

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

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- 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 net ecosystem productivity (NEP) which integrates fluxes over the entire forest ecosystem. Here, we investigated the unexpectedly close relationship between NEP and DR and asked for causalities.
- NEP (positive values indicate carbon sink) measured by eddy covariance over 11 yr was analysed at three time scales alongside automated point dendrometer DR data from a Swiss subalpine Norway spruce forest.
- On annual and monthly scales, the remarkably close relationship between NEP and DR was positive, whereas on a half-hourly scale the relationship was negative. Gross primary production (GPP) had a similar explanatory power at shorter time scales, but was significantly less correlated with DR on an annual scale.
- The causal explanation for the NEP–DR relationship is still fragmentary; however, it is partially attributable to the following: radial stem growth with a strong effect on monthly and annual increases in NEP and DR; frost-induced bark tissue dehydration with a parallel decrease in both measures on a monthly scale; and transpiration-induced DR shrinkage which is negatively correlated with assimilation and thus with NEP on a half-hourly scale.

Introduction

Eddy covariance (EC) CO₂ flux measurements allow the quantification of net ecosystem productivity (NEP). However, they represent net carbon fluxes and thus do not allow a direct quantification of flux components, that is, the contributions of vegetation vs soil or of wood vs leaves and fruits (Buchmann & Schulze, 1999; Baldocchi, 2003). EC measurements provide an integrated view of net CO₂ fluxes in and out of a (forest) ecosystem by including different CO₂ sources and sinks within the so-called flux footprint (Schmid, 2002). The CO₂ sources (respiration) and CO₂ sinks (assimilation) are large budget components of opposite directions that sum to a relatively small NEP over a year (Barford *et al.*, 2001; Körner *et al.*, 2005; Navarro *et al.*, 2008). As the net balance of these components is measured directly with EC, it is generally assumed that the accuracy

of the annual estimates of NEP should be better than the accuracy of the estimates of the two large components [gross primary production (GPP) and total ecosystem respiration (TER)] separately (Buchmann & Schulze, 1999). The main carbon sink of a forest is usually represented by the assimilation of trees, leading to an accumulation of biomass (wood, leaves, fruits, etc.). This carbon sink is balanced by the carbon losses via the respiration of living tissues, and the carbon losses from soils (Monson *et al.*, 2006), including the decomposition of biomass and soil organic matter (Damesin *et al.*, 2002).

By adding point dendrometers for the continuous measurement of stem radius changes (DR) of trees within the footprint area of an EC site, we can obtain independent information about one of the dominant carbon sinks of the ecosystem, that is, wood and phloem growth of trees. The tree stem biomass-related accumulation of carbon has

been 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 in the long term. Continuous DR measurements allow for an intra-annually resolved interpretation of growth processes and the investigation of tree water relations as a result of the (under-) pressure-related swelling and shrinking of bark (Steppe *et al.*, 2006).

Generally, DR is determined by stem water content and wood and bark growth, including the degradation of dead phloem cells. The water-related fraction is a short-term effect lasting over hours to weeks that can either have positive or negative effects on stem radius depending on the changing turgor of stem tissues (Zweifel *et al.*, 2001). Mainly the phloem (contributes > 90% to the total change in 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 are replenished during 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 tree water deficits lasting several weeks with shrinking stems even during the wood growth period (Zweifel *et al.*, 2006). In addition to this diurnal rhythm, 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 become lignified and die when mature and the stem size is no longer altered by these woody structures. In addition, their response to tissue saturation changes is then strongly reduced and DR is only affected by minimal changes in cell wall sizes as a result of water content variations. By contrast, phloem cells remain elastic and undergo diurnal water-related size changes even when mature and, after a few years, they die, shrink and, finally, are shed (Lockhart, 1965; Gricar *et al.*, 2009). Continuously measured DR therefore has 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 on how integrated ecosystem measures, such as NEP, can be related to tree physiological processes of growth at various time scales (Barford *et al.*, 2001; Gough *et al.*, 2008, 2009; Rocha & Goulden, 2009). Thus, to the best of our knowledge, our study is the first to address the relationship between continuously changing stem radii and corresponding ecosystem productivity over integration times from 30 min 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 NEP patterns (and its derived quantities GPP and TER) on the basis of underlying tree physiological processes that distinguish between growth (xylem and phloem) and water-related changes in DR (Steppe *et al.*, 2006; Zweifel *et al.*, 2006).

