Link between continuous stem radius changes and net ecosystem productivity of a subalpine Norway spruce forest in the Swiss Alps

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Summary

- Continuous stem radius changes (DR) include growth and water-related processes on the individual-tree-level. DR is assumed to provide carbon turnover information complementary to the net ecosystem carbon productivity (NEP) which integrates fluxes over the entire forest ecosystem. We investigated the unexpectedly close relationship between NEP and DR and ask for causalities.

- NEP (positive values=C sink) measured by eddy covariance over eleven years were analyzed at three timescales alongside automated point dendrometer DR data from a Swiss subalpine Norway spruce forest.

- On an annual and monthly scale, the remarkably close relationship between NEP and DR was positive, whereas on a half-hourly scale the relationship was negative. Gross primary production had a similar explanatory power at shorter timescales but was significantly less correlated to DR on an annual scale.

- Causal explication for the NEP-DR relationship is still fragmentary however it is partially attributable to: (i) radial stem growth with a strong effect on the monthly and annual increase of NEP and DR, (ii) the frost-induced bark tissue dehydration with a parallel decrease of both measures on a monthly scale, and (iii) the transpiration-induced DR shrinkage which is negatively correlated to assimilation and thus to NEP on a half-hourly scale.
Introduction

Eddy covariance (EC) CO$_2$ flux measurements allow the quantification of net ecosystem productivity (NEP). They, however, represent net C fluxes and thus do not allow a direct quantification of its components, i.e. the contributions of the vegetation vs. the soil or the wood vs. the leaves and fruits (Buchmann & Schulze, 1999; Baldocchi, 2003). The EC measurements provide an integrated view of net CO$_2$ fluxes in and out of a (forest) ecosystem by including different CO$_2$ sources and sinks within the so-called flux footprint (Schmid, 2002). The CO$_2$ sources (respiration) and CO$_2$ sinks (assimilation) are large budget components of opposite direction that sum up to a relatively small NEP over a year (Barford et al., 2001; Körner et al., 2005; Navarro et al., 2008). Since the net balance of these components is directly measured with EC, it is generally assumed that the accuracy of annual estimates of NEP should be better than those which estimate the two large components (gross primary production GPP and total ecosystem respiration TER) separately (Buchmann & Schulze, 1999). The main C sink of a forest is usually represented by the assimilation of trees leading to an accumulation of biomass (wood, leaves, fruits etc). This C sink is balanced with the C losses by respiration of living tissues, and the C sources from the soil (Monson et al., 2006), including the decomposition of biomass and soil organic matter (Damesin et al., 2002).

By adding point dendrometers for continuously measuring stem radius changes of trees (DR) within the footprint area of an EC site, we can obtain independent information of one of the dominant C sinks of the ecosystem in the form of wood and phloem growth of trees. The tree-stem-biomass related accumulation of C is reported to have a strong weight on NEP (Barford et al., 2001; Rocha et al., 2006; Stoy et al., 2009), at least on an annual scale. However, DR contains much more information than wood growth on the long term. Continuously measured DR allow for an intra-annually resolved interpretation of growth
processes and the investigation of tree water relations due to the (under-) pressure related swelling and shrinking of the bark (Steppe et al., 2006).

Generally, $DR$ is determined by (i) stem water content, and by (ii) wood and bark growth including the degradation of dead phloem cells. (i) The water-related fraction is a short-term effect lasting over hours to weeks that can either have positive or negative effects on the stem radius depending on the changing turgor of stem tissues (Zweifel et al., 2001). Mainly the phloem (contributes $> 90\%$ to the total change of $DR$) but also the cambium and the cell walls of the xylem undergo a volume change depending on the actual tree water status (Steppe et al., 2006). Usually, cells lose water during periods of transpiration (daytime) and get replenished during the night and rainy or foggy periods. Accordingly, stems shrink during the day and expand at night. In dry periods, the daily balance between water uptake and water loss can be negative and therefore lead to several-weeks-lasting tree water deficits with shrinking stems even during the wood growth period (Zweifel et al., 2006). In addition to this diurnal rhythm, (ii) seasonal growth periods contribute to the dynamics of $DR$. New xylem and phloem cells are built and elongated to their predisposed size. The xylem cells get lignified and die when matured and the stem size is not altered by these woody structures any more. Also, their response to tissue saturation changes is then strongly reduced and $DR$ is only affected by minimal changes of the cell wall sizes due to water content variations. In contrast, phloem cells remain elastic and undergo diurnal water-related size changes even when matured and, after a few years, they die, shrink, and finally are shed (Lockhart, 1965; Gricar et al., 2009). Continuously measured $DR$ has therefore the potential to link EC-based measures ($NEP$, $GPP$, $TER$) to intra-annually resolved wood growth and water-related physiological processes of trees (Daudet et al., 2005; Steppe et al., 2006).

There is still very scarce information available about how such integrated ecosystem measures like $NEP$ can be related to the tree physiological process of growth at various
timescales (Barford et al., 2001; Gough et al., 2008; Gough et al., 2009; Rocha & Goulden, 2009). Thus, to the best of our knowledge, our study is the first to address the relationship of continuously changing stem radii with the corresponding ecosystem productivity over integration times from 30 minutes to years. This approach offers a new link between ecophysiological plant responses and the processes occurring at larger scales ranging from forests to landscapes. Moreover, it enables us to interpret the NEP patterns (and its derived quantities GPP and TER) based on underlying tree physiological processes that distinguish between growth (xylem and phloem) and water-related changes of DR (Steppe et al., 2006; Zweifel et al., 2006).

