20 to 0.53 when previous year’s weather was considered in statistical regression models. Updated data processing procedures, which were implemented after the publication of Chapter 2, led to changes in the annual NEP of the Davos forest. To assess whether our results concerning the relevance of the previous year’s weather for the Davos forest were still true, we repeated our analysis with the new data. Although lower than before, considering previous year’s weather still increased explained inter-annual variability of NEP by 30%, which gave us further confidence in the robustness of our result.

Consequentially, the next step was to validate the findings concerning the relevance of the delayed response of forest’s NEP from one forest site at other forests of different species composition, which are also diverse in terms of climate and site characteristics. Chapter 4 of this thesis comprises a multi-site analysis, covering strongly differing temperate and boreal forests in Europe as well as the USA and thus, tackles the question concerning an wide-spread occurrence of the delayed response. We were able to show that NEP of the majority of the analysed sites (eight out of nine) in fact showed a response to previous year’s weather with the average explained variability of NEP increasing by 30% (rise of \( \text{adj. } r^2 \) from 0.49 to 0.64), however, the magnitude of this response varied strongly among sites. Since the goal of this Ph.D. study was not only to explore and quantify patterns, yet also aimed at uncovering their underlying mechanisms, we further identified causes responsible for forests to show difference strength of the delayed response. Our analysis revealed that exposure to cold climatic conditions, a low productivity as well as an old stand age led to a stronger response of forest’s current year NEP to previous year’s weather, possibly due to frost-induced damages to tree parts (Pederson et al., 2004) associated with C losses due to increased C costs for repair, productivity-related carbon storage (e.g. Carbone et al., 2013) as well as age dependent differences in timing of leaf flush and cambial activity (Seiwa, 1999; Rossi et al., 2008). Thus, this chapter provides yet another piece in the puzzle that is the C balance of forest ecosystems. We were able to confirm that the findings from our single-site study concerning the delayed
response of forest NEP hold true on a much broader spatial scale, and beyond that, provided a first understanding of underlying ecophysiological mechanisms of delayed responses. Thus, we delivered strong evidence for delayed response of the C balance in a forest ecosystem. With that, we laid the foundation for the application of our findings to C budget modeling efforts, which we expect to lead to an increase in quality of forest C budget estimates.

7.3 Linking tree growth and forest net ecosystem productivity

Deriving NEP of forests as a result of EC measurements over large spatial scales is restricted due to the limited number of measurement sites. On the other hand, however, data of tree growth, the major component of the forest C budget, is often available at a higher spatial resolution and comes at lower costs. Thus, being able to explain and predict NEP via tree growth bears great potential to determine fast and instantaneous trends of forests’ C budget on large spatial scales. In Chapter 6, we showed that tree growth as measured by tree-ring width has a strong and positive weight on EC-derived NEP of a subalpine coniferous Swiss forest ($r = 0.661$), a link that has often been shown to lead to contradictory or only weak results so far (e.g. Rocha et al., 2006; Grant et al., 2009; Metsaranta and Kurz, 2012). Showing the same relationship, however, with tree growth derived from high-resolution dendrometer data is even more rare and, to our knowledge, has only been done for one forest site (Zweifel et al., 2010). Yet, using the high temporal resolution of continuous tree growth data would enable us to explore the link to NEP on intra-annual scales, as instead of inter-annual scales only, to which we are usually bound by tree-ring data. In the Appendix A, we first introduced a methodology to separate dendrometer data into stem growth and tree water deficit which then served as the foundation for a multi-site study linking stem growth and forest NEP (Appendix B). In this study with six European forests, we were able to explain on average 85% of daily NEP with stem growth alone, with among-site differences being determined by the so-called “time to grow”, the growth amplitude over time. Thus, we could build a strikingly simple (uni-variate), yet powerful statistical model which outperformed many multi-variate and often highly-complex ecosystems models (cf. Keenan
et al., 2012). These chapters highlight the integral qualities of trees, incorporating information on meteorological and biological conditions driving the C balance of the entire forest ecosystem.

The strong link between tree growth and the ecosystem C balance, which our results show, is striking and on the first glance surprising. Tree growth, as measured here, only represents the C sink activity of the C balance since once-built woody matter is not lost again. The release of C is the second major component of the C balance, yet is not directly accounted for in our measurements. However, given the close link tree growth and the C balance, the former has to be related to the release of C from the entire forest to some extent. This is supported by the repeatedly shown link between assimilation and respiration (mainly autotrophic) in forest ecosystems (e.g. Ekblad and Hogberg, 2001; Högberg et al., 2001; Knöhl et al., 2005). Consequently, the unexplained part of the C balance by tree-growth might therefore be attributed to the heterotrophic respiration, which seems to be largely independent from the sink C activity of trees (at least on shorter time scales, and thus, not including e.g. the supply of C via litter or dead wood for microbial decomposition). In case of the dendrometer approach, measuring tree growth which can include the degradation of phloem cells in the bark, and thus, shrinkage of the stem radius might also be responsible for an unexplained part of the relationship between the C balance and tree growth.

7.4 Open questions and future work

Although this Ph.D. thesis contributes towards the understanding of temporal dynamics and feedbacks of the carbon balance of forests, it also reveals remaining knowledge gaps and poses new questions. With delayed responses of forest NEP to weather of the previous year being the core of this project, we focus hereupon in this outlook onto future scientific work.

One of the main questions, which our work arose, is on the physiological mechanisms responsible for delayed responses of forest NEP. Although we proposed several explanations potentially causing such delays, e.g. year-to-year changes in the build-up of stored C in the previous year, the pre-formation of buds as well as prolonging effects of frost events (cf. Chapter 2), it is not even clear yet, whether delays in
NEP are evoked by delays in growth (GPP), respiration (TER), or a combination of both. Analysing the component fluxes for delayed responses could lead to valuable insights and provide first explanations. However, it has to be kept in mind, that component fluxes are themselves calculated involving climate variables, and thus, identifying climatic drivers of (delayed) component responses remains challenging. Also, it needs to be assessed how climate change alters the above mentioned eco-physiological mechanisms and their likely superimposition, since alterations, e.g. in mechanism strength and relative contribution, will have an effect on forest NEP.

Additionally, in this Ph.D. thesis we only focused on delayed responses of NEP to weather conditions of the previous year. However, longer time periods between triggering weather conditions and the respective response of the forest appear to be likely as well. For example, it has been shown recently that stored C reaches ages of up to a decade and is still utilized by trees (Richardson et al., 2013). Given the likely relationship between stored C and a delayed response of tree growth, and thus, forest NEP, it has to be studied whether and to what extent multi-year delays might influence the C balance of forests.

Finally, the findings of delayed responses of forest NEP to previous year’s weather have to find their way into terrestrial biosphere models, which, to our knowledge, is not the case so far. It has to be tested, whether and to what extent their implementation will increase model performance. Acceptance and feasibility of our findings in terrestrial biosphere models will also be highly dependent on knowledge of underlying mechanisms, whose identification is of utmost importance, as stated above.
7.5 References


CHAPTER 7. GENERAL CONCLUSION


Appendix A

Partitioning dynamic stem radius changes into stem growth and tree water deficit

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This chapter is intended for submission to the Journal of Experimental Botany
Continuous stem radius changes (DR) measured with high precision point dendrometers contain real-time information about tree water relations and stem tissue growth dynamics in an unmatched quality and resolution. Here we present the physiological and mathematical background for partitioning DR into growth-induced irreversible stem expansion (GRO) and tree water deficit-induced reversible stem shrinkage (TWD), based on the premise of no growth during TWD-periods of contracted stems. The approach was tested with DR data obtained from 15 trees at three Swiss TreeNet sites, covering four deciduous and evergreen species over one year.

We found that >95% of annual GRO was correctly associated to stem increment periods. The rest occurred during TWD periods, indicating a low cambial activity during periods of contracted stems. Longer TWD periods prior to a GRO period significantly increased the average GRO rates in two of the five investigated combinations (site x species), but only for two hours at maximum. TWD was largely explicable with a weighted difference between air vapour pressure deficit and soil water potentials, confirming the strong dependency of tree water relations on humidity conditions in air and soil.

Overall, the partitioning approach with the premise of no growth during periods of TWD works very well and opens up completely new avenues for real-time growth analyses of mature trees with a temporal resolution of minutes to hours. Furthermore, TWD is proposed as a biological indicator for drought stress of trees, since the shrinkage of tree stems is an integrated signal over any environmental factor relevant for tree water relations.
A.1 Introduction

Continuous stem radius changes (differences in radius, DR) measured with automatic point dendrometers have been recognised as valuable data to analyse wood growth (Downes et al., 1999; Daudet et al., 2005; Zweifel et al., 2006; Deslauriers et al., 2007b; Camarero et al., 2010) and tree water relations (Herzog et al., 1995; Zweifel et al., 2001; Steppe et al., 2005; Camarero et al., 2010; Fernández and Cuevas, 2010; Drew et al., 2011), including practical applications for forest management (Duchesne and Houle, 2011) and irrigation systems (Steppe et al., 2006; Cuevas et al., 2010; Fernández et al., 2011). In order to understand the physiological processes underlying DR, DR measurements need to be interpreted in terms of (i) irreversible growth of new wood and bark cells, and (ii) water-related expansion and shrinkage of the stem. The partitioning into these two fractions can be based on well-known physiological processes, however, needs a premise to overcome the uncertainty of potentially overlapping growth and water-related swelling processes (Drew and Downes, 2009). Here we present and validate an approach to partition DR into growth-induced irreversible stem expansion (GRO) and tree water deficit-induced shrinkage and swelling (TWD), with the aim to resolve this biological information of DR real-time at a temporal resolution of minutes to hours.

A.1.1 Physiological background

DR data from woody structures like stems, branches or roots consist of two main components: (i) radius increments due to growth, thus related to the carbon cycle, and (ii) radius fluctuations due to changes in water content, i.e., swelling and shrinking of wood and bark, thus related to the water relations of a tree (Zweifel et al., 2014).

(i) Stem growth, including cell division and cell enlargement, is attributable to the activity in the cambium, a meristem between bark and wood. The cambium builds new cells towards the centre of the stem mainly differentiating to xylem, while it builds cells towards the periphery of the stem mainly differentiating to phloem (Schweingruber et al., 1996). In both cases, cambial activity leads to an irreversible increase of stem radii, i.e. growth (Rossi et al., 2008; Downes et al., 2009; Drew et al., 2010). This growth rate is mainly driven by turgor conditions in
the cambium (Lockhart, 1965; Steppe et al., 2005). In contrast to wood which is accumulating over time, cells in the bark also undergo catabolic processes, e.g. the seasonal degradation of phloem cells (Gričar et al., 2009), which may be size relevant and may lead to decreasing stem radii. Very little is known about the impact and the timing of this bark degradation on DR.