Here, we analyse two long-term datasets 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 annual (DR_{yr} vs NEP_{yr}), monthly (DR_m vs NEP_m) and half-hourly (DR_{hh} vs NEP_{hh}) data integration times over 11 yr. We ask to what degree the relationship between DR and NEP is of a correlative nature and what aspects of it can be explained by causal mechanisms. Thus, we analyse the general relationships between DR and NEP and also their most prominent anomalies at three time scales. Further, we test the hypothesis that a close link between DR and NEP vanishes at time scales below annual resolution. This is expected because of the decreasing impact of wood growth and the increasing impact of tree water relations on DR at shorter integration times. We compare the results for NEP with the results for GPP and TER and discuss to what degree the relationships are explicable by physiological processes. Finally, we test the hypothesis that annual stem growth only rudimentarily explains NEP because of the many other components contributing to the carbon balance of a forest ecosystem.

Materials and Methods

Site description

The Seehornwald Davos research site (Fig. 1) is located at 1640 m a.s.l. 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 to be moderately productive in the regional context at this altitude. The tree age of the dominant trees ranges between 200 and 400 yr. European larch (*Larix decidua* Miller) plays only a marginal role with < 1% abundance. The understorey vegetation is rather patchy, covering *c.* 30% of the surface, and is mainly composed of dwarf shrubs, primarily *Vaccinium myrtillus* and *Vaccinium gaultherioides*, as well as mosses. Sustainable forest management was introduced in Switzerland in 1876, in the same year that instrumental records of climate variables started at Davos. For a documented period over the last 21 yr, only seven of 500 trees on the 0.6-ha long-term ecosystem monitoring plot have been removed from the site, most following a severe storm in 1990. At the end of October 2006, an area of 25 × 70 m (1750 m²) within the north-east part of the EC footprint was harvested. This area was estimated to have a contribution of *c.* 20–30% to the EC measurements before cutting.



Fig. 1 Satellite image, location of flux tower (cross) and footprint area of Seehornwald Davos, Swiss Alps, computed with the footprint model of Kljun *et al.* (2004). 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 in bold. Background image © 2010 swisstopo (JD082776).

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 (DR, *difference in radius over time*) were measured with 12 automated point dendrometers every 10 s and averaged every 30 min. Some sensors failed for a certain time or were mounted at different locations within the investigated research period of 11 yr. However, between eight and 12 sensors were permanently mounted at stems *c.* 1.5 m above ground level. Analyses and graphs were performed with averaged DR values of 8–12 individual trees. The original type of dendrometer (LVTD; Agricultural Electronics Corporation, Tucson, AZ, USA; measured temperature sensitivity, $0.5 \mu\text{m } ^\circ\text{C}^{-1}$) has been successively replaced by a less temperature sensitive type (ZB06; Zweifel Consulting, Hombrechtikon, Switzerland; measured temperature sensitivity, $0.27 \mu\text{m } ^\circ\text{C}^{-1}$), starting in 2006. The temperature sensitivity was corrected for both instruments accordingly.

EC flux measurements and microclimatic profile

Turbulent fluxes of CO_2 and H_2O were measured on a 35-m-tall tower with a Solent R2 ultrasonic anemometer–thermometer (Gill Instruments Ltd, Lymington, UK) and a Li-Cor 6262 (Li-Cor, Lincoln, NE, USA) closed-path infrared gas analyser (IRGA) from 1997 to 2005 and an open-path system (Li-Cor 7500) from 2005 onwards, 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 performed on 9–10 August 2005. The ultrasonic anemometer–thermometer was replaced by its successor model Solent R3-50 (Gill Instruments Ltd) on 19–20 December 2006. As open-path systems and closed-path systems require 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 Li-Cor 7500 analyser (Burba *et al.*, 2006, 2008) had to be incorporated in our data processing. We used the fitting method described in Järvi *et al.* (2009), based on an empirically approximated temperature difference between the instrument and air as reported for a different locality (Rogiers *et al.*, 2008). The fraction of heat flux produced by the open-path instrument ξ was set to 0.085 as suggested for a forest ecosystem by Järvi *et al.* (2009). This approach closely follows Burba *et al.* (2006, 2008) with a site-specific correction factor for sensor tilt angle (see eqn 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 IRGAs, respectively, and density fluctuation effects (Webb *et al.*, 1980; only applied in the case of the open-path instrument). EC data were processed according to the CarboEurope standard methodology which is based on Aubinet *et al.* (2000). Thirty minute averages of CO_2 fluxes were calculated by the in-house software *ethflux*. Details on 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 good agreement with the reference software TK2 over tall vegetation, with *ethflux* estimates being only slightly larger than those of TK2 (Mauder *et al.*, 2008).