Here we analyse two long-term data sets of DR and NEP from the Seehornwald Davos research site, located in a subalpine Norway spruce forest in the Swiss Alps, in the light of current tree physiological knowledge, on an annual (DR_{yr} vs. NEP_{yr}), on a monthly (DR_{m} vs. NEP_{m}) and on a half-hourly data integration time (DR_{hh} vs. NEP_{hh}) over eleven years. We ask up to what degree the relationship between DR and NEP is of correlative nature and what aspects of it can be explained with causal mechanisms. For this, we analyse the general relationships between DR and NEP and also the most prominent anomalies at the three timescales investigated. Further, we test the hypothesis that a close link between DR and NEP vanishes at timescales below the annual resolution. This is expected because of the decreasing weight of wood growth and the increasing weight of tree water relations on DR with shorter integration times. We compare the results for NEP with the results for GPP and TER and discuss up to what degree the relationships are explicable with physiological processes. And finally, we test the hypothesis that annual stem growth only rudimentarily explains NEP due to the many other components contributing to the C balance of a forest ecosystem.
Materials and Methods

Site description

The Seehornwald Davos research site (Figure 1) is located at 1640 m asl at 46°48'55.2" N, 9°51'21.3" E in the eastern part of the Swiss Alps. The coniferous forest is dominated by Norway spruce (*Picea abies* (L.) Karst.) with a maximum canopy height of 27 m, and is considered moderately productive in the regional context at this altitude. Tree age of the dominant trees ranges between 200 and 400 years. European larch (*Larix decidua* Miller) plays only a marginal role with less than 1% abundance. The understorey vegetation is rather patchy, covering roughly 30% of the surface, and is mainly composed of dwarf shrubs, primarily *Vaccinium myrtillus* and *Vaccinium gaulterioides*, as well as mosses. Sustainable forest management was introduced in Switzerland in 1876, the same year when instrumental records of climate variables started at Davos. For a documented period over the last 21 years, only 7 out of 500 trees on the 0.6 ha long-term ecosystem monitoring plot had been removed from the site, most of them following a severe storm in 1990. At the end of October 2006, an area of 25 x 70 m (1750 m²) within the NE-part of the footprint of the EC site was harvested. This area was estimated to have a weight of about 30% on the EC measurements before the cutting.

Continuous stem radius changes \( DR \)

Stem radii continuously respond to tree water relations and cell growth (xylem and phloem) by diurnal stem expansion and contraction. These stem radius changes \( (\text{DR} = \text{difference in radius over time}) \) were measured with 12 automated point dendrometers every 10 seconds and averaged every 30 minutes. Some sensors failed for a certain time or were mounted at different locations within the investigated research period of 11 years. However, between 8-12 sensors were permanently mounted at stems around 1.5 m above ground level.
Analyses and graphs were done with averaged $DR$ values of the 8-12 individual trees. The original type of dendrometers (LVTD, Agricultural Electronics Corporation, Tucson, USA; measured temperature sensitivity: $0.5 \, \mu m \, °C^{-1}$) has been successively replaced by a less temperature sensitive type (ZB06, Zweifel Consulting, Hombrechtikon, Switzerland; measured temperature sensitivity: $0.27 \, \mu m \, °C^{-1}$) starting in 2006. The temperature sensitivity was accordingly corrected for both instruments.

**Eddy covariance flux measurements and microclimate profile**

Turbulent fluxes of CO$_2$ and H$_2$O were measured on a 35 m tall tower with a Solent R2 ultrasonic anemometer-thermometer (Gill Instruments Ltd., Lymington, UK) and a Licor 6262 (Licor, Lincoln, USA) closed-path infrared gas analyser (IRGA) from 1997 to 2005 and an open path system (Licor 7500) from 2005 on, 18 m above the aerodynamic displacement height of the forest. The closed-path IRGA used a 2.60 m long intake hose with its inlet below the sonic anemometer’s sensor head. The instrumental upgrade was done on 9/10 August 2005. The ultrasonic anemometer-thermometer was replaced by its successor model Solent R3-50 (Gill Instruments Ltd., Lymington, UK) on 19/20 December 2006. Since open-path systems and closed-path systems need different treatment in data processing, great care was taken to minimize the systematic effects of replacing old, fading equipment with new instruments.

In particular, an unwanted, and at the time of replacement yet unknown effect of sensor self-heating of the Licor 7500 analyzer (Burba et al., 2006; Burba et al., 2008) had to be incorporated in our data processing. We used the fitting method as described in Järvi et al. (2009) based on an empirically approximated temperature difference between the instrument and air as it is presented for a different locality (Rogiers et al., 2008). The fraction of the heat flux produced by the open-path instrument $\xi$ was set to 0.085 as suggested for a forest ecosystem by Järvi et al. (2009). This approach closely follows Burba et al. (2006 and 2008).
with a site-specific correction factor for sensor tilt angle (see Eq. 1 in Rogiers et al., 2008). Flux measurements were compensated for high frequency damping losses of the instruments (Eugster & Senn, 1995); damping constants of 1.0 and 0.15 s for closed-path and open-path IRGA, respectively) and density fluctuation effects (Webb et al., 1980; only applied in case of the open-path instrument). EC data were processed according to the CarboEurope standard methodology which is based on Aubinet et al. (2000). 30 min averages of CO$_2$ fluxes were calculated by the in-house software ethflux. Details about the flux calculation and data processing can be found in Rogiers et al. (2005) and Hiller et al. (2008). The ethflux software participated in the CarboEurope intercomparison of EC software and showed over tall vegetation good agreement to the reference software TK2, with ethflux estimates being only slightly larger than those of TK2 (Mauder et al., 2008).