(ii) The water related processes are driven by changes in water potential gradients in the tree, mainly induced by transpiration and altered by hydraulic flow limitations to transport water from the roots to the leaves (Zweifel et al., 2007; Ehrenberger et al., 2012; Steppe et al., 2012; Dawes et al., 2014) and by osmotic processes in the bark (De Schepper and Steppe, 2010; Sevanto et al., 2011; Mencuccini et al., 2013). The transpiration-induced tension in the xylem (i.e. negative water potential) leads to a dehydration of living tissues, which provides the main physical force to transport water within the tree according to the cohesion-tension theory (van den Honert, 1948). During the day, when transpiration is high, the stem loses water from elastic tissues, mainly the bark and the cambium, but also from immature xylem as recently shown by Zweifel et al. (2014). This loss of water is proportional to a decrease in DR (µm) (Zweifel et al., 2000; Drew et al., 2011; De Schepper et al., 2012) and is called a tree water deficit-induced stem shrinkage (TWD, µm) according to Hinckley and Bruckerhoff (1975) and Zweifel et al. (2005). A TWD of zero means a fully saturated stem tissue and increasing values of TWD indicate increasing amounts of missing water. The primary unit of TWD is given in µm and can be transformed into the unit litre (or kg) water per tree (stem) with estimations of stem (or entire tree wood) volume (Zweifel et al., 2000). TWD usually decreases in absence of transpiration, when the water potential gradients within a tree cease, and depleted tissues get replenished. Decreasing DR are thus always attributable to loss of water and thus exclusively attributable to increasing TWD. Increasing DR, however, are induced either by a replenished water status of tissues and/or growth-induced irreversible cell expansion (GRO) and hence need a premise of how increasing DR are separated into TWD and GRO.

A.1.2 Existing partitioning concepts and premises

Besides various numerical approaches to use characteristics of DR without explicitly disentangling the two fractions driving DR (King et al., 2013; van der Maaten et al.,
there are two partitioning approaches described in the literature, which are based on different assumptions of how growth processes develop during periods of shrunken stems, i.e., increased TWD (Fig. A.1). During such TWD periods, the stem radius is below a previously measured maximum (DR$_\text{max}$), i.e. any increase in radius is at least partially associated with replenishing stem tissues and most likely not attributable to growth (Herzog et al., 1995). However, a potential cambial activity (cell division or elongation) cannot be ruled out for this period. A first approach assumes linear growth between two peaks in DR over such a shrinking period, resulting in an envelope curve encompassing peaks in DR (Zweifel et al., 2005; Drew et al., 2011; Vieira et al., 2013) (Fig. A.1). Beside some processing difficulties with short and irregular time series of DR, this approach needs an empirical parameter characterizing the maximum time allowed between two DR peaks (Zweifel et al., 2005). Consequently, the growth curve changes its shape depending on the set parameter (see different blue lines in Fig. A.1a). Another disadvantage of this approach is that the partitioning of DR into TWD and GRO is not possible in real-time but needs to be done retrospectively when knowing the timing and the amplitude of DR peaks. Furthermore, a constant growth rate during TWD periods is very unlikely, considering the non-linear relationship between turgor pressure in the cambium and the respective threshold-dependent processes of cell division and cell expansion (Lockhart, 1965; Steppe et al., 2005). Overall, this first approach is of limited value for our purposes.

The second approach to separate growth- and water-related changes in DR is based on the premise of no growth during TWD periods (Deslauriers et al., 2007a; Drew and Downes, 2009; Deslauriers et al., 2011; Ehrenberger et al., 2012) and associates any potential growth-induced expansion (GRO) to the time after TWD has completely ceased. Accordingly, GRO remains zero during periods of TWD, and it increases when the current maximum of the radius (DR$_\text{max}$) is exceeded (see the stepwise red line in Fig. A.1a). The partitioning procedure is very simple, needs no parameterisation, and can be done in real-time. However, the question arises how large a potential artefact is when assuming no growth during periods of shrunken stems, i.e. under not fully saturated conditions. From a physiological point of view, it is likely that (reduced) cell division and elongation processes are ongoing at least under slightly non-saturated conditions (Lockhart, 1965).

With the aim to develop a real-time analysis approach for DR of hundreds of trees
measured in parallel (www.treenet.info), we adapted the second approach to partition tree water deficit (TWD) and growth-induced irreversible stem expansion (GRO) from DR. Our approach assumes no growth-induced irreversible expansion during TWD periods (Fig. A.1). However, in contrast to the cited applications of this approach, we do not restrict DR \(_{\text{max}}\) to a certain period (in most cases 24 hrs back in time), but refer to the all-time-high back in time, independent of the length of this period. To test the validity of our approach, we posed the following questions:

1. How good is the premise of no GRO during TWD periods? Or in other words, can we quantify potential growth activities attributable to TWD periods and thus estimate the fraction of GRO which occurred during TWD and thus might be incorrectly attributed in time? In order to test this premise, we compared GRO rates after different lengths of TWD periods. We expected no differences in GRO rates after TWD periods of different lengths, assuming cambial activity being indeed close to zero during the TWD periods.

2. Can we relate TWD, as the mathematical counterpart of GRO in our DR analysis approach, to known physiologically drivers such as vapour pressure deficit (VPD) and soil water potentials (\(\Psi_{\text{Soil}}\))? We used a model with a weighted difference between VPD and Soil to estimate TWD (Zweifel et al., 2005) and test the validity of our approach.

3. Is our approach to partition DR measurements applicable to different species in different environments? What is the value of GRO and TWD for the growth-climate relationship of trees?

A.2 Materials and methods

A.2.1 Sites

The stem radius changes were measured at three Swiss forest sites, at Visp, Davos and Lägeren. These sites belong to the dendrometer measurement network TreeNet (www.treenet.info) and to the Swiss Long-Term Forest Monitoring Program LWF (www.wsl.ch/lwf). The study covered deciduous and evergreen species from dry to wet conditions (Tab. A.1).
APPENDIX A. PARTITIONING DYNAMIC STEM RADIUS CHANGES INTO STEM GROWTH AND TREE WATER DEFICIT

A.2.2 Point dendrometers and data acquisition

Continuous stem radius changes (DR, differences in radius over time) were measured with automated high-precision point dendrometers of the type ZN11-T-WP at Visp and Lägeren, and with type ZB06 at Davos (both: Natkon.ch, Hombrechtikon, Switzerland). Both dendrometer types consisted of the same electronic components, but differed slightly in the design of the carbon fibre frame attaching the sensor to the tree stem. The temperature sensitivity of both sensor types was found to be $\leq -0.28$.

Data were collected with a data logger of the type DecentBase (DecentLab GmbH, Dubendorf, Switzerland) at Visp (data acquisition: measurement every 30 sec, averaged every 7 min by the logger, and interpolated to achieve a 10 min resolution) and with a CR1000 (Campbell Sci. Ltd., Shepshed, UK) at Davos and Lägeren (data acquisition: measurement every 20 sec, averaged every 10 min).

A.2.3 Concept of analyses and definitions

A.2.3.1 Partitioning growth-induced irreversible stem expansion (GRO) and tree water deficit-induced stem shrinkage (TWD) from stem radius changes (DR)

Growth-induced irreversible stem expansion (GRO) is defined as the positive deviation between the current DR reading (DR$^t$) and the highest DR record of the past (DR$_{max}$) when DR$^t$ is exceeding DR$_{max}$ (Fig. A.1). DR$_{max}$ is not restricted to a certain period and may date back in time for minutes, days, or even months. Tree water deficit induced stem shrinkage (TWD) is defined as the negative deviation between DR$^t$ and DR$_{max}$ when DR$^t < DR_{max}$. After each iteration step, DR$_{max}$ is reset to a new higher DR$_{max}$ when current DR$^t$ exceeded DR$_{max}$. Mathematically this is formulated as:

$$TWD(t) = \begin{cases} \max[DR(< t)] - DR(t) & \text{if } DR(t) < \max[DR(< t)] \\ 0 & \text{otherwise} \end{cases}$$

$$GRO(t) = \begin{cases} DR(t) - \max[DR(< t)] & \text{if } DR(t) \geq \max[DR(< t)] \\ 0 & \text{otherwise} \end{cases}$$

where $t$ refers to the current record, $<t$ refers to historic records, DR$_{max}$ equals
max[DR(<t)], and DR<sub>t</sub> equals DR(t). The unit of DR, TWD and GRO are given in µm. According to the partitioning approach, the general relationship between DR, GRO and TWD is:

\[ DR = GRO - TWD \]

**A.2.3.2 Definition of “dry periods”**

In this study, dry periods are defined as periods when tree water relations are not balanced over 24h, i.e. stem tissues are not fully water saturated and TWD does not cease completely overnight. This corresponds to the often used pre-dawn water potential which decreases when a plant is not able to fully re-saturate its tissues overnight (Larcher, 2003). A dry period ends when TWD returns to 0. Accordingly, a dry period lasts at least one day and has no upper time limit. Within a dry period, the stem may increase in size due to water-related swelling of stem tissues, however, it never reaches the previous maximum (DR<sub>max</sub>), i.e. it shows an uninterrupted TWD > 0 (Fig. A.1).

**A.2.3.3 Definition of “growth periods”**

We distinguish between periods of consecutive growth (GRO periods) and the wood growth period (WGP), in which GRO is accumulated over a season. WGP starts in spring when DR<sub>t</sub> exceeds DR<sub>max</sub> (of the past year) and ends with the date when DR<sub>max</sub> of the current year is reached. Since the seasonal growth curve has an asymptotical character and thus the date of the last DR<sub>max</sub> of the year may strongly depend on the last few micrometers of stem radius increase, a 97.5% threshold was introduced to define the date of the last DR<sub>max</sub> of the year (Zweifel et al., 2006).

**A.2.3.4 Estimation of the fraction of growth which occurs during TWD periods**

Under the premise of no GRO during TWD periods, we expected equal GRO rates within a GRO period independent of the precedent TWD period lengths. However, if there will appear larger GRO rates after longer TWD periods, we attribute this
increase to an accumulation of growth induced tissue expansion during TWD periods, which only becomes visible in the first hours of the following GRO period. We thus assumed that this increased GRO rate above an average quantified the fraction of GRO over an entire season which actually occurred during TWD periods and was temporally incorrectly attributed to the GRO period. The ratio between the wrongly attributed GRO and the total annual GRO was interpreted as a measure of quality for our initial premise of no GRO during TWD periods.