In addition, CO_2 concentrations have been 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 obtain a homogeneously treated dataset and as the storage term had only a minor influence on the carbon budget ($< 1 \text{ g C m}^{-2} \text{ yr}^{-1}$), we have not corrected EC fluxes for the storage term since the start of profile measurements. However, we used the 35-m CO_2 concentration from the profile system as a reference for the older Li-Cor 6262 EC IRGA to correct for sensor drift and pressure effects that resulted from the fact that Li-Cor 6262 was always calibrated with zero and span gases at low flow rates, but was operated at high flow rates in EC 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

Li-Cor 6262. For the years 1997–99 and early 2000 before installation of the profile system, the seasonal trend of CO₂ measured from 2000 to 2005 was projected backwards in time and used for drift correction. This correction was performed on annual data (more frequently in 1997). Thus, the working dataset used for this study is consistent with the increase in annual CO₂ concentrations since 1997 and the pronounced seasonality of CO₂ 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 between temperature-normalized night-time fluxes and 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 the possible underestimation of nocturnal respiration by the EC method. Data gaps of < 2 h were linearly interpolated, longer day-time gaps were filled with logistic sigmoid light response curves (A.M. Moffat, pers. comm.), 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 two main wind directions from the north-east and south-west (Fig. 1). Flux footprint computations with the parameterized 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 south-west of the tower (Fig. 1). No influence was found from the nearby lake, clearly outside the footprint area. Recently started advection experiments do not indicate a major bias for long-term NEP estimates (data not shown) but, on completion, will allow us to reassess the absolute numbers presented here.

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

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 winter time, the starting point for annual radial stem increments (DR_{yr}) was set to the culmination point of the cumulative DR curve of the previous year (zero-line in Fig. 2).