Additionally, CO$_2$ concentrations were measured since 2000 in a profile on the tower at 2, 10, 20, 25, and 35 m above ground level to correct for CO$_2$ storage inside the forest canopy. In order to get a homogenously treated data set and as the storage term had only a minor influence on the carbon budget (<1 gC m$^{-2}$ yr$^{-1}$), we did not correct EC fluxes for the storage term since the start of the profile measurements. We however used the 35 m CO$_2$ concentration from the profile system as a reference for the older Licor 6262 eddy covariance IRGA to correct for (i) sensor drift, and (ii) for pressure effects that resulted from the fact that the Licor 6262 IRGA was always calibrated with zero and span gas at low flow rates, but then operated at high flow rates in eddy covariance mode. In a special field campaign in September 2004 with an independent instrument (CIRAS, PP Systems, Amesbury, MA, USA) this pressure effect was quantified and used as a correction factor (1.114) for all fluxes obtained with the old Licor 6262. For the years 1997-1999 and early 2000 before installation of the profile system, the seasonal trend of measured CO$_2$ from 2000 to 2005 was projected backwards in time and used for drift correction. This correction was done on annual data
(more frequently in 1997). Thus, the working data set used for this study is consistent with the increase of annual CO$_2$ concentrations since 1997 (measurements exist since fall 2000), the pronounced seasonality of CO$_2$ concentrations, and considers all currently known sources of error.

Data were screened for quality by instrumental failure, snow, dew or ice on the sensor, out-of-range fluxes and low turbulence conditions. The threshold of friction velocity $u^*$, as a measure of turbulence, was derived from the relationship of temperature-normalised night-time fluxes to classes of $u^*$ (0.05 intervals) and was set to 0.2 m s$^{-1}$ (Goulden et al., 1996).

Fluxes measured during nocturnal periods with low turbulence ($u^* < 0.2$ m s$^{-1}$) were replaced by modelled data (Aubinet et al., 2003; Gu et al., 2005). This procedure accounts for possible underestimation of nocturnal respiration by the EC method. Data gaps of less than two hours were linearly interpolated, longer day-time gaps were filled with logistic sigmoid light response curves (Moffat, personal communication), and longer night-time gaps with a temperature response function (Lloyd & Taylor, 1994).

The wind direction is strongly channelled by the valley wind system at the measurement site. Thus, the flux footprint is dominated by the two main wind directions from NE and SW (Figure 1). Flux footprint computations with the parameterised Kljun-model (Kljun et al., 2004) indicated that flux measurements are mostly influenced by the Norway spruce forest with a marginal influence (< 5%) of the loosely built-up Davos area at the far end of the footprint area to the SW of the tower (Figure 1). No influence was found from the nearby lake clearly outside of the footprint area. Recently started advection experiments do not indicate a major bias for long-term NEP estimates (data not shown), but upon completion will allow us to reassess the absolute numbers we present here.

$NEP$ was partitioned into its two gross fluxes, that is gross primary production ($GPP$) and total ecosystem respiration ($TER$). $NEP$ equals $GPP$ minus $TER$. During the night the
assimilation and thus $GPP$ is assumed to be zero, and therefore $NEP$ equals $TER$. Night-time $TER$ were calculated as a function of air temperature according to Lloyd & Taylor (1994) and the derived temperature response functions were accordingly applied to day-time conditions.

**Definitions**

To distinguish between growth and water-related processes that jointly affect $DR$, and to avoid confounding effects of rapid, freezing-temperature-induced $DR$ changes in wintertime, the starting point for annual radial stem increments ($DR_{yr}$) is set to the culmination point of the cumulative $DR$ curve of the previous year (zero-line in Figure 2). Coupled to this definition is the assumption that shrinking stems never loose wood volume; instead, they shrink due to decreasing water content in the elastic tissues of the stem (mainly the phloem) (Zweifel et al., 2001; Daudet et al., 2005; Steppe et al., 2006) or due to decomposing phloem tissue. The $DR$ zero-line represents the stem status at which the stem contraction of the previous winter is fully recovered and positive values therefore indicate growth (xylem and phloem).

Accordingly, the $NEP$ zero-line was set to the maximum $NEP_{sum}$ value (positive values indicate C sink) of the previous year (Figure 2). The $NEP$ zero-line therefore represents the ecosystem status at which the cumulative net respiration of the previous winter is compensated and positive values mean a net C sink of the ecosystem in the current year.

These predispositions explain why the cumulative curves of $DR_{sum}$ and $NEP_{sum}$ do not begin at zero on January 1st. Besides the terms $DR_{sum}$ and $NEP_{sum}$, we use $DR_{yr}$ and $NEP_{yr}$ to denote annual sums in $DR$ and $NEP$, $DR_m$ and $NEP_m$ for monthly sums, and $DR_{hh}$ and $NEP_{hh}$ for half-hourly sums. Being well aware of the fact that $NEP$ is typically used for annual periods from January 1st to December 31st, the definition used here is physiologically more meaningful and essential for comparing $NEP$ to $DR$. The periods of $GPP_{yr}$ and $TER_{yr}$ are corresponding to $NEP_{yr}$. A similar approach is taken in hydrology where annual budgets are computed from
October to September of the next year to minimize artefacts that would otherwise be introduced when using calendar years.

Furthermore, the period during which the maximum stem contraction in wintertime (MSC) recovers is defined as the winter rehydration period according to Zweifel & Häsl er (2000). It ends with the date when $DR_{sum}$ crosses the zero-line into the positive range. Accordingly, this end point is the day of the year on which the winter shrinkage is compensated ($DOY_{Comp_{MSC}}$) and is identical with the start of the radial wood growth (RWG) period. The RWG period ends when $DR_{Sum}$ reaches its annual maximum. Accordingly, the period in which the winter respiration ($WRES$) recovers is defined as the winter respiration compensation period, ending with the day of the year at which winter respiration is compensated ($DOY_{Comp_{WRES}}$). The period between $DOY_{Comp_{WRES}}$ and the time when $NEP_{Sum}$ reaches its maximum is referred to as the ‘net C sink accumulation period’ hereafter. The period between the minimum and the maximum $NEP_{Sum}$ is defined as the C sink period (CSP) (Figure 2).