A.2.3.5 Testing the dependency of TWD from vapour pressure deficit of the air (VPD) and soil water potentials ($\Psi_{Soil}$)

Tree water deficit-induced shrinkage and swelling of stems (TWD) has been shown to be related to water potentials of the respective plant tissues (Steppe et al., 2006a; Ehrenberger et al., 2012), and to the humidity conditions in air (vapour pressure deficit, VPD) and soil (soil water potentials, $\Psi_{Soil}$) (Zweifel et al., 2005). According to Zweifel et al. (2005), using a weighted difference between VPD and $\Psi_{Soil}$, explains 49% to 64% of the variance of TWD for three different tree species ($P$. sylvestris, Picea abies, Quercus pubescens). To obtain an alternative quality indicator of the partitioning of DR into TWD and GRO in our study, we compared weighted differences of VPD and $\Psi_{Soil}$ to TWD as follows:

i) calculate weighted differences with

$$TWD_{modelled} = (VPD - a\Psi_{Soil}) \times k$$

where $TWD_{modelled}$ is a weighted difference between VPD and $\Psi_{Soil}$, with the weighting factor $a$ and the unit conversion factor $k$ [\(\mu m/kPa\)]. Set $a = 1$.

ii) calculate regression coefficients between TWD and $TWD_{modelled}$.

iii) optimize the quality of the regression coefficients by adjusting “$a$”, further optimize the quality of the regression coefficients by introducing a time shift between the two sets of VPD and $\Psi_{Soil}$ data.
A.3 Results

A.3.1 Rates of growth-induced irreversible stem expansion (GRO rates)

Average GRO rates per site and species were lowest at the dry site Visp (Scots pine: 4.4 \( \mu \text{m/h} \); Fig. 2a), and highest at Lägeren (beech: 6.3 \( \mu \text{m/h} \), ash: 8.9 \( \mu \text{m/h} \), spruce: 9.3 \( \mu \text{m/h} \); Fig. A.2e, g, i). The subalpine site Davos showed intermediate GRO rates (spruce: 6.6 \( \mu \text{m/h} \); Fig. 2c). GRO periods, defined as consecutive periods with irreversible stem radius increase and thus a TWD of zero, lasted from 10 min (measurement resolution) up to 16 hrs. 90% of GRO, however, occurred on average within the first 4 hrs of the respective GRO periods (Fig. A.2). Remarkably, the driest site with the lowest GRO rates and the lowest annual GRO (Visp) had the longest consecutive GRO periods (on average about 9hrs, Fig. 2b).

To test whether GRO rates (\( \mu \text{m/h} \)) differed after different lengths of TWD periods, we grouped data of GRO rates according to the length of the TWD period prior to a GRO period: growth rates after TWD periods of less than 16 hrs (group 1), and growth rates after periods TWD periods of more than 16 hrs (group 2). The 16 hrs-threshold was found to lead to the most distinctive separation of GRO rates between the two groups (data not shown). The analyses were done for each site and species separately (Fig. A.2). Since our partitioning approach of DR into GRO and TWD is based on the premise of no growth during TWD periods by definition, we hypothesized that GRO rates did not differ after TWD periods of different lengths (objective i in introduction). However, we found higher GRO rates after the longer TWD period (group 2) for two of the five combinations investigated (species x site, Fig. A.2), i.e., for pines at the dry site Visp (Fig. A.2a) and for Norway spruce at the subalpine site Davos (Fig. 2c, see horizontal black bars as indication for significance between the two groups of GRO rates). Although GRO rates of the species at the Lägeren site did not significantly differ between the two groups, they also showed the similar trend (higher GRO rates for group 2 than group 1). Potential differences between the two groups at all sites and all species leveled off after 2 hours.

To determine how much of GRO potentially occurred during TWD periods, we summed up the positive deviations from species- and site-specific average GRO
rates over the entire season (Fig. A.2). This annual GRO sum was assumed to be attributable to growth activities during TWD periods and was thus labeled as “incorrectly associated GRO” (dark grey bars showing these annual sums in relation to the length of the GRO period in Fig. 2b, d, f, h, j). This fraction of this incorrectly attributed GRO during a growing season of the total annual GRO varied between 1% (Beech at Lägeren) and 5% (Norway spruce at Davos). Overall, this was only a small fraction of annual GRO, independent of site and species (Fig. A.2), and thus negligible.

A.3.2 Tree water deficit (TWD)

Tree water deficit (TWD) is intrinsically coupled to (the quality of) GRO due to the partitioning approach chosen (Eq. 3). TWD showed in general a regular diurnal pattern within a consecutive TWD period, with increasing values during daylight and decreasing ones during night-time (Fig. A.3). Since the data shown in Fig. 3 were averaged values of pooled data respective to the starting time of the respective TWD periods, the 24-hr cycle indicated the strong general dependency on diurnal climatic changes, particularly on VPD. The modelled curves of weighted differences between vapour pressure deficit (VPD) and soil water potentials ($\Psi_{\text{soil}}$) followed the measured curves generally very well. We found regression coefficients ($r^2$) between measured and modelled TWD values ranging between 0.60 and 0.92 (Fig. A.3, Tab. A.2). The TWD model explained the variance in measured TWD always better than VPD and $\Psi_{\text{soil}}$ alone (Tab. A.2). Furthermore, TWD appeared to be considerably lagged behind VPD (Tab. A.2), indicating a physiological delay of the response to atmospheric driving factors. The delay was quantified by maximizing the regression coefficient between VPD and TWD as well as between modelled TWD and measured TWD by shifting VPD forward in half-hourly steps (Tab. A.2). The relationship between measured and modelled TWD held also when pooling all the sites and species (data not shown).
A.4 Discussion

A.4.1 The premise of no growth during periods of shrunken stems

Growth processes (cell division and cell elongation) in the cambium are known to mainly occur under high turgor pressure conditions, i.e. in water saturated tissues (Lockhart, 1965) and thus fully expanded stem radii. Under non-saturated conditions, the cambium activity has been found to first reduce cell expansion and later also to inhibit cell division (Lockhart, 1965; Hsiao and Acevedo, 1974; Hinckley and Lassoie, 1981). Current (mechanistic) model applications have taken up these findings and showed that using a turgor threshold for growth led to very good simulations of measured stem radius changes (Steppe et al., 2005; Zweifel et al., 2006; Steppe et al., 2008; De Schepper and Steppe, 2010). However, to efficiently extract the growth contribution to temporally highly resolved dynamic stem radius changes (DR) – without applying a complex tree water relations and growth model – it is necessary to assume no growth-induced irreversible expansion of stem tissue (GRO) during non-saturated conditions (= increased tree water deficit, TWD). This premise implicitly means that any shrinkage of the stem is induced by a lack of water (Hinckley and Bruckerhoff, 1975; Zweifel et al., 2005) and theoretically excludes any growth processes during periods of increased TWD. This is a simplification of the known growth mechanisms (Drew et al., 2010) and thus this work aimed to judge about the quality and the usefulness of such an approach. We found direct (growth rates, Fig. 2) and indirect (water related stem fluctuations, Fig. A.3) indications for a high degree of validity of our approach, which are discussed in the following.

A.4.2 How well does GRO derived from dynamic stem radius data represent real growth processes?

The investigation of GRO rates after different lengths of TWD periods revealed an existing but largely negligible impact of the non-growth period (= TWD period) on subsequent growth rates (Fig. A.2), most likely due to very minor growth activities during TWD periods of our tree species investigated (two deciduous and evergreen species at a dry site, and two more humid sites in Switzerland, Tab. A.1). Only
pine trees at the dry site (Visp) and Norway spruce at one of the wet sites (Davos) showed significantly increased GRO rates after TWD periods of more than 16 hours (Fig. A.2). These increased GRO rates, which never lasted for more than two hours, suggested the presence of newly divided cells built during the precedent TWD period. These new cells did not seem to be size relevant during the TWD period, because they have been built but did not expand yet due to the limiting water availability (Larcher, 2003) and were thus masked by the larger change of DR by TWD. However, as soon as the turgor pressure increased during the GRO period, the cells elongated and became visible as extra growth rate in the stem radius measurements. In such a case, the GRO period ‘benefited’ from cell division processes happening during the precedent TWD period. The extent of this incorrectly associated growth summed up over a year, however, was found to be very small (<5% of the annual GRO) even for the two combinations (site x species) with a significant growth rate response to TWD. In any of the five investigated combinations (site x species), real growth processes were found to be largely attributable to GRO periods and thus strongly supporting our partitioning approach with the premise of no growth during periods of shrunken stems.

Overall, we conclude that our approach chosen does make a small error when interpreting GRO as real growth, but with an accuracy of >95% it was found to be very reliable for all tree species and sites investigated. However, we cannot rule out that other tree species not studied here may behave differently.

A.4.3 TWD as an indirect indicator for the quality of the partitioning approach

We posed the question whether there is a potential quality check for our disentangling approach for DR on the TWD side, comparable to the one presented for GRO. Tree water deficit-induced stem shrinkage (TWD) is intrinsically coupled to GRO due to the partitioning approach chosen (Eq. 3). Consequently this means that the qualities of TWD and GRO are also related. If the partitioning procedure leads to physiologically meaningful GRO, the same should be true for TWD and vice versa. We found no direct quality check, however applied an indirect prove-of-concept, by checking for TWD quality in terms of its reported relationship to vapour pressure deficit of the air (VPD) and soil water potential ($\Psi_{\text{Soil}}$) (Zweifel et al., 2005). A
A.4. DISCUSSION

tree is exposed to air and soil and both ends are known to induce drought stress. A weighted difference between the two driving variables (VPD and Soil) was found to explain TWD up to a high degree (correlation coefficients $r^2$ between 0.49 to 0.64 (Zweifel et al., 2005). In contrast to the work presented here, Zweifel et al. (2005) used a linear growth approach during periods of TWD (according to the blue lines in Fig. A.1). Even higher $r^2$ between measured and modelled TWD (between 0.6 and 0.92, Fig. A.3 and Tab. A.2) were found in the presented work here with the premise of no GRO during periods of TWD (according to red line in Fig. A.1). The better model fit of TWD in this study is interpreted as an indicator for the quality of our partitioning approach. The improved fit may also be partially explained with the additional optimizing step in which a time lag of 0.5–3 hours of TWD lagging behind VPD was eliminated (Tab. A.2). This time lag of TWD behind VPD reflects the temporal sequence of the determining forces in tree water relations over a day starting with transpiration in the leaves (driven by a combination of VPD, light and wind, (Penman, 1948; Monteith, 1965)), being followed by the flow resistance- and storage capacitance-induced delay of sap flow in twigs, branches and the stem (Steppe et al., 2006a), to finally a delayed depletion of elastic stem storage tissues (i.e. increased TWD) at breast height (Zweifel et al., 2007) where the point dendrometers were mounted. Since TWD is closely coupled to the water potential conditions in the stem section measured (Ehrenberger et al., 2012), any environmental impacts of air and soil on tree water relations is affecting TWD. Trees are coupled to the air by many square meters of leaf area and to the soil by many square meters of root surface. It is therefore physiologically plausible that VPD and $\Psi_{\text{Soil}}$ determine TWD up to a very high degree (Tab. A.2). However, we are aware of other factors affecting TWD like growth rate (De Swaef et al., 2009), fruit load, tree size, and season (Fernández and Cuevas, 2010), temperature (Molz and Klepper, 1973), stomatal regulation (Zweifel et al., 2005), CO$_2$-treatment (Dawes et al., 2014) etc. which all may alter the pure physical effect from air and soil. Further, a potential effect of degrading bark cells (mainly phloem) on decreasing DR is ignored. Such an artefact is assumed to be of minor importance on a daily to weekly scale but may be of more importance on the seasonal to annual scale which is not further discussed here. Overall, the comparison of measured and modelled TWD has been found to be a convincing indirect quality check for our partitioning approach of DR with the premise of no growth during periods of shrunken stems.
A.4.4 Applicability of the partitioning approach and potential implications for climate-growth relationships

Based on our results, we argue that growth-induced irreversible expansion of tree stems (GRO) as well as tree water deficit induced stem shrinkage (TWD) as the two fractions of DR measured by point dendrometers are representing real growth and water deficits in tree stems very well. The new partitioning approach is easily applicable in real-time and works very well with all four tree species investigated. It opens up new opportunities to analyse stem growth and tree water relation patterns and their dependencies on environmental drivers. Wood growth rates resolved into integration periods from minutes to years are now determinable from DR and become comparable to tree physiological processes like water flow and storage dynamics, carbohydrate storage dynamics, carbon exchange dynamics on the ecosystem level by the Eddy covariance method, related respiration activities, and seasonal patterns like bud burst, leaf senescence, and winter dormancy. The opportunity to analyse both tree carbon and water relations simultaneously will be a major step forward to understand forest responses to climate extremes, expected to increase in magnitude and frequency in the future (Reichstein et al., 2013).