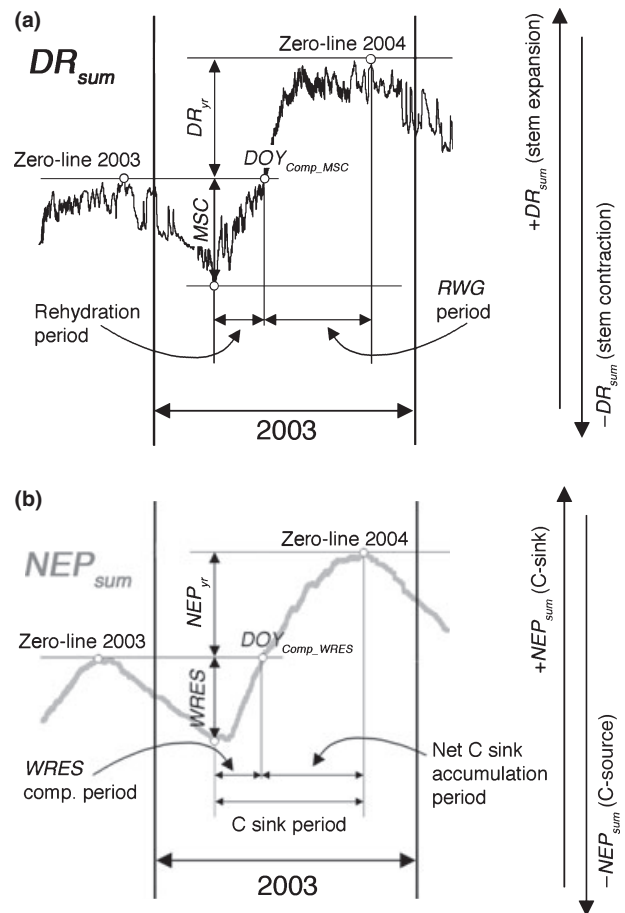


Fig. 2 Definitions of measures and periods for dendrometer measurements (a) and eddy covariance measurements (b): cumulative stem radius changes (DR_{sum}), radial stem increment over the year (DR_{yr}), maximum winter stem contraction (MSC), day of year when MSC is compensated (DOY_{Comp_MSC}), radial wood growth period (RWG period), cumulative net ecosystem productivity (NEP_{sum}), ecosystem productivity over the year (NEP_{yr}), maximum winter respiration (WRES), and day of year when WRES is compensated (DOY_{Comp_WRES}). The zero-line of the current year corresponds to the respective culmination point of the past year.

Coupled with this definition is the assumption that shrinking stems never loose wood volume; instead, they shrink as a result of 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 of decomposing phloem tissue. The DR zero-line represents the stem status at which stem contractions of the previous winter are 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 carbon sink) of the previous year (Fig. 2). The NEP zero-line therefore represents the ecosystem status at which cumulative net respiration of the previous winter is compensated and positive values indicate a net ecosystem carbon sink in the current year.

These predispositions explain why cumulative curves of DR_{sum} and NEP_{sum} do not begin at zero on 1 January. In addition to 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 1 January to 31 December, the definition used here is physiologically more meaningful and essential for comparing NEP with DR. The periods of GPP_{yr} and TER_{yr} correspond to NEP_{yr} .

Furthermore, the period during which the maximum stem contraction (MSC) in winter time recovers is defined as the winter rehydration period according to Zweifel & Häslér (2000). It ends with the date at which DR_{sum} crosses the zero-line into the positive range. Accordingly, this end point is the day of the year at which 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 winter respiration (WRES) recovers is defined as the WRES compensation period, ending with the day of the year at which WRES is compensated (DOY_{comp_WRES}). The period between DOY_{comp_WRES} and the time at which NEP_{sum} reaches its maximum is referred to as the 'net carbon sink accumulation period' hereafter. The period between the minimum

and maximum NEP_{sum} is defined as the carbon sink period (CSP) (Fig. 2).

Results

Close relationship between DR and NEP independent of integration times

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

GPP and TER are derived quantities from NEP and are therefore not independent measures. However, they showed a different relationship to DR compared with NEP (Table 1). GPP was as closely correlated as NEP with DR

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 time scales

| | NEP | NEP | GPP | GPP | TER | TER | DR | DR |
|--|------------|-------------|------------|-------------|------------|-------------|------------|-------------|
| | adj. R^2 | P | adj. R^2 | P | adj. R^2 | P | adj. R^2 | P |
| Analyses on a half-hourly time scale | | | | | | | | |
| $DR_{hh(I)}^a$ | 0.59 | < 0.0001*** | 0.65 | < 0.0001*** | 0.01 | 0.21 | – | – |
| $DR_{hh(II)}^a$ | 0.43 | < 0.0001*** | 0.52 | < 0.0001*** | 0.00 | 0.28 | – | – |
| $DR_{hh(III)}^a$ | 0.25 | < 0.001*** | 0.31 | < 0.001*** | 0.00 | 0.28 | – | – |
| $DR_{hh(IV)}^a$ | 0.12 | 0.008** | 0.15 | 0.003** | 0.00 | 0.28 | – | – |
| $DR_{hh(V)}^a$ | 0.00 | 0.30 | 0.00 | 0.35 | 0.00 | 0.31 | – | – |
| Analyses on a monthly time scale | | | | | | | | |
| DR_m | 0.35 | < 0.0001*** | 0.47 | < 0.0001*** | 0.30 | < 0.0001*** | – | – |
| DR_m (without May) | 0.53 | < 0.0001*** | 0.53 | < 0.0001*** | 0.31 | < 0.0001*** | – | – |
| Analyses on an annual time scale | | | | | | | | |
| DR_{yr} | 0.85 | < 0.001*** | 0.35 | 0.03* | 0.04 | 0.27 | – | – |
| Analyses comparing specific periods and dates with annual measures | | | | | | | | |
| MSC | 0.27 | 0.06 | –0.03 | 0.41 | 0.04 | 0.26 | 0.40 | 0.02* |
| DOY_{comp_MSC} | 0.39 | 0.02* | 0.01 | 0.32 | 0.08 | 0.21 | 0.37 | 0.03* |
| WRES | 0.51 | 0.01** | –0.02 | 0.38 | 0.22 | 0.08 | 0.38 | 0.03* |
| DOY_{comp_WRES} | 0.88 | < 0.001*** | 0.51 | 0.01** | –0.08 | 0.65 | 0.76 | < 0.0001*** |
| CSP | 0.18 | 0.1 | 0.57 | < 0.001*** | 0.25 | 0.05* | 0.04 | 0.25 |
| RWG period | –0.08 | 0.64 | –0.09 | 0.72 | –0.11 | 0.9 | –0.10 | 0.73 |