Results

Close relationship between DR and NEP independent of integration times

The net ecosystem productivity ($NEP$) was closely correlated to changes in stem radii ($DR$) on an annual (1998-2008: adj. $R^2 = 0.85$), on a monthly (1998-2008 without the month of May: adj. $R^2 = 0.53$) and for days with an average daytime temperature $> 0^\circ C$ even on a half-hourly timescale (Table 1, Figure 3). On annual and monthly timescales, the regressions were found to be positive. On a daily timescale, however, the regression was found to be negative. This means that increasing stem radii significantly correlated to increasing $NEP$ when integrating over periods of months and longer, but they significantly correlated to
decreasing NEP when using half-hourly data. Thus, the length of the integration time changed the quality of the relationship between the two measures but it did not lead to a general loss of interdependence (Table 1).

Gross primary production (GPP) and total ecosystem respiration (TER) are derived quantities from NEP and therefore not independent measures. However, they showed a different relationship to DR (Table 1). GPP was similarly closely correlated to DR as NEP on the short timescales but lost most of the significance of this relationship on the annual scale. An exception was the GPP relation to the C sink period (CSP) which was closer than the one of NEP with CSP. Total ecosystem respiration (TER) correlated to DR on the monthly scale only.

Some exceptions of the above mentioned general relationships between DR and NEP were found on a monthly timescale for the month of May and on a half-hourly scale for the winter values of freezing days. In the first case, the exclusion of May data significantly increased the regressions between $DR_m$ and $NEP_m$ (Table 1, Figure 3). In case of the half-hourly data, the annual sets of data were split into five classes of days (sunny summer/cloudy summer/rainy summer/temperature > 0 °C winter/ temperature < 0 °C winter) which led to a gradual decrease in adj. $R^2$ in this order and the complete loss of a correlation for the last group of days with freezing temperatures (Table 1). Remarkably, no exceptional values were observed for the years after the tree harvesting at the end of 2006 (Figure 3a).

**Annual and monthly timescales**

Years with a large annual radial stem increment ($DR_{yr}$), including wood and phloem growth, always ended with a high annual $NEP_{yr}$. This close relationship is remarkable since the period of radial growth (about 3 months, Figure 4) was much shorter than the period in which the ecosystem assimilation exceeded respiration (C sink period, about 7 months, Figure 4). And, remarkable as well, the close annual correlation between $DR_{yr}$ and $NEP_{yr}$ is not
explicable with $GPP$ and $TER$ per se (Table 1), since these measures are not ($TER$) or not comparably well ($GPP$) related to $DR_{yr}$. On a monthly timescale, even negative $DR_{m}$ values fitted very well into the regression between $DR_{m}$ and $NEP_{m}$ (Figure 3b) because shrinking stems induced by freezing temperatures went in parallel with ecosystem C losses due to an increased ratio of respiration to assimilation in the winter months (Figure 4).

Relying on the definitions made in Figure 2, the recurrent annual patterns started with shrunken stems (negative $DR_{sum}$) and a C balance deficit (negative $NEP_{sum}$) in January (Figures 4-5). This meant tree stems lost volume since last year’s maximum stem size. Correspondingly, the ecosystem was a net C source since last year’s maximum $NEP_{sum}$. In February/March, $DR_{sum}$ started to increase and on average about one month later $NEP_{sum}$ followed (Figure 4). During the period of negative but increasing $DR_{sum}$, the stem expansion is defined as recovery from the current tree water deficit (mainly in the bark) and is not attributable to growth in a physiological sense (Figure 2). Accordingly, negative but increasing $NEP_{sum}$ indicated the ecosystem’s recovery from winter respiration C losses ($WRES$) and cannot be attributed to the net C sink. Both curves, $DR_{sum}$ and $NEP_{sum}$, crossed the respective compensation points ($DOY_{Comp\_MSC}$ and $DOY_{Comp\_WRES}$) on average within 4 days around May/June. However, the variation among years was large. The maximum deviation occurred in 1999 with 56 days when extraordinarily much snow covered the forest floor until mid of May (data not shown). The maximum stem radii were reached in August/September, whereas the culmination point of the $NEP_{sum}$ time course was reached 1-2 months later in October/November (Figure 4). During the winter months, $DR_{sum}$ shrank disproportionately fast at temperatures below the freezing point.

**Half-hourly timescale**

On a half-hourly timescale, the negative regression between $DR_{hh}$ and $NEP_{hh}$ was consistent over the entire year except for days with averaged daytime temperatures $< 0^\circ C$.
Table 1. Sunny summer days appeared to have the closest relationship between $DR_{hh}$ on the one hand and $NEP_{hh}$ and $GPP_{hh}$ on the other hand, followed by cloudy and rainy summer days, and (winter) days with temperatures between 0°C and 5°C. No correlation at all was found for winter days with temperatures below 0°C (Table 1, Figure 3d). This ranking of grouped days corresponded with the ranking of decreasing transpiration intensities (data not shown).

The intra-annual courses of $DR_{sum}$ and $NEP_{sum}$ on a half-hourly resolution were closely linked over the entire measurement period from 1998 to 2008 (Figure 5). This was true for the annual extremes, for year-specific characteristic patterns within the season, and in parts, also for processes on an intra-daily timescale (Figure 6). Within summer days, the onset of net CO$_2$ uptake (positive $NEP_{hh}$) occurred almost at the same time when the stem started to shrink, and the highest $NEP_{hh}$ values occurred always when stems were shrinking. When stems started to expand again in the afternoon, also $NEP_{hh}$ changed its sign, and the ecosystem became a net C source.