TWD as the second main process extracted from DR measurements represents not only a proportional measure for missing water to fully saturated plant tissues (in µm stem radius shrinkage), but the shrinkage of tree stems also integrates over any environmental factor affecting the tree water balance. Since the plant is a hydraulic system in which every living part is connected via the water flow paths, TWD is proposed to be a valuable biological indicator for missing water in a tree, the level of dryness of its direct environment, and thus its current sensitivity to an even further prolonged drought (see also Klein et al., 2014), much more direct than e.g. minimum water potentials as used by Choat et al. (2012). TWD of multiple trees within a stand is thus proposed to be at least as good as a measure for potential drought stress in a forest ecosystem – if not better – than any combination of physical soil and microclimate sensors. Particularly in combination with net ecosystem flux measurements of water vapour and CO₂ (e.g. Zweifel et al., 2010; Wolf et al., 2013), TWD has the potential to provide the necessary mechanistic understanding of forest responses to environmental change such as drought.
Acknowledgements

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drivers of hourly to yearly tree radius variations along a 6 C natural warming

assessment of the hydrological vulnerability of forests to climate change-induced


APPENDIX A. PARTITIONING DYNAMIC STEM RADIUS CHANGES INTO STEM GROWTH AND TREE WATER DEFICIT


A.6 Tables and figures
Table A.1: Investigated sites and trees species with the respective climatic conditions

<table>
<thead>
<tr>
<th>Site</th>
<th>Coordinates, altitude</th>
<th>Species investigated</th>
<th>Dendrometer Measurement period</th>
<th>Avg. annual sum of precip. [mm]</th>
<th>Avg. annual mean Temp [°C]</th>
</tr>
</thead>
<tbody>
<tr>
<td>Davos</td>
<td>46.82°N, 9.86°E, 1640 m a.s.l.</td>
<td><em>Picea abies</em></td>
<td>2012</td>
<td>1000 (^1)</td>
<td>3.4 (^1)</td>
</tr>
<tr>
<td>Lägeren</td>
<td>47.48°N, 8.36°E, 694 m a.s.l.</td>
<td><em>Picea abies</em></td>
<td>2013</td>
<td>1000 (^1)</td>
<td>7.4 (^1)</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Fraxinus excelsior</em></td>
<td>2013</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Fagus sylvatica</em></td>
<td>2013</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Visp</td>
<td>46.30°N, 7.86°E, 695 m a.s.l.</td>
<td><em>Pinus sylvestris</em></td>
<td>2012</td>
<td>615 (^2)</td>
<td>8.8 (^2)</td>
</tr>
</tbody>
</table>

\(^1\) Etzold et al. (2011), \(^2\) Walthert et al. (2003)
Table A.2: Regression coefficients ($r^2$) between measured tree water deficit (TWD) and vapour pressure deficit (VPD), soil water potential ($\Psi_{Soil}$), as well as a linear model using a weighted difference between VPD and $\Psi_{Soil}$ ($TWD_{modelled}$). Regression coefficients were maximized by shifting VPD accordingly (VPD shift in hours). A positive shift indicates a delayed response of TWD to VPD (in comparison to $\Psi_{Soil}$).

<table>
<thead>
<tr>
<th>Site/species</th>
<th>$r^2$ (VPD)</th>
<th>$r^2$ ($\Psi_{Soil}$)</th>
<th>$r^2$ ($TWD_{modelled}$)</th>
<th>VPD shift</th>
</tr>
</thead>
<tbody>
<tr>
<td>Visp/pine</td>
<td>0.28</td>
<td>0.72</td>
<td>0.92</td>
<td>+2h</td>
</tr>
<tr>
<td>Davos/spruce</td>
<td>0.75</td>
<td>0.80</td>
<td>0.87</td>
<td>+3h</td>
</tr>
<tr>
<td>Lägeren/spruce</td>
<td>0.34</td>
<td>0.75</td>
<td>0.81</td>
<td>+0.5h</td>
</tr>
<tr>
<td>Lägeren/ash</td>
<td>0.15</td>
<td>0.51</td>
<td>0.60</td>
<td>+1h</td>
</tr>
<tr>
<td>Lägeren/beech</td>
<td>0.14</td>
<td>0.69</td>
<td>0.73</td>
<td>0h</td>
</tr>
</tbody>
</table>
A.6. TABLES AND FIGURES

Figure A.1: Continuous stem radius changes (DR) partitioned into tree water deficit-induced stem shrinkage (TWD) and growth-induced irreversible expansion (GRO) with the premise of no GRO during periods of TWD. a) DR over 35 days measured by point dendrometer (black line). Shrinking stems indicate a loss of water from the elastic tissues. Increasing stems indicate either refilling with water (swelling tissue) or GRO (red line). Growth-induced irreversible expansion curves assuming linear growth during periods of TWD are shown with blue lines (not part of our approach but showing an alternative way of disentangling DR, described in Zweifel et al. (2005). The linear growth approach needs additional assumptions to define which of the blue curves is chosen. b) TWD is the difference between the actual DRt and the maximum DR of the past (DR_{max}). TWD has been shown to represent the missing water for fully saturated and thus expanded stem tissues (Hinckley and Bruckerhoff, 1975) (not the inverse scale). c) GRO represents the sum of growth-induced irreversible stem expansion processes including cell division and cell elongation (red curve). Shaded areas highlight periods of GRO. Dry periods are defined as periods when TWD does not return to zero (DR_t < DR_{max}) for more than 24 hrs.
Figure A.2: Average stem radius growth rates (GRO) following two different lengths of tree water deficit (TWD) periods. **a)** Average GRO rates (μm/h) after TWD periods of less than 16hrs (data group 1: black curve, dark grey area showing range of values) and after more than 16h (data group 2: grey curve, light grey area) for three pine trees at the dry site Visp. **b)** Frequency distribution of summed up growth increments for consecutive GRO intervals within a GRO period (light grey bars, data of one season). Estimated sums of incorrectly associated GRO in time (dark grey bars) due to the chosen partitioning approach. The horizontal arrow indicates the time within an average GRO period in which 90% of GRO occurred. The same analyses are shown for three subalpine Norway spruce trees at Davos (**c–d**), and for three beech (**e–f**), three Norway spruce (**g–h**), and three ash trees (**i–j**) at Lägeren.
Figure A.3: Tree water deficit (TWD) and its driving factors vapour pressure deficit (VPD) and soil water potential ($\Psi_{\text{Soil}}$). a) Scots pine, Visp: Averages of TWD within consecutive TWD periods: individual pine trees (light grey curves), average of the three measured trees (black curve) and modelled curve (broken grey curve). b) VPD and $\Psi_{\text{Soil}}$. c) Number of data points (n) contributing to a) and b) The measurement resolution was 10 min. d)–f) According analyses for Norway spruce, Davos, g)–i) for Beech, Lägeren, j)–l) for Norway spruce, Lägeren, and j)–l) for Ash, Lägeren. Regression coefficients between measured and modelled TWD are listed in Tab. A.2.
Appendix B

High resolution stem radial increments to predict daily net carbon uptake in European forests

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This chapter is in preparation for publication in a peer-reviewed scientific journal
Abstract

Predicting day-to-day cumulative net ecosystem productivity ($\text{NEP}_c$) of forest ecosystems as measured by the eddy covariance (EC) has shown to be difficult. Trees stem radius increments ($\text{SRI}_c$), as measured by dendrometers, reflect both tree growth and tree water-relations, as a direct result from meteorological conditions and biological processes. Hence, we hypothesized that $\text{SRI}_c$ may better predict $\text{NEP}_c$ than meteorological variables alone, as many currently used models are limited to. We included 45 site years highly resolved time series from $\text{SRI}_c$, $\text{NEP}_c$, and meteorological data from six forest sites within a broad gradient of continental Europe. We found that linear regression models built with only $\text{SRI}_c$ were significantly superior to those using meteorological variables alone. Furthermore, the slope of the linear regression models were determined by an intrinsic site-specific value by so-called ‘speed of growth’ and even better with the inverse thereof (‘time to grow’, $t_g$). Speed of growth is the averaged ratio between the difference of annual maxima and minima of $\text{SRI}_c$ and the time period in between the two. The higher $t_g$ (as the inverse of speed of growth), the lower were the slope of the curve and therefore the lower the corresponding $\text{NEP}_c$ values to the $\text{SRI}_c$ values. In other words, the more time tree required to grow (high $t_g$), the lower the productivity of the forest in terms of annual $\text{NEP}_c$. Many terrestrial biological models were outperformed by the empirical model presented here, which highlights the need to include more ecophysiological data for predicting $\text{NEP}_c$ (i.e. with dendrometers) in order to better represent the biological processes within forest ecosystems in forest C uptake estimations.
APPENDIX B. HIGH RESOLUTION STEM RADIAL INCREMENTS TO PREDICT DAILY NET CARBON UPTAKE IN EUROPEAN FORESTS

B.1 Introduction

The eddy covariance (EC) technique is an established and widely-used direct method to measure net C fluxes, integrating over all component fluxes within terrestrial ecosystems, such as forests (Baldocchi et al., 1988; Baldocchi, 2003; Burba and Anderson, 2010; Aubinet et al., 2012). Single components can be modelled (e.g. soil respiration; Reichstein et al., 2005), yet, it is impossible to quantify directly single component fluxes, e.g. the tree’s single contribution to the forest with EC alone. On the other hand, it is difficult to integrate single component measurements, such as tree growth measurements, over a whole forest ecosystem. Usually, these integrated estimates of C storage changes are very sensitive to the numerous assumptions that have to be made to overcome temporal and spatial limitations. For example, forest inventories are typically made every couple of years (Etzold et al., 2011) or soil respiration measurements are conducted over few selected locations within the forest (Ruehr and Buchmann, 2010).