Data of half-hourly time scales are grouped into five classes of days: I, sunny summer days; II, cloudy summer days; III, rainy summer days; IV, winter days with average temperature $> 0^\circ\text{C}$; V, winter days with average temperature $< 0^\circ\text{C}$. Maximum stem contraction (MSC), maximum cumulative winter respiration (WRES), day of year when MSC (DOY_{comp_MSC}) and WRES (DOY_{comp_WRES}) are compensated, carbon sink period (CSP), radial wood growth (RWG) period. Significant negative correlations are marked in grey (* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$). ^aAdj. 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.

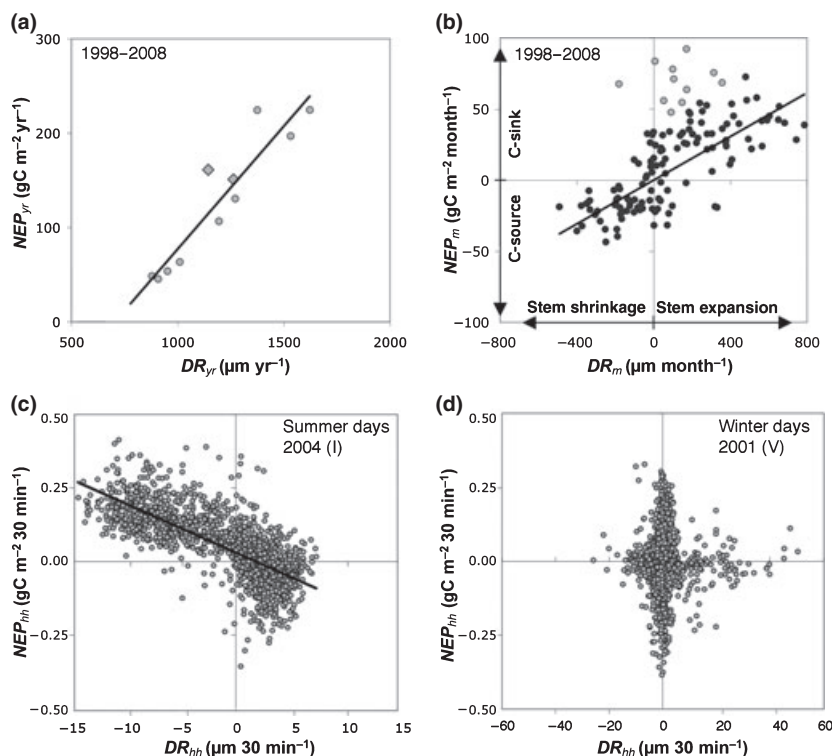


Fig. 3 Stem radius changes (DR) of Norway spruce (*Picea abies*) trees and corresponding net ecosystem productivity (NEP) on three different time scales. (a) Annual values (subscript 'yr') from 1998 to 2008 (adj. $R^2 = 0.85$). The years 2007 and 2008, that is, after harvesting in one part of the footprint in autumn 2006, are depicted with diamond symbols. (b) Monthly values (subscript 'm'); May values are shown as light grey circles. Half-hourly values (subscript 'hh') for the sunny summer days of 2004 (day class I) (c) and for winter days with average day temperatures below the freezing point (day class V) (d). Statistical analyses and details for the day classes can be found in Table 1.

on short time scales, but this close relationship was lost on annual scales. One exception was the relationship of GPP to CSP, which was closer than that of NEP to CSP. TER correlated with DR on monthly scales only.