330 Winter and spring processes as indicators for $NEP_{yr}$

Besides the close relationships between $DR$ and $NEP$ of corresponding time periods as shown above, we found unexpectedly strong relationships between special dates and periods in winter and spring and the productivity of trees ($DR_{yr}$) and ecosystem ($NEP_{yr}$) in the following growing season (Table 1). The best explanatory power had the cumulative winter respiration of the ecosystem ($WRES$). $WRES$ is known in March already and predicted $NEP_{yr}$ (adj. $R^2 = 0.51$, $p < 0.01$) and $DR_{yr}$ (adj. $R^2 = 0.38$, $p < 0.03$) surprisingly well. The smaller $WRES$, the larger were $NEP_{yr}$ and $DR_{yr}$ of the corresponding season. No correlation was found between $WRES$ and $GPP_{yr}$ and $TER_{yr}$ (Table 1). Even better predictions were possible with the day of the year when the cumulative winter respiration was compensated by assimilation ($DOY_{Comp_{WRES}}$). The earlier the winter respiration was compensated, the larger was $NEP_{yr}$.
(adj. $R^2 = 0.88$, $p < 0.001$), $DR_{yr}$ (adj. $R^2 = 0.76$, $p < 0.001$), and also $GPP_{yr}$ (adj. $R^2 = 0.51$, $p < 0.01$). The maximum stem contraction in winter ($MSC$) had a significant explanatory power for $DR_{yr}$ ($p < 0.02$), a strong but not significant tendency for $NEP_{yr}$ ($p = 0.06$), and no relevance for $GPP_{yr}$ and $TER_{yr}$ (Table 1). The larger $MSC$ was, the smaller were $NEP_{yr}$ and $DR_{yr}$ and the earlier in the year MSC was compensated, the larger became $NEP_{yr}$ and $DR_{yr}$.

Less well related to either $NEP_{yr}$ or $DR_{yr}$ was the length of the C sink period ($CSP$, Table 1). However $GPP_{yr}$ and $TER_{yr}$ were significantly correlated to $CSP$. No explanatory power was found for the radial wood growth ($RWG$) period.
The comparison of continuous stem radius changes (DR) of individual trees and the eddy covariance-based net ecosystem productivity (NEP) of the corresponding forest ecosystem revealed an intriguingly close relationship between the two measures DR and NEP on three different timescales (Table 1). This close relationship was not a priori expected since one measure (DR) is an averaged physiological response of individual, mature trees, whereas the other one (NEP) integrates over the entire ecosystem represented in the EC footprint (Kljun et al., 2004). The finding is even more surprising when considering that DR is the product of growth and water-related processes in the stem and that both of them contribute to the close relationship to NEP with changing weights depending on the integration time. There is no simple physiological approach available that could fully explain this relationship in all its details (Table 1). However, there is good evidence that at least parts of this relationship between NEP and DR can be functionally understood. In the following we discuss to what degree physiological causes and effects can build a link between the two measures.

Integration time-dependent information content of DR

Stem radius changes are determined by water- and growth-related processes (Daudet et al., 2005; Steppe et al., 2006). The analytical distinction between the two fractions of DR is possible either with statistical (Zweifel et al., 2005; Deslauriers et al., 2007) or process-based modelling approaches (Zweifel et al., 2007; Steppe et al., 2008). However, such a distinction is never absolute precise and depends up to a certain degree on assumptions about wood and phloem properties (Zweifel et al., 2006). In general, the longer the time period for data aggregation, the stronger is the importance of the growth-related processes on DR (Zweifel et al., 2006; Steppe et al., 2008). And conversely, the shorter the time period, the stronger is the influence of the water-related processes (Zweifel et al., 2001). This is particularly true for our slow growing trees with a maximum growth rate of about 10-20 µm per day (data not shown),
whereas the water related changes of DR are a magnitude larger with 100-300 µm per day (Zweifel & Häsl er, 2001). The understanding of how these two processes, integration-time dependent, alter DR is essential for the physiological interpretation of the relationship between DR and NEP.

**Close relationship between DR and NEP**

Since NEP represents the budget of CO₂ fluxes in and out of the ecosystem, it was reasonable to expect that only the long-term, growth-related (and thus C-related) fraction of DR would show a close relationship to NEP. Such a relationship on an annual timescale has been reported before in a study of tree ring widths in combination with NEP (Rocha et al., 2006). The interdependence of the two measures in a Black spruce stand in central Manitoba, Canada, was less strong (R² = 0.73) than in our study (adj. R² = 0.85) but still convincing.

Nevertheless, the statistically highly significant regression found between annual NEP<sub>yr</sub> and DR<sub>yr</sub> was expected to disappear with shorter integration times due to the increasing weight of the water-related changes of DR. However, this was not the case (Table 1). Our analyses have clearly shown that the relationship remained close from the annual to the half-hourly timescale, yet with a switch of the algebraic sign for the regression from positive to negative. This switch can be attributed to the changing weight of growth-related (positive regression) and water-related (negative regression) contributions to DR from long (annual) integration times to short ones (half-hourly).

**Approaching causalities on different timescales**

On an annual timescale, wood growth – known as the main C sink of a forest ecosystem (Barford et al., 2001; Rocha et al., 2006) – is the main driver of DR<sub>yr</sub> and NEP<sub>yr</sub> and therefore responsible for the close relationship between the two measures (Figure 5). However, the correlation between the two measures was closer than what has been reported from a tree ring study of Rocha et al. (2006) and it was also closer than what we have found from own
preliminary tree ring data (data not shown). Since DR includes not only woody growth but also the growth (and death) of phloem cells, we hypothesize that annual phloem size changes may have substantially contributed to the patterns found. However, at the current state of knowledge this remains speculation because there is little data available about inter-annual phloem size changes (Gricar & Cufar, 2008; Gricar et al., 2009). Interesting is that neither

\[ GPP_{yr} \] nor \[ TER_{yr} \] showed a similar close relationship to \[ DR_{yr} \] at this timescale (Table 1). This supports recent findings that wood growth is not directly controlled by \[ GPP \] (Rocha et al., 2006; Stoy et al., 2009) but involves complex processes such as carbohydrate storage and allocation (Hoch et al., 2003; Carbone et al., 2007). Wood growth is thus affected by environmental conditions that occurred weeks, months or years ago (Gough et al., 2008).