The combination of both forest integrated and single component measurements have shown promising, although both concepts are methodologically independent and therefore also the sources of errors have to be independently analysed (Curtis et al., 2002; Etzold et al., 2011). In dendrochronology, strong links have been found between tree growth as shown in tree-ring data and annually cumulative net ecosystem productivity (NEP$_c$, as derived by EC) (e.g., Babst et al., 2012). However, these studies focus on inter-annual time scales only. Extracting intra-annual information is still challenging (Zweifel et al., 2006). It is therefore crucial to fill the yet fragmentary link between tree growth and forest C uptake on high temporal resolutions.

Continuous measurements of stem radius increments (SRI$_c$), capture not only tree water relations in trees, but also tree growth. Zweifel et al. (2010) have shown that empirically, there is a remarkably close link between SRI$_c$ (as continuously measured with automatic point dendrometers) and forest C uptake (as measured by EC) on both inter- and intra-annual time scales at a subalpine forest in Switzerland. The authors suggested, that tree water relations and stem growth, have considerable explanatory power for the forest’s C uptake (NEP$_c$).

Here, we analyse long-term datasets of highly temporal resolved SRI$_c$ and NEP$_c$ data sets at six forest sites within Europe. We asked to what degree the purely
empirical relationship between SRI\textsubscript{c} and NEP\textsubscript{c} is of a correlative nature and what aspects of it can be explained by causal mechanisms. We hypothesize, that SRI\textsubscript{c} incorporate meteorological conditions in a way, which makes it to a better modelling time series than meteorological variables themselves. The specific objectives were: (1) To quantify the empirical link between SRI\textsubscript{c} and NEP\textsubscript{c} on time scales from half-hourly to annual resolution; (2) To compare SRI\textsubscript{c} as a variable alone to meteorological variables and in combination; (3) To identify the drivers on intra-annual time scales to build a model with SRI\textsubscript{c} predicting NEP\textsubscript{c}; And (4) to compare measures to predicting NEP\textsubscript{c} from (independent) data from SRI\textsubscript{c}.

B.2 Materials and methods

B.2.1 Study sites

The study is based on dendrometer and CO\textsubscript{2} flux data from six eddy covariance (EC) forest sites within Europe (Tab. B.1, Fig. B.1): Collelongo (1997–2006), Davos (1998–2011), Jastrebarsko (2008–2010), Laegeren (2006–2012), Loobos (2008–2011) and Tuczno (2010–2011). The selected sites were chosen according to the following criteria: (i) continuous and complete data sets from eddy covariance (EC) measurements and at the same time dendrometer data from within the footprint of the EC measurements are available; (ii) No relevant disturbances in recent measurement years; (iii) The forests are C sinks and not C sources. The vegetation at these sites is classified broadly into two main plant functional types, with three evergreen needle leaf forests (ENF) and two deciduous broad leaf forests (DBF).

B.2.2 CO\textsubscript{2} flux measurements (net ecosystem productivity, NEP)

Half-hourly CO\textsubscript{2} flux data (net ecosystem productivity, NEP, processed data) were post-processed for all sites. First we filtered out unrealistically high values (±50 μmol m\textsuperscript{-2} s\textsuperscript{-1}) and unfavourable atmospheric conditions (snow, heavy rain and/or dust, window dirtiness > 70%). A u*-filter with a threshold of u* < 0.2 m s\textsuperscript{-1} was chosen for all sites. After gapfilling with standardized methods (Reichstein et al., 200
we filtered out large (negative) night-time CO₂ fluxes, which by definition indicate CO₂ uptake, and thus are physiologically unrealistic. Both negative and positive night-time CO₂ fluxes (symmetric filtering) outside the range of ±3 standard deviations a moving 14-day mean were dismissed. CO₂ is converted to units of carbon in g C m⁻² s⁻¹. NEPₒ (Fig. B.2a) is defined as the cumulative integrated sum of NEP (Fig. B.2c), yielding net C uptake by the forest. Positive NEPₒ indicates that the forest is a C sink, while negative NEPₒ indicates C source.

B.2.3 Tree growth measurements (stem radius increments, SRI)

Stem radius increments (SRIₒ) where measured with dendrometers of different types from within the EC footprint of the six flux towers. All dendrometers measured either circumference changes or instantaneous stem radii at breast height and showed a limited temperature sensitivity. Collelongo used the classical metal model until 2009 (Matteucci, 2013), and from then the UMS plastic model (Umweltanalytische Mess-Systeme UMS, 2001), measuring circumference differences every month between February and October. Daily values have been modelled with local polynomial regression fitting by loess (R Core Team, 2012). At the Davos site, dendrometers of type ‘Natkon’ (model ZN11-T-IP) were used (Zweifel, 2014) measuring instantaneous stem radii continuously every five to ten minutes (averaged to half-hourly values). In Jastrebarsko, classical dendrometer bands were used and installed according to Keeland and Young (2007). They measured diameter roughly bi-weekly. Missing daily values have been modelled with local polynomial regression fitting (loess, R Core Team (2008)). We then calculated radius changes from the circumference change measurements according to Marjanović (2009) as described in Marjanović et al. (2011). At the Laegeren site, dendrometers of type ‘Natkon’ where used (type ZN11-T-IP). They measured stem radii continuously and were averaged to half-hourly values. At the Loobos forest, data came from classical metal dendrometer bands, measured with built-in data loggers (Environmental Measuring System EMS Brno, 2012) on a continuous time scale (averaged to half hour). In Tuczno, also ‘Natkon’ dendrometers (type ZN11-T-WP) continuously measured stem radius increments, also on half-hourly basis (Zweifel, 2014).

In contrast to the EC based measurements, not the rate of change from one time
B.2. MATERIALS AND METHODS

unit to the other were measured, but the instantaneous and continues cumulative sum of changes of stem radius increments. Hence, SRIc (Fig. B.2d) was measured and not SRI (Fig. B.2b). For all measured dendrometer data, we used an R package (treegro) to clean, to filter outliers and to apply basic gap-filling strategies for shorter time periods (< four hours).

B.2.4 Statistics

All analyses were performed using R statistical software, version 3.0.1 (R Core Team, 2012). As a major difference to previous studies (cf. Zweifel et al., 2010), highly resolved sequentially measured variables were analysed. We first built five models (Fig. B.3, MOD0–MOD4) either with a one-step approach of using univariate linear regression modelling (one time series predicting another: MOD2), or with a two-step approach (MOD0, MOD1, MOD3, MOD4). This two-step approach consisted of (1) choosing the time series variables with multivariate adaptive regression splining (MARS, explained more in detail below) and of (2) building multivariate linear regression models. The six meteorological time series (air temperature, \(T_a\); soil temperature, \(T_s\); global radiation, \(R_g\); vapour pressure deficit, \(VPD\); relative humidity, \(rH\); precipitation, \(Precip\); and if available soil respiration, \(S_{resp}\) and soil water potential, \(SWP\)), are all also integrated up over time, then yielding twelve time series variables. In addition air and soil temperature daily maxima and minima were calculated, yielding in total 14 time series meteorological variables. From these, a maximum of three were forced to be chosen by the backward and forward pruning technique of MARS (multiple adaptive regression splining). This, because more than three variables would overparametrise the models in relation to the dependent variable (six sites).

Both approaches (the one-step and the two-step approaches) are based on linear regressions, whether univariate (one-step approach) or multivariate (two-step approach). Thus, the models are comparable by conducting analyses of variance (ANOVA) and by comparing the significance levels. In a second step, one model (MOD5) was built overall data. MOD5 is based on the linear regression models of MOD2 (NEPc predicted by SRIc), by finding explanations for the differences in slopes and intercepts of the site-individual models (MOD2). All coefficients of determination (R squared) are calculated as adjusted \(R^2\) (adjR\(^2\)).
Multiple adaptive regression splining (MARS) is a so-called non-parametric regression technique (Friedman, 1991). The MARS algorithm searches for all possible knot locations for each variable. The forward stepwise addition procedure can produce a large collection of basis functions (Zakeri et al., 2010). The best-fitting model in the stepwise sequence is chosen to minimize the generalized cross-validation (GCV) criterion (cf. Craven and Wahba, 1978):

\[
GCV(M) = \frac{\sum_{i=1}^{n} [y_i - f_M(x_i)]^2}{n[1 - (C(M)/n)]^2}
\]  

(B.1)

where n is the number of observations, and C(M) is the cost complexity measure of a model containing M basis functions (Zakeri et al., 2010). The numerator is the sum of squared residuals from the fitted model, and the denominator contains a penalty for model complexity, which is related to the number of parameters estimated in the model. An empirical rule proposed by Friedman (1991) is used to determine C(M).

Three of the five models (MOD0, MOD1, MOD3) have been forced to use a maximum of three variables, considering having between 13 (MOD0, MOD1: only meteo) and 14 variables (MOD3: meteo and SRIc) for choosing. Using more than three variables would have over-parametrized the models, considering the number of sites included (six). The remaining models MOD2 and MOD4 used one and two variables only, respectively. The choice of the best meteorological variable for MOD4 was based on the best variable, as found in MOD3. To compare the variables’ importances, we used the method of the β-coefficient, also called the standardized regression coefficient (Vittinghoff et al., 2005; Schroeder et al., 1986; Quinn and Keough, 2001). This β-coefficient ranged from −1 (greatest importance, yet a negative correlation) to +1 (greatest importance, positive correlation). To compare the models, we chose to compare the differences of adjR² of the linear regressions and the significance levels. Significance levels were calculated using the test for differences of mean under serial dependence by Wilks (2011), by calculating the effective sample size with the following equation:

\[
n' \approx n \frac{1 - \rho}{1 + \rho}
\]  

(B.2)
where $\rho$ (‘rho’) is the time correlation and $n$ is the sample size. The time correlation is calculated with time lag 1 between modelled and the measured NEP$_c$. To assess overall uncertainty of the predictions, we modelled NEP$_c$ (every single point within the NEP$_c$ curve) using MOD4 and MOD5 to compare the modelled with the measured data on an ideal time resolution. To evaluate the confidence interval at 95%, a leave-one-out cross-evaluation was conducted.

B.3 Results

B.3.1 Choosing time resolution

To choose the time resolution for modelling, we built linear regression models between SRI$_c$ and NEP$_c$ at all available time resolutions (data not shown). Based on the half-hourly to annual time resolutions, the highest adjR$^2$ (averaged over all sites) were found at half day time resolution (adjR$^2 = 0.83$). The averaged adjR$^2$ for higher time resolution (half hour) were only marginally lower (absolute $< 0.01$). The quality of prediction however for lower time resolution decreased to 0.57 for the yearly time resolution. Half day time resolution is not commonly used, hence, daily time resolution was chosen for the modelling.