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

Annual and monthly time scales

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 as the period of radial growth (c. 3 months; Fig. 4) was much shorter than the period in which ecosystem assimilation exceeded respiration (CSP, c. 7 months; Fig. 4). Also remarkable was the observation that the close annual correlation between DR_{yr} and NEP_{yr} was not explicable with

GPP and TER *per se* (Table 1), as these measures were not related to DR_{yr} (TER) or not as well (GPP) as NEP_{yr} . On monthly time scales, even negative DR_m values fitted very well into the regression between DR_m and NEP_m (Fig. 3b), because shrinking stems induced by freezing temperatures went in parallel with ecosystem carbon losses as a result of an increased ratio of respiration to assimilation in winter months (Fig. 4).

Relying on the definitions shown in Fig. 2, the recurrent annual patterns started with shrunken stems (negative DR_{sum}) and a carbon balance deficit (negative NEP_{sum}) in January (Figs 4, 5). This meant that tree stems lost volume from the previous year's maximum stem size. Correspondingly, the ecosystem was a net carbon source from the previous year's maximum NEP_{sum} . In February–March, DR_{sum} started to increase and, on average, c. 1 month later NEP_{sum} followed (Fig. 4). During the period of negative but increasing DR_{sum} , stem expansion is defined as recovery from current tree water deficits (mainly in the bark) and is not attributable to growth in a physiological sense (Fig. 2). Accordingly, negative but increasing NEP_{sum} indicated the ecosystem's recovery from WRES carbon losses and could not be attributed to the net carbon sink. Both curves, DR_{sum} and NEP_{sum} , crossed the respective compensation points (DOY_{Comp_MSC} and DOY_{Comp_WRES}), on average, within 4 d around May/June. However, the variation among years was large. The maximum deviation occurred in 1999 with 56 d when, extraordinarily, much snow covered the forest floor until mid-May (data not shown). The

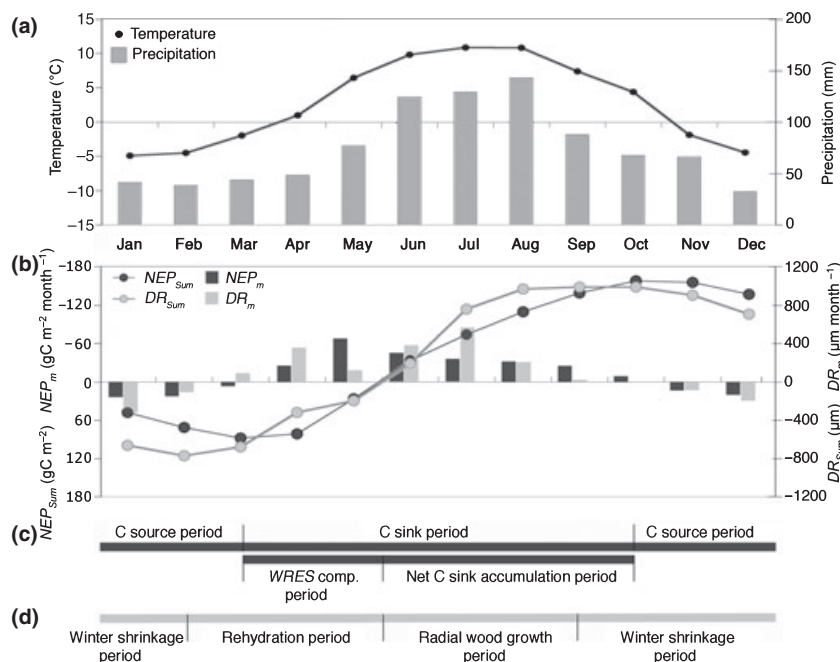


Fig. 4 Averaged monthly values of temperature (circles) and precipitation (bars) (a) and net ecosystem productivity (NEP) and stem radius changes (DR) (b) of a Norway spruce (*Picea abies*) forest over 11 yr (1998–2008). NEP and DR are given as changes per month (subscript 'm') and cumulative curves (subscript 'sum'). NEP-relevant periods of the year: C source period, period in which the ecosystem respiration exceeds the total ecosystem assimilation; C sink period, period in which assimilation exceeds respiration; winter respiration compensation (WRES comp.) period, period in which the respiration excess of the winter months is compensated; net C sink accumulation period, period in which the ecosystem is a net C sink (c). DR-relevant periods: winter dehydration period, period in which tree stems are shrinking due to freezing processes; rehydration period, period in which tree stems are expanding due to rehydration processes of the bark; radial wood growth period, period in which stems are expanding due to stem tissue growth (d).