Overall, it became evident that wood and phloem growth, independent of water-related fluctuations of \[ DR \], represented \[ NEP \] up to an unexpectedly high degree on the annual scale.

On a monthly scale, a mixture of growth- and water-related processes determined \[ DR_m \] with distinctly differing ratios in summer and winter. The combination of the two processes was therefore also responsible for the close relationship between \[ DR_m \] on the one hand and \[ NEP_m \], \[ GPP_m \] and \[ TER_m \] on the other hand (Table 1). Only on this timescale all three EC-based measures showed significant correlations to \[ DR \]. The reason for that is not completely clear to us but might have something to do with the split contributions of growth and tree water relations to \[ DR_m \]. During the summer, \[ DR_m \] increased up to 750 µm per month (Figure 4), of which about two thirds are attributable to radial growth and one-third to water-related fluctuations (Zweifel & Häslar, 2001). Positive \[ NEP_m \] in summer are thus linked to good wood growth conditions and water relations that do not induce large \[ DR_m \]-reducing tree water deficits (Zweifel et al., 2005). Such conditions lead to increased \[ NEP_m \], \[ GPP_m \] and \[ TER_m \], however, obviously in a ratio that favours assimilation over respiration as the positive \[ NEP_m \] show (Figure 4).
In winter, $DR_m$ decreased with up to 400 µm per month (averages, Figure 4) and even more than 1000 µm for individual trees (Zweifel & Häsl er, 2000; Zweifel & Häsl er, 2001). There was no growth at that time of the season and the shrinkage is mainly attributable to freezing processes in the stem which lead to a very rapid dehydration of the elastic bark tissue with a consequent decrease of $DR$ (Zweifel & Häsl er, 2000). This winter shrinkage is thus a water-related process, although it is mainly induced by freezing temperatures (Ameglio et al., 2001; Mayr et al., 2007). The negative $NEP_m$ in winter, when $TER_m$ exceeds $GPP_m$ as reported before by e.g. Monson et al. (2006) or Lipson et al. (2009), was not a priori expected to be so closely linked to the negative $DR_m$ since lower temperatures should also lead to decreasing respiration (Schwalm et al., 2010). Thus, we expected smaller and not bigger $TER_m$, as it was measured in this study in the form of negative $NEP_m$ (Figure 3).

Furthermore, this finding at the monthly scale produces an apparent discrepancy to the winter findings at shorter timescales as it is discussed below. As a synthesis of the monthly resolved results we can say that growth and water-related processes of trees in summer and temperature-induced, water-related processes in winter contributed to the close relationships measured. A clear mechanism, however, that explains these correlative findings with physiological causes and effects awaits further research.

On a half-hourly timescale, the relationship between $DR_{hh}$ and $NEP_{hh}$ is highly water-related due to the influence of changing water contents on mainly the bark and thus $DR$ (Steppe et al., 2006; Zweifel et al., 2007). In contrast to longer integration times investigated, the linear regression was found to be negative (Figure 3), what is not surprising when considering the dominant physiological processes at this temporal scale. The sunnier the conditions, the more the trees are transpiring and consequently, the more depleted get the tree-internal water storages e.g. in the bark (Steppe et al., 2006). The same conditions also lead to higher assimilation rates by photosynthesis and consequently to an increased ecosystem CO$_2$
uptake in parallel to shrinking stem radii. This relationship can be altered by drought stress-
related stomatal closure (Pena-Rojas et al., 2004; Buckley, 2005). Although midday stomatal
closure on sunny days have been reported for the trees at our site (Zweifel et al., 2002), it did
apparently not reduce $NEP_{hh}$ to an extent that would have forced the discussed relationship to
disappear. Overall, the longer and more pronounced the stems were shrinking over a day, the
larger was the assimilation and therefore $NEP_{hh}$ (Figures 3 and 6). A causal link between $DR_{hh}$
and $NEP_{hh}$ must have, thus, to do with biotic and physical conditions (Stoy et al., 2009) that
induce large diurnal stem fluctuations which do not only represent the trees net assimilation
but also the productivity of the entire forest ecosystem. This general relationship between
$DR_{hh}$ and $NEP_{hh}$ has been found to be true for days with temperatures above the freezing point
and is further supported by the close correlation between $DR$ and $GPP$ at the half-hourly scale
(Table 1).

**Exception and anomalies**

There are exceptions from the discussed general relationship between $DR$ and $NEP$.
Such anomalies indicate that the two measures have similar drivers but may be only indirectly
linked to each other. One such exception to be discussed here is the month of May. May is the
month with the highest $NEP_m$ on average, but with little change in $DR_m$ (Figure 4). Wood
growth has not started yet but stem rehydration of the winter shrinkage, which mostly occurs
in April at this site, has nearly finished. This succession of first rehydration of the stem and
second initial wood growth has been found in other studies as well (Larcher, 2003; Monson et
al., 2005; Zweifel et al., 2006) and shows, besides the well-known limitations by temperature
(Rossi et al., 2008), the importance of balanced tree water relations for initiating wood growth
(Lockhart, 1965; Steppe et al., 2006; Steppe et al., 2008; Turcotte et al., 2009). The
relationships of $DR_m$ to $GPP_m$ and $TER_m$, respectively, were much less affected by the month
of May (data not shown). In combination, however, the increased $GPP_m$ and the slightly
decreased TER_m led to the over-proportional large NEP_m in relation to DR_m. This delay of radial wood growth after NEP_m explains, at least partially, the somewhat disturbed relationship between DR_m and NEP_m in May (Figure 3, Table 1) and is a strong indication for two, at least partially decoupled, mechanisms determining DR_m and NEP_m from the same climatic drivers.