B.3.2 Diel cycles (24-hour cycles)

The comparison between the monthly averaged diel cycles of NEP and the monthly averaged diel cycles of SRI revealed a methodological difference between the two time series (data not shown). On the one hand, NEP values uniformly peak maximized during the day and remained at a negative value during the night. On the other hand, SRI showed an opposite pattern in the months April to October, showing minimum peaks during the day and maximum peaks during the night. In the remaining months (November to March), SRI synchronized with a similar pattern to NEP. This methodological difference in the diel cycle is an non-ideal prerequisite for the comparison of the two time series at time resolutions higher than days, and hence, this was another reason for choosing daily time resolution for the modelling.
APPENDIX B. HIGH RESOLUTION STEM RADIAL INCREMENTS TO PREDICT DAILY NET CARBON UPTAKE IN EUROPEAN FORESTS

B.3.3 Variability of annual NEP\(_c\) and SRI\(_c\)

Annual cumulative NEP\(_c\) ranged in average from 221 (Davos) to 771 g C m\(^{-2}\) yr\(^{-1}\) (Loobos; Tab. B.2). Jastrebarsko showed the smallest inter-annual variability with a standard deviation of ±30 g C m\(^{-2}\) yr\(^{-1}\). Together with Tuczno, this site included the smallest number of years (three each). The largest inter-annual variability of NEP\(_c\) occurred at Collelongo sites (±200 g C m\(^{-2}\) yr\(^{-1}\)). Standard deviations of annual NEP\(_c\) of all sites did not exceed the annual NEP\(_c\) values.

Annual stem radius increments varied in average between 354 (Loobos) and 2'056 µm yr\(^{-1}\) yr\(^{-1}\) (Laegeren), with standard deviations ranging between ±78 (Loobos) and ±565 µm yr\(^{-1}\) (Tuczno). Standard deviations of annual SRI\(_c\) of all sites did not exceed the annual SRI\(_c\) values.

B.3.4 Modelling results

In general, all site-specific linear regression models showed high and highly significant relationships, with adjR\(^2\) values ranging from averages between 0.85 for MOD2 and 0.94 for MOD4 (Tab. B.3). The highest adjR\(^2\) were found for MOD4 (0.94) for SRI\(_c\) and \(T_a\)-sum (cumulative sum of air temperature) as explaining variables for NEP\(_c\). The model with the lowest adjR\(^2\) average was MOD2 (the only univariate linear regression) with 0.85 for the prediction of NEP\(_c\) with SRI\(_c\) alone. All models have shown to be highly significant, for both using the sample size and the effective sample size (Equation B.2).

The comparison between MOD1, MOD2 and MOD4, revealed that calculated NEP\(_c\) with MOD2 and MOD4 were closer to the measured NEP\(_c\) curve than calculated with MOD1 (Fig. B.4, Davos, all other sites are in supplementary material). This was not only true visually on the inter-annual time scales (Fig. B.4), but also on the intra-annual time scale.

The ANOVAs (Fig. B.4) revealed that for all sites except for Collelongo, MOD4 was significantly (p < 0.05) superior to MOD2 and moreover, MOD2 was significantly (p < 0.05) superior to MOD1. For Collelongo, MOD4 was significantly superior to MOD2, but MOD2 and MOD1 did not show a significant difference.
B.3.5 Drivers of NEP<sub>c</sub> prediction

The analysis of which variables drove the quality of prediction in MOD2 (SRI<sub>c</sub> predicts NEP<sub>c</sub>) did not reveal a consistent or significant pattern explaining the differences between the qualities of prediction of the NEP<sub>c</sub> from SRI<sub>c</sub> of the six individual forest sites (Tab. B.5). Basal area alone was able to explain the adjR<sup>2</sup> of the linear regression model with an R<sup>2</sup> of 0.68 (not significant however). For basal area, the β-coefficient was negative, indicating a negative relationship: The lower the basal area of the site, the higher adjR<sup>2</sup> of the linear regression between SRI<sub>c</sub> and NEP<sub>c</sub> for that site individually (MOD2). Canopy height did not improve the two-variable model. The inclusion of speed of growth, calculated as the averaged difference between the annual minima and maxima over the time period did improve the R<sup>2</sup> by 0.05 (0.73 instead of 0.68), improved the three-variable model, however not insignificant.

B.3.6 Uncertainty of prediction

To assess the quality of the empirical analysis between SRI<sub>c</sub> and NEP<sub>c</sub> at daily time resolution, modelled and measured NEP<sub>c</sub> values were compared. Differences between modelled and measured NEP<sub>c</sub> were aggregated for all years (Fig. B.5a), as well as for all years and all sites (Fig. B.5b). Moreover, 95% confidence intervals were calculated. Daily differences were then aggregated (Fig. B.5c). In general, all sites showed a relatively similar pattern and size of the 95% confidence interval envelopes (Fig. B.5a). The largest differences occurred in the months of March and April and in September and October (vertical size of gray envelope in Fig. B.5a). Overall, the mean difference between modelled and measured NEP<sub>c</sub> was −5.2 g C m<sup>−2</sup> and the standard deviation 95.7 g C m<sup>−2</sup>.

B.3.7 Slope of correlation (MOD5)

To build model 5 (MOD5) based on MOD2, differences between the site specific linear regression models needed to be found. For linear regression models, the differences could be either caused by differing slopes, intercepts, or both. The site-specific linear regression model slopes (MOD2, NEP<sub>c</sub> predicted by SRI<sub>c</sub>) differed substan-
tially from one another, with a very steep slope for Loobos (1.6) and a relatively flat one for Davos (0.2). The only significant relationship found was the speed of growth and the inverse thereof (time to grow, \( t_g \)) (Fig. B.6f, g). Speed of growth was negatively correlated with the slope, with an \( R^2 \) of 0.80, while \( t_g \) was positively correlated with an \( R^2 \) of 0.97. Speed of growth is the calculated average ratio between the difference of the annual maximum and the minimum and the time period in between the two, in \( \mu m \ h^{-1} \).

The highly correlative nature between the slope of the individual MOD2 allowed the building of MOD5. For any given day \( i \) in the year:

\[
NEP_c(i) = t_g \ast SRI_c(i)
\]  
(B.3)

where \( NEP_c(i) \) is the instantaneous cumulative \( NEP_c \) value within the curve in \( g \ C \ m^{-2} \ yr^{-1} \); \( t_g \) is \textit{time to grow} in \( h \ \mu m^{-1} \), the inverse of the speed of growth in the growing period in \( \mu m \ h^{-1} \); \( SRI_c(i) \) is the instantaneous continuous stem radius increment at any given day \( i \) of the day in \( \mu m \). A constant factor (an intercept) was not included due to the fact that no explanation for the intercept could be found, using the same characteristics as for the slope. Intercepts, however, ranged substantially between –48.1 (Collelongo) to 155.5 g C m\(^{-2}\) (Loobos). We then used this MOD5 to calculate \( NEP_c \) for all sites and all years. Moreover, the deviation of the measured and the \( NEP_c \) modelled by MOD5 were small during almost the whole year and only increased during the start of the growing period and at the year end (Fig. B.7b), with the mean difference amounting to –51.6 g C m\(^{-2}\) d\(^{-1}\).

### B.4 Discussion

Continuously measured stem radius changes (\( SRI_c \)) and cumulative net ecosystem productivity (\( NEP_c \)) are two time series empirically closely related. All modelling efforts in this study showed highly significant correlative natures between these two time series at all sites. We hypothesized that sequentially measured \( SRI_c \) incorporates meteorological and biological information within a forest and therefore, this time series is better in predicting \( NEP_c \) than meteorological variables alone. Model 2 (MOD2) — the model where only \( SRI_c \) predicts \( NEP_c \) — was superior to MOD1
(where only meteorological data predicted NEP_c) in five out of six forest sites, hence, confirming our hypothesis (Tab. B.4). MOD4, the combination of SRI_c and meteorological conditions have shown to be even superior over MOD2. When focusing only on the relationship between SRI_c and NEP_c, we found that time to grow \( t_g \), as the inverse of the averaged speed of growth, determined the linear regression models between SRI_c and NEP_c. The less time required for the annual growth to take place in a forest \( t_g \), the higher the slope of the model. Hence, sites with high \( t_g \) (such as Davos) showed a low daily to annual productivity \( \text{NEP}_c \). With this, model 5 was built, where \( \text{NEP}_c(i) = t_g \times \text{SRI}_c(i) \) (B.3). This model outperforms other commonly used soil–biosphere–atmosphere models (examples to be found in Keenan et al. (2012). This is mainly due to the fact that SRI_c (as a basis for the prediction) integrates over a wide range of meteorological and biological conditions and processes within a forests, as experienced by trees. Trees incorporate information e.g. from soil moisture, to temperature to water vapour pressure deficits or even from radiation. SRI_c, and hence, trees serve as integrals for forests C uptake.

### B.4.1 Time resolution

Highly resolved data allowed an in-depth analysis of the effect of time resolution on overall model qualities. While many studies focus on combining methods primarily at an annual scale \( \text{cf. Zweifel et al., 2010; Babst et al., 2012, 2013} \), we found that a daily time resolution increases the predictory power from as much as 0.57 (annual time resolution) to 0.87 (daily time resolution), which is an increase of absolute 0.30, i.e. 27\% (data not shown). In comparison to other methods, i.e. tree rings, we find this to be a remarkable increase in prediction quality. Going beyond daily time resolution (i.e. half-hourly, hourly), has not shown to increase the modelling quality (data not shown). This may be due to the fact that the two time series show considerable differences in the diel cycles (data not shown). While half-hour to half-hour changes of stem radii were synchronized with NEP in the non-transpiring months, in the transpiring months, stem radius changes reflect actual tree water-relations, where maximum peaks were not during the day, but during the night, when water replenishes the stem (Zweifel et al., 2006, 2005).
B.4.2 Small deviation of modelled and measured NEP<sub>c</sub> during growing period

Intra-annual variability of daily NEP<sub>c</sub> was better reflected during the growing season and less in the dormancy period (gray 95% confidence interval envelope in Fig. B.5b and B.7a). In February and March and in August and September, modelled NEP<sub>c</sub> (MOD4) underestimated measured NEP<sub>c</sub>. In the first period, around the transition between winter (March) and spring (April), measured NEP<sub>c</sub> was already strongly increased while modelled NEP<sub>c</sub> was at a lower level and not increasing yet. A delay of a couple of weeks may be explained by the contribution to C exchange processes of the understory in the forests. While CO<sub>2</sub> exchange of the understory of a forest is reflected and measured with the eddy covariance (EC) method, it is not reflected in tree dendrometers. Carbon (C) uptake by the understory can therefore lead to the earlier increase of NEP<sub>c</sub> in comparison to SRI<sub>c</sub>.