maximum stem radii were reached in August–September, whereas the culmination point of NEP_{sum} was reached 1–2 months later in October–November (Fig. 4). During the winter months, DR_{sum} shrank disproportionately rapidly at temperatures below the freezing point.

Half-hourly time scale

On half-hourly time scales, the negative regression between DR_{hh} and NEP_{hh} was consistent over the entire year, except for days with averaged daytime temperatures < 0°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, 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, Fig. 3d). This ranking of grouped days corresponded to 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 (Fig. 5). This was true for annual extremes, for year-specific characteristic patterns within the season and, in part, also for processes during a day (Fig. 6). For summer days, the onset of net CO₂

uptake (positive NEP_{hh}) occurred almost at the same time as when stems started to shrink, and the highest NEP_{hh} values occurred always when the stems were shrinking. When stems started to expand again in the afternoon, NEP_{hh} also changed its sign, and the ecosystem became a net carbon source.

Winter and spring processes as indicators of NEP_{yr}

In addition to the close relationships between DR and NEP of the 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). Cumulative WRES of the ecosystem provided good explanatory power. WRES is already known in March 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 NEP_{yr} and DR_{yr} of the corresponding season. No correlation was found between WRES and GPP_{yr} or TER_{yr} (Table 1). Even better predictions were possible with the day of year when cumulative WRES was compensated by assimilation (DOY_{Comp_WRES}). The earlier WRES was compensated, the larger were 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. $R^2 = 0.51$, $P < 0.01$).

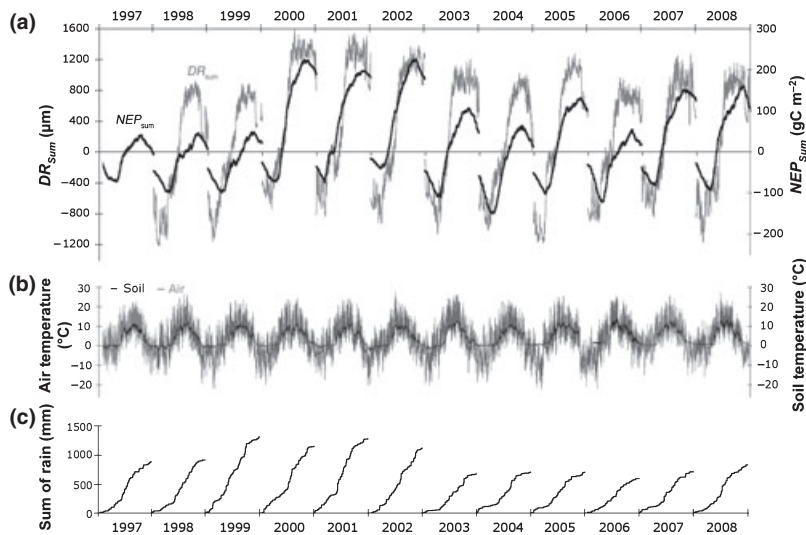


Fig. 5 Eddy covariance (EC)-based net ecosystem productivity (NEP_{sum} , positive values indicate carbon sink) in comparison with point dendrometer records (DR_{sum}) and climatic factors at the subalpine research site, Seehornwald Davos, Swiss Alps. (a) NEP_{sum} and DR_{sum} are shown as annual cumulative values from 1997 to 2008. Air temperatures at 35 m above ground (tree tops at c. 27 m) and soil temperatures 0.1 m below ground (b) and cumulative sum of rain (c) represent the climatic conditions within this period.