In contrast to what was discussed for monthly values in wintertime, half-hourly DR_{hh} and NEP_{hh} were found to be uncorrelated on days with freezing conditions (Figure 3d). This anomalous short-term behaviour can be interpreted as a stem dehydration effect which decouples frost-induced stem radius fluctuations from respiration processes and thus NEP_{hh}. This should not be surprising per se since DR is expected to be decoupled from transpiration (and photosynthesis) under such cold conditions, and a direct coupling between DR and transpiration (and thus NEP) is only expected during the physiologically active period (Zweifel & Häslar, 2000). However, surprising is that despite this short-term decoupling of DR_{hh} from NEP_{hh}, dehydrated stems at cold temperatures tend to lead to a higher winter ecosystem respiration on a monthly scale. The increased ecosystem respiration might in this case not be functionally linked to stem physiological processes.

The ecological relevance of DR measurements for NEP

In summary, DR is, with some reservations, closely correlated to NEP at all timescales investigated. This is not explicable in detail with mechanisms and it is not necessarily what was expected beforehand. It raises, however, the question, why NEP measured by EC over this ecosystem seems to be mostly driven by the metabolism of the trees. Other components of the ecosystem, namely heterotrophic (soil respiration) and understory vegetation could have added substantial contributions to NEP (Carbone et al., 2007; Paterson et al., 2009; Subke et al., 2009). Hence, our results suggest that these contributions are proportional to the changes in stem radius. From this we can deduce that other ecosystem components
contributed either very little to \( \text{NEP} \) or more likely, they contributed mostly in phase with the mature trees measured. A similar close relationship was found in a boreal forest in central Manitoba, Canada (Rocha et al., 2006). This may be a coincidence, or more likely, a characteristic of these subalpine (Davos) and boreal (Manitoba) regions and may differ in lowland deciduous forests where spring ephemerals can be a relevant short-term C sink which is not synchronous with the dominant tree species (Knohl et al., 2003). Particularly, the freezing conditions in winter and spring seem to play an important role for the annual \( DR_{yr} \) and \( NEP_{yr} \) as indicated by the high predictive power of the compensation day of the cumulative winter respiration (Table 1). Overall, the course of \( DR \) appeared to be a fingerprint of the ecosystem’s \( NEP \) at all temporal scales investigated, describing the short-time metabolism, the tree water relations and most remarkably the annual ecosystem productivity.

Conclusions

\( NEP \) of the subalpine coniferous forest Seehornwald Davos in the Swiss Alps, is intriguingly highly predictable from \( DR \) at various integration times. This strong correlation between an integrative measure of \( NEP \) (which represents the whole ecosystem) and a measure from individual trees (\( DR \), which reflects a subordinate component of the ecosystem) suggests that tree water-relations and stem growth are representative for the productivity of this forest ecosystem.

Two major physiological processes determine variations in \( DR \): tree water relations and stem growth, including wood and phloem tissue. Both fractions of \( DR \) have considerable explanatory power for \( NEP \). There is reasonable indication that phloem growth, so far an unquantifiable fraction of stem growth, could be a reason for the higher explanatory power of \( DR \) for \( NEP \) in comparison to the pure wood-related tree ring widths. The relationships between \( DR \) and \( NEP \), however, are a function of the timescale under consideration. In
general, we observed a shift from a water-related dominance on short-term DR changes towards a more growth-related dominance at seasonal to annual timescales.

Furthermore, tree physiological responses to winter and spring conditions seem to play a decisive role in the seasonal cycles of DR and NEP of this subalpine forest. However, some exceptions from the typically close relationship between DR and NEP also indicate that NEP is physiologically and mechanistically not directly but actually indirectly linked to DR via its climatic and biotic drivers. What the biotic drivers are and through what mechanisms they are linking DR and NEP needs to be subject of future investigations. Particularly, it remains to be tested at other localities, with different forest types and climates, whether such close correlations between DR and NEP are only specific to cold climates (subalpine, boreal) or whether they are more abundant.

Acknowledgments

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References


Table 1. Regression analyses for stem radius changes ($DR$) vs. net ecosystem productivity ($NEP$), gross primary production ($GPP$), and total ecosystem respiration ($TER$) on three different timescales. Data of the half hourly timescale is grouped into five classes of days: (I) sunny summer days, (II) cloudy summer days, (III) rainy summer days, (IV) winter days with an average temperature $> 0$ °C, and (V) winter days with an average temperature $< 0$ °C. Maximum stem contraction ($MSC$), maximum cumulative winter respiration ($WRES$), day of the year when $MSC$ ($DOY_{comp\_MSC}$) and when $WRES$ is compensated ($DOY_{comp\_WRES}$), C sink period ($CSP$), radial wood growth ($RWG$) period. Significant negative correlations are marked in grey.