Another effect might have evoked the slightly larger uncertainty in the winter-spring transition period. Deciduous trees show a delayed onset of photosynthetic activity in spring compared to coniferous trees, because of the necessity of energy for bud burst and leaf flushing (cf. Epron et al., 1996; Jurik, 1986; Koike, 1990; Reich et al., 1991; Suni et al., 2003). In contrast, photosynthetic capacity in coniferous forests may be attained after only a few days upon exposure to optimal environmental conditions (Ottander and Öquist, 1991; Ottander et al., 1995; Suni et al., 2003). Since our study included coniferous, deciduous, and mixed forests, we expected NEP<sub>c</sub> to precede stem expansion by some days, especially in the forests with the deciduous trees. Even though our findings are well aligned with these expectations, we could not quantitatively disentangle the effects of the understory (mentioned above) from the effect of deciduous trees delay for the onset of assimilation.

Opposite to the first period, in the transition from summer (August) to autumn (September), modelled NEP<sub>c</sub> was not increasing at the same rate as measured NEP<sub>c</sub>. This might be explained by the earlier termination of tree stem growth compared to net C uptake at the end of the growing season. This finding is well aligned with other studies, e.g. by Longdoz and Granier (2012). Similar to the energy requirements of the deciduous trees for the bud burst, there are processes in the transition from fall to winter, where a switch from structural carbon production, i.e. growth, to carbon storage occurs (cf. Epron et al., 2012; Carbone et al., 2013). Carbon storage
products include sugars, starch, amino acids and lipids, which do not effect tree growth in the same period.

**B.4.3 Uncertainty of NEP<sub>c</sub> prediction**

Most biosphere–atmosphere models of predicting NEP<sub>c</sub> are built on the basis of annual time scales. Hence, most modelling comparison studies look at inter-annual variability of NEP<sub>c</sub> and not at intra-annual patterns (cf. Keenan et al., 2012). In this study we were able to model on a daily basis and therefore, we can compare the uncertainty of our model at the end of the year to the uncertainty of other models. The mean difference between measured and modelled (MOD5) NEP<sub>c</sub> was −51.6 g C m<sup>−2</sup> yr<sup>−1</sup>, and thus, relatively skewed to an underestimation in comparison to other models studied in Keenan et al. (2012). According to the authors of that study, observed inter-annual variability of many models was as high as the magnitude of the mean fluxes. MOD5 outperforms this systematic error of many presently used biosphere–atmosphere models. The standard deviation of MOD5 was with 101.1 g C m<sup>−2</sup> yr<sup>−1</sup> almost double the uncertainty of the EC method (±50 g C m<sup>−2</sup> yr<sup>−1</sup>; Hollinger and Richardson, 2005; Papale et al., 2006). However, we assume that the incorporation of many systematic errors in the responses of the trees leads to overcoming large uncertainties and will further increase the already high predictive power of MOD5 for modelling forest NEP<sub>c</sub>. These systematic errors include, according to Keenan et al. (2012), the underrepresentation of variability in spring phenology, soil thaw and snowpack melting, and difficulties in reproducing the lagged response (compare also with Zielis et al., 2014). We conclude that even though the models are usually only taking into account annual values, our model is based on day-to-day predictions.

**B.4.4 Synthesis**

The novelty of this study lay in the analyses and modelling of sequentially measured variables of cumulative net ecosystem productivity (NEP<sub>c</sub>), of continuously measured stem radius increments (SRI<sub>c</sub>), and of meteorological time series. These highly resolved time scales were accompanied by spatially expanding from one site in Switzerland to six forest sites in a broad gradient within continental Europe. Data
APPENDIX B. HIGH RESOLUTION STEM RADIAL INCREMENTS TO PREDICT DAILY NET CARBON UPTAKE IN EUROPEAN FOREST

derived from measurements of tree stem radius expansion and shrinkage with automatic dendrometers represent an integral of the forest, incorporating meteorological and biological conditions and processes at a highly resolved time scale. Predictions of forest C uptake based on dendrometer measurements therefore outperforms other predictions which e.g. only take meteorological data as a predicting basis. Meteorological data influences tree processes (tree growth and tree water-relations), which are in turn representative for powerful prediction of forest NEP budgets, on daily to annual time scales.

B.5 Acknowledgements

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B.6 References


B.7 Tables and figures
Table B.1: Detailed description of the selected sites in this study (Fig. B.1, European Fluxes Database Cluster (2013)). Sites are abbreviated with the original three letter FLUXNET codes not including the country code. Forest types: DBF = deciduous broad leaf forests, ENF = evergreen needle leaf forests, MF = mixed forests. Species = dominant species in the forest. Latitude and longitude positive, when North or East respectively. Years used are the years analysed. Precipitation = mean annual sum. Annual air temperature = mean annual temperature at the top of the flux towers. Altitude = average in meters above sea level. Age = average age of the mature trees in the stand. Height = maximum of the canopy height above ground. LAI = leaf area index. Data access = either download from the European Database Cluster in mostly Level 4 (highest) quality, or receipt directly from the PIs.

| Site       | FLUXNET Abbr. | Forest Type | Dominant Species | Lat. | Long. | Yrs used | Precip. [mm] | Air Temp. [°C] | Altitude [m asl] | Age [years] | Canopy height [m] | LAI [m² m⁻²] | Data access                      | Processing     |
|------------|---------------|-------------|------------------|------|-------|----------|-------------|----------------|-----------------|-------------|----------------------|-------------|----------------------------------|----------------|--------------------------|
| Collelongo, IT | COL          | DBF         | Fagus sylvatica  | 41.85| 13.59 | 1997–2006 | 1'180       | 6.3            | 1'550          | 105         | 25                   | 5.0         | download, L4 post-processed |                |
| Davos, CH   | DAV          | ENF         | Picea abies      | 46.81| 9.86  | 1998–2011 | 1'000       | 3.4            | 1'639          | 240         | 35                   | 3.9         | own site post-processed         |                |
| Jastrebarsko, HR | JAS    | DBF         | Quercus robur   | 45.62| 15.69 | 2008–2010 | 960         | 10.6           | 115            | 40          | 23                   | 5.6         | direct from PI post-processed  |                |
| Laegeren, CH | LAE          | MF          | Mixed            | 47.48| 8.37  | 2006–2012 | 1'000       | 7.4            | 682            | 140         | 31                   | 3.6         | own site own processing      |                |
| Loobos, NL  | LOO          | ENF         | Pinus sylvestris | 52.17| 5.74  | 2008–2011 | 966         | 10.0           | 25             | 90          | 18                   | 3.0         | download, L2 post-processed   |                |
| Tuczno, PL  | TUC          | ENF         | Pinus sylvestris | 53.21| 16.10 | 2010–2011 | 625         | 7.8            | 105            | 54          | 20                   | 1.1         | direct from PI post-processed  |                |
Table B.2: Overview of years analysed, averaged cumulative annual net ecosystem productivity (NEP$_c$) and annual stem radius increments (SRI$_c$) with standard deviations for each of the included six sites.

<table>
<thead>
<tr>
<th>Site</th>
<th>FLUXNET Abbr.</th>
<th>Years used</th>
<th>NEP$_c$ ±SD [g C m$^{-2}$ yr$^{-1}$]</th>
<th>SRI$_c$ ±SD [µm yr$^{-1}$]</th>
</tr>
</thead>
<tbody>
<tr>
<td>Collelongo</td>
<td>COL</td>
<td>1997-2006</td>
<td>605 ±200</td>
<td>974 ±180</td>
</tr>
<tr>
<td>Davos</td>
<td>DAV</td>
<td>1998-2011</td>
<td>221 ±80</td>
<td>1'520 ±317</td>
</tr>
<tr>
<td>Jastrebarsko</td>
<td>JAS</td>
<td>2008-2010</td>
<td>464 ±30</td>
<td>1'871 ±180</td>
</tr>
<tr>
<td>Laegeren</td>
<td>LAE</td>
<td>2006-2012</td>
<td>618 ±164</td>
<td>2'056 ±469</td>
</tr>
<tr>
<td>Loobos</td>
<td>LOO</td>
<td>2008-2011</td>
<td>771 ±81</td>
<td>354 ±78</td>
</tr>
<tr>
<td>Tuczno</td>
<td>TUC</td>
<td>2010-2011</td>
<td>669 ±33</td>
<td>1'097 ±565</td>
</tr>
</tbody>
</table>
Table B.3: Results (adjusted R^2, adjR^2 and variable choices, with β-coefficients) of the modelling with multiple adaptive regression splining (MARS) and the linear regression models for all six sites. The variables included: air temperature (T_a), soil temperature (T_s), global radiation (R_g), vapour pressure deficit (VPD), relative humidity (rH), precipitation (Precip), and if available soil respiration (S_{resp}) and soil water potential (SWP). All meteorological variables were also included in their integrated form, e.g. the sum of air temperature over the course of the year (T_a-sum). For temperatures, we also calculated the daily maxima and minima (e.g. T_a-max). A maximum of three variables is enforced to avoid over-parametrization of the models for MOD0, MOD1, and MOD3. MOD2 chooses from one variable only, i.e. cumulative stem radius increments (SRI_c). MOD4 includes the SRI_c from MOD2 and includes one more meteorological variable, as chosen from the MOD3 (T_a-sum). To compare variable importances, the β-coefficients were used. This so-called standardized regression coefficient (Vittinghoff et al., 2005; Schroeder et al., 1986; Quinn and Keough, 2001), ranging from –1 (negative correlation, yet greatest importance) to +1 (positive correlation, greatest importance). To compare the models, adjR^2 values are compared and analyses of variance were conducted (ANOVA).

<table>
<thead>
<tr>
<th></th>
<th>Collelongo</th>
<th>Davos</th>
<th>Jastrebarsko</th>
<th>Laegeren</th>
<th>Loobos</th>
<th>Tuczno</th>
<th>Averaged</th>
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<tr>
<td><strong>MOD0</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>var1</td>
<td>T_a-sum 0.818</td>
<td>T_s-sum 0.658</td>
<td>T_s-sum 0.769</td>
<td>T_a-sum 0.890</td>
<td>T_a-sum 0.867</td>
<td>T_a-sum 0.952</td>
<td>0.87</td>
</tr>
<tr>
<td>var2</td>
<td>T_s 0.185</td>
<td>T_r 0.412</td>
<td>T_r 0.377</td>
<td>T_r 0.326</td>
<td>VPD -0.113</td>
<td>Precip 0.035</td>
<td></td>
</tr>
<tr>
<td>var3</td>
<td>Precip 0.048</td>
<td>VPD -0.078</td>
<td>T_a-max -0.132</td>
<td></td>
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<tr>
<td><strong>MOD1</strong></td>
<td></td>
<td></td>
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<td></td>
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<td>SRI_c 0.493</td>
<td>SRI_c 0.318</td>
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<td>SRI_c 0.463</td>
<td>T_r 0.115</td>
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</tbody>
</table>
Table B.4: Significant differences between models 4, 2 and 1 (MOD4, MOD2, MOD1). A ‘greater than’ symbol (>) indicates that the model is significantly (p < 0.05) superior over the other. A ‘not greater than’ (great than symbol, but crossed out) symbol indicates that there was no significant difference found between the two models.