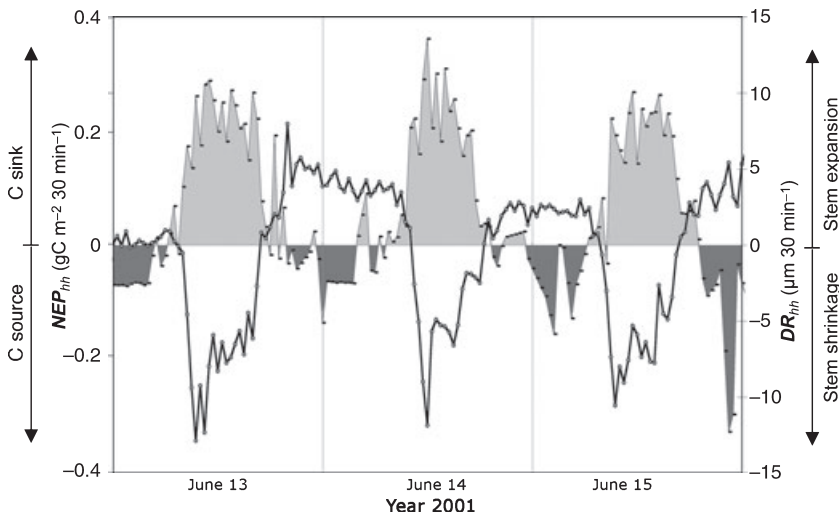


Fig. 6 Relationship between net ecosystem productivity (NEP_{hh} ; grey symbols, bold line) and stem radius changes (DR_{hh} ; black symbols, grey line) on half-hourly time scales for 3 d in June 2001 at the subalpine research site, Seehornwald Davos, Swiss Alps. The ecosystem turns into a carbon (C) source (dark grey) at the time at which stems start to expand as a result of replenishment of their bark tissue, and becomes a carbon sink (light grey) at the moment when trees start to shrink.

MSC in winter 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, the smaller NEP_{yr} and DR_{yr} . The earlier MSC was compensated in a year, the larger NEP_{yr} and DR_{yr} . The length of CSP (Table 1) was less well related to either NEP_{yr} or DR_{yr} . However, GPP_{yr} and TER_{yr} were significantly correlated with CSP. No explanatory power was found for the RWG period.

Discussion

The comparison of continuous stem radius changes (DR) of individual trees and the EC-based NEP of the corresponding forest ecosystem revealed an intriguingly close relationship between the two measures DR and NEP on three different time scales (Table 1). This close relationship was not expected *a priori* as one measure (DR) is an averaged physiological response of individual mature

trees, whereas the other (NEP) integrates over the entire ecosystem represented in the EC footprint (Kljun *et al.*, 2004). This finding is even more surprising when considering that DR is the product of growth and water-related processes in the stem and that both processes contribute to the close relationship to NEP with changing weights depending on integration time. There is no simple physiological approach available that could fully explain this relationship in all of its detail (Table 1). However, there is good evidence that at least part 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 with either statistical (Zweifel *et al.*, 2005; Deslauriers *et al.*, 2007) or process-based (Zweifel *et al.*, 2007; Steppe *et al.*, 2008) modelling approaches. However, such a distinction is never absolutely precise and depends, 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 the importance of growth-related processes in DR (Zweifel *et al.*, 2006; Steppe *et al.*, 2008). Conversely, the shorter the time period, the stronger the influence of water-related processes (Zweifel *et al.*, 2001). This is particularly true for our slow-growing spruce trees with a maximum growth rate of *c.* 10–20 $\mu\text{m d}^{-1}$ (data not shown), whereas water-related changes in DR are a magnitude larger at 100–300 $\mu\text{m d}^{-1}$ (Zweifel & Häsler, 2001). Understanding how these two integration time-dependent processes alter DR is essential for the physiological interpretation of relationships between DR and NEP.

Close relationship between DR and NEP

As NEP represents the budget of CO₂ fluxes in and out of the ecosystem, it was reasonable to expect that only long-term, growth-related (and thus carbon-related) fractions of DR would show a close relationship with NEP. Such a relationship on an annual time scale has been reported previously 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 ($R^2 = 0.73$) than in our study (adj. $R^2 = 0.85$), but still convincing. Nevertheless, the statistically highly significant regression found between annual NEP_