<table>
<thead>
<tr>
<th></th>
<th>NEP adj. R$^2$</th>
<th>NEP P</th>
<th>GPP adj. R$^2$</th>
<th>GPP P</th>
<th>TER adj. R$^2$</th>
<th>TER P</th>
<th>DR adj. R$^2$</th>
<th>DR P</th>
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<tr>
<td><strong>Analyses on a half-hourly timescale</strong></td>
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<td>$DR_{hh(I)}$$^a$</td>
<td>0.59</td>
<td>$&lt;0.001$***</td>
<td>0.65</td>
<td>$&lt;0.001$***</td>
<td>0.01</td>
<td>0.21</td>
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<td>$DR_{hh(II)}$$^a$</td>
<td>0.43</td>
<td>$&lt;0.001$***</td>
<td>0.52</td>
<td>$&lt;0.001$***</td>
<td>0.00</td>
<td>0.28</td>
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<tr>
<td>$DR_{hh(III)}$$^a$</td>
<td>0.25</td>
<td>$&lt;0.001$***</td>
<td>0.31</td>
<td>$&lt;0.001$***</td>
<td>0.00</td>
<td>0.28</td>
<td>-</td>
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<tr>
<td>$DR_{hh(IV)}$$^a$</td>
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<td>0.008**</td>
<td>0.15</td>
<td>0.003***</td>
<td>0.00</td>
<td>0.28</td>
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<td>$DR_{hh(V)}$$^a$</td>
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<td>0.30</td>
<td>0.00</td>
<td>0.35</td>
<td>0.00</td>
<td>0.31</td>
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<td>0.47</td>
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<td>$DR_{m}$ (without May)</td>
<td>0.53</td>
<td>$&lt;0.001$***</td>
<td>0.53</td>
<td>$&lt;0.001$***</td>
<td>0.31</td>
<td>$&lt;0.001$***</td>
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<td>$DR_{yr}$</td>
<td>0.85</td>
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<td>0.35</td>
<td>0.03*</td>
<td>0.04</td>
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<td><strong>Analyses comparing specific periods and dates to annual measures</strong></td>
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<td>$MSC$</td>
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<td>-0.03</td>
<td>0.41</td>
<td>0.04</td>
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<td>0.01</td>
<td>0.32</td>
<td>0.08</td>
<td>0.21</td>
<td>0.37</td>
<td>0.03*</td>
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<td>0.01**</td>
<td>-0.02</td>
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<td>0.03*</td>
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<td>0.01**</td>
<td>-0.08</td>
<td>0.65</td>
<td>0.76</td>
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<td>0.1</td>
<td>0.57</td>
<td>$&lt;0.001$***</td>
<td>0.25</td>
<td>0.05*</td>
<td>0.04</td>
<td>0.25</td>
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<td>$RWG$ period</td>
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<td>0.64</td>
<td>-0.09</td>
<td>0.72</td>
<td>-0.11</td>
<td>0.9</td>
<td>-0.10</td>
<td>0.73</td>
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$^a$ Adj. R$^2$ and p were calculated separately for each day, and the median of the frequency distribution of all adj. R$^2$ and p per class for the years 1998-2008 is shown.
Figure 1. Satellite image, location of flux tower (cross), and footprint area of Seehornwald Davos computed with the Kljun et al. (2004) footprint model. The isolines show lines of equal relative footprint weights with respect to the point of maximum contribution during the time interval 1997-2004. The 20% and 50% relative contribution lines are drawn with bold lines. Background image © 2010 swisstopo (JD082776).
Figure 2. Definitions of measures and periods for a) the dendrometer measurements and b) the eddy covariance measurements: cumulative stem radius changes ($DR_{\text{sum}}$), radial stem increment over the year ($DR_{\text{yr}}$), maximum winter stem contraction ($MSC$), day of the year when $MSC$ is compensated ($DOY_{\text{Comp\_MSC}}$), radial wood growth period (RWG period), cumulative net ecosystem productivity ($NEP_{\text{sum}}$), ecosystem productivity over the year ($NEP_{\text{yr}}$), maximum winter respiration ($WRES$), and day of the year when $WRES$ is compensated ($DOY_{\text{Comp\_WRES}}$). The zero-line of the current year corresponds to the respective culmination point of the past year.
Figure 3. Stem radius changes ($DR$) of Norway spruce trees and the corresponding net ecosystem productivity ($NEP$) on three different timescales. **a)** Annual values (subscript yr) from 1998 to 2008 (adj. $R^2=0.85$). The years 2007 and 2008 after the harvesting in one part of the footprint in autumn 2006 are depicted with squared symbols. **b)** Monthly values (subscript m); May values are shown as light grey shaded circles. **c)** Half-hourly values (subscript hh). Shown are the sunny summer days of 2004 (day class I) and **d)** the corresponding values from winter days with an average day temperature below the freezing point (day class V). Statistical analyses can be found in Table 1.
Figure 4. Averaged monthly values of a) temperature and precipitation, and b) net ecosystem productivity (NEP) and stem radius changes (DR) of a Norway spruce forest over eleven years (1998-2008). NEP and DR are given as changes per month (subscript m) and cumulative curves (subscript sum). c) NEP-relevant periods of the year (WRES = winter respiration) and d) DR-relevant periods. For details about the definitions of these periods refer to Figure 2.
Figure 5. Eddy covariance (EC) based net ecosystem productivity (\(NEP_{sum}\), positiv values = C sink) in comparison to point dendrometer records (\(DR_{sum}\)) and climatic factors at the subalpine research site, Seehornwald, Davos. 

a) \(NEP_{sum}\) and \(DR_{sum}\) are shown as annual cumulative values from 1997 to 2008. 

b) Air temperatures at 35 m above ground (tree tops at about 27 m) and soil temperatures 0.1 m below ground, and 
c) cumulative sum of rain represent the climatic conditions within this period.
Figure 6. Relationship between the net ecosystem productivity ($NEP_{hh}$) and the stem radius changes ($DR_{hh}$) on a half-hourly timescale for three days in June 2001. The ecosystem turns into a C source at the time when the stems start to expand due to the replenishment of their bark tissue and it becomes a C sink at the moment the trees start to shrink.