<table>
<thead>
<tr>
<th>Location</th>
<th>Differences</th>
</tr>
</thead>
<tbody>
<tr>
<td>Collelongo</td>
<td>MOD4 &gt; MOD2 ≯ MOD1</td>
</tr>
<tr>
<td>Davos</td>
<td>MOD4 &gt; MOD2 &gt; MOD1</td>
</tr>
<tr>
<td>Jastrebarsko</td>
<td>MOD4 &gt; MOD2 &gt; MOD1</td>
</tr>
<tr>
<td>Laegeren</td>
<td>MOD4 &gt; MOD2 &gt; MOD1</td>
</tr>
<tr>
<td>Loobos</td>
<td>MOD4 &gt; MOD2 &gt; MOD1</td>
</tr>
<tr>
<td>Tuczno</td>
<td>MOD4 &gt; MOD2 &gt; MOD1</td>
</tr>
</tbody>
</table>
Table B.5: Stepwise multiple regression models (SMRM) and $\beta$-coefficients ($\beta$-coefs) for three site specific characteristics which all could not significantly explain the quality of NEP$_c$-by-SRI$_c$ prediction by one to three variables (vars).

<table>
<thead>
<tr>
<th>Drivers of $R^2$</th>
<th>$R^2$</th>
<th>SMRM ($\beta$–coefs)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>alone</td>
<td>1 var</td>
</tr>
<tr>
<td>Basal area</td>
<td>0.68</td>
<td>-1.00</td>
</tr>
<tr>
<td>Canopy height</td>
<td>0.63</td>
<td>–</td>
</tr>
<tr>
<td>Speed of growth</td>
<td>0.57</td>
<td>–</td>
</tr>
<tr>
<td><strong>Total $R^2$</strong></td>
<td>–</td>
<td>0.68</td>
</tr>
</tbody>
</table>
Figure B.1: Spatial distribution of the six sites included in this study. The original three letter FLUXNET abbreviations (not including the country codes) are used as identifiers (European Fluxes Database Cluster, 2013).
Figure B.2: Time series (example from Davos, year 2012) used in this study as rate of change (panels a: net ecosystem productivity, NEP; panel b: stem radius increments, SRI) and cumulative time series (cumulative net ecosystem productivity, NEP\textsubscript{c}; continuously measured stem radius increments, SRI\textsubscript{c}). Panel a) shows an example of a measured NEP time series as daily cumulative sums of half-hourly NEP values (either C uptake or C release). b): Time series of day-to-day averaged discrete differences of SRI values, as calculated from dendrometer readings in the case of the ‘Natkon’ dendrometers (Davos, Laegeren and Tuczno) or as calculated from the circumference change readings from Collelongo, Jastrebarsko and Loobos. c) and d): The cumulative curves of NEP\textsubscript{c} and SRI\textsubscript{c}, respectively. e): The overlay of both the cumulative NEP\textsubscript{c} and the SRI\textsubscript{c} values (as read directly from the dendrometer readings in the case of the ‘Natkon’ dendrometers, or as calculated from the diameter readings from the others). Note that the units in e) are different for both the time series with g C m\textsuperscript{-2} for NEP\textsubscript{c} and \(\mu\text{m}\) for SRI\textsubscript{c}. 
Figure B.3: Five models were built on different sets of time series variables. These included next to cumulative net ecosystem productivity \( \text{NEP}_c \) and continuously measured stem radius increments \( \text{SRI}_c \) meteorological time series: air temperature \( (T_a) \), soil temperature \( (T_s) \), global radiation \( (R_g) \), vapour pressure deficit \( (VPD) \), relative humidity \( (rH) \), precipitation \( (Precip) \), and if available soil respiration \( (S_{resp}) \) and soil water potential \( (SWP) \). All meteorological variables were also included in their integrated form, e.g. the sum of air temperature over the course of the year \( (T_a\text{-sum}) \). For temperatures, we also calculated the daily maxima and minima (e.g. \( T_a\text{-max} \)). MOD0: chooses from all meteorological time series variables to predict stem radius increments (cumulative, \( \text{SRI}_c \)). MOD1: \( \text{NEP}_c \) as predicted by a maximum of three time series variables. MOD2: \( \text{NEP}_c \) as predicted by \( \text{SRI}_c \) alone. MOD3: \( \text{NEP}_c \) as predicted by meteorological data and \( \text{SRI}_c \), choosing a maximum of three time series variables. MOD4: \( \text{NEP}_c \) as predicted by \( \text{SRI}_c \) and one meteorological time series variable alone. The choice for this meteor-variable is based on MOD3, using the variable used the most by MARS. MOD5: One model built for all sites based on dendrometer data only. To assess model quality, \( \text{adjR}^2 \) and ANOVAa were conducted.
Figure B.4: Overlay of modelled net ecosystem productivity (NEP$_c$, black curves) as calculated with MOD1 (meteo variables only), MOD2 (stem radius increments only), and MOD4 (both stem radius increments and sum of air temperature) over the measured NEP$_c$ (gray). The closer the black curve to the gray, the better the modelling approach, at least visually. The figures for all other sites are attached to this chapter in the Sect. *Supplementary materials*.
APPENDIX B. HIGH RESOLUTION STEM RADIAL INCREMENTS TO PREDICT DAILY NET CARBON UPTAKE IN EUROPEAN FORESTS

Figure B.5: Quality of the prediction (adjR² of linear regression) of cumulative net ecosystem productivity (NEPc) calculated from cumulative stem radius increments (SRIc) (model 2, MOD2). Panel (a): For each single site individually the measured NEPc curves as measured and then aggregated over the years. The gray envelope depicts the 95% confidence interval for every day. Indicating we would expect a 5% chance that measured NEPc is outside of the gray envelope. Gray areas indicate the accuracy of the modeling within a year. Panel (b): All sites measured and aggregated in one curve. The gray solid line indicates the averaged NEPc of all sites within a year. All sites measured and aggregated in one curve. The black solid line indicates the accuracy of the modeling within a year. Panel (c): All data as measured and then aggregated in a histogram (leave-one-out cross-evaluation) of cumulative net ecosystem productivity (NEPc) calculated from cumulative stem radius increments (SRIc) (model 2, MOD2).
Figure B.6: Eight panel (a-h) overview of possible explaining factors for the slope of the individual site specific linear regression models between $SRI_c$ and $NEP_c$ (MOD2). Significant linear dependencies are indicated with linear lines and a larger text of $R^2$. 

- **a)** Basal area of the forests, estimated; 
- **b)** Average diameter at breast height (DBH); 
- **c)** Wood density, as estimated according to the species at the site; 
- **d)** Stem density in trees per ha; 
- **e)** Leaf area index (LAI); 
- **f)** Speed of growth, which is the averaged distance ($\mu m$) between the minimum of $NEP_c$ and the maximum of $NEP_c$, divided by the time between these two points. 
- **g)** Time to grow is the inverse of (1 over) speed of growth, which is the ratio between the average distance between the minimum of $SRI_c$ and the maximum of $SRIc$ within a year, over the time between these two points (unit = $\mu m \ h^{-1}$); 
- **h)** the averaged gross primary productivity (GPP) over total ecosystem respiration (TER) ratio.
Figure B.7: Modelling of net ecosystem productivity \( (\text{NEP}_e) \) from cumulative stem radius increments \( (\text{SRL}_e) \) alone, considering different slopes and intercepts within the linear regression model, departing from site-specific models (MOD0–MOD4) to a global model \( (\text{NEP}_e(i) = t_g * \text{SRL}_e(i)) \).

\( \text{a): Average day-to-day modelling of NEP}_e \) with MOD5, with gray envelope indicating the averaged 95% confidence interval.

\( \text{b): Aggregated in the histogram the absolute deviations as stacked in the frequency of modelled minus measured differences of NEP}_e \), including the 95% confidence intervals, mean and standard deviation (SD, on daily time resolution).
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This thesis would have not come to life in this way without the support, help, and encouragement of many people who deserve great acknowledgment. So, here we go – many thanks to:

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EDUCATION

ETH Zurich, Zurich, Switzerland
- **PhD** in biogeochemistry and micrometeorology
- **Focus**: on multi-site and multi-year data analysis and modeling of the carbon balance of European and US forest ecosystems
- **Thesis**: Climatic and biological drivers of temporal dynamics and feedbacks of the carbon balance of forests
- **Member**: of mid-level faculty departmental conference and resource committee as well as treasurer of mid-level faculty
- **Leading**: student assistants and apprentices

Trier University, Trier, Germany
- **Diploma** in Applied Environmental Sciences
- **Top 5%** of the graduating class in 2010, Grade: 1.1
- **Thesis**: Litter decomposition in different forest stands and inferences on ion export

WORK EXPERIENCE

DATASCIENTIST.ch, Zurich, Switzerland
- **Co-Founder**
  - Co-founded company aiming at analyzing big data and digging up information otherwise hidden and never explored. We quest to create social and economic value for businesses, public agencies, and non-profits

AMR International, Frankfurt, Germany
- **Intern – Management consulting**
  - Developed growth strategy for German company in the technical ceramics sector by identifying new market areas and restructuring the sales department. Efficiency of sales force substantially increased right after roll-out
  - Consulted British client in the “Renewables” domain on market identification and go-to-market strategy. Three out of five recommended markets are under consideration for market entry
  - Evaluated the sustainability of the business model for PE investor’s target company of the DIY business. Investor followed the advice and backed out of buying decision
ETH Zurich, Zurich, Switzerland
December 2011 – November 2012
*International Symposium “Plants replacing fossil fuels?”*

**Head of Program Organization**
- Managed program and speaker organization for international symposium with >200 attendees and 14 speakers from the US, the UK, Germany and Switzerland. Attained extremely positive participant feedback.

Forschungsanstalt für Waldökologie, Trippstadt, Germany
August 2009 – September 2009
*Institute for forest ecology and forestry*

**Intern – Forest monitoring and environmental precautions**
- Acquired, validated, and analyzed forest inventory data, later used in the annual status report of the federal state forest.

Green Manitoba, Winnipeg, Canada
February 2009 – April 2009
*Special operating agency for sustainability issues*

**Intern – Government consulting**
- Formed concept and managed project of provincial organic and electronic waste survey including telephone and on-site interviews. Report served as guide and decision making tool for the Manitoba Government.

Trier University, Trier, Germany
July 2008 – March 2009
*Department of Soil Sciences*

**Research Assistant**
- Analyzed and acquired soil and tree specific data and reported findings to project partners. Project results led to new insights highly important for crucial flood control measures.

**LANGUAGE AND IT-SKILLS**

Languages: German (native), English (fluent), French (basic)
IT-Skill: MS Office, R statistical programming, SPSS, LateX, ArcGIS

**INTERESTS**

Music: Playing drums and guitar
Sports: Tennis, running, fitness training, snowboarding
Culture: Architecture, modern art, photography

**REFERENCES (contact details on request)**

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ETH Zurich: Prof. Nina Buchmann, Head of Grassland Sciences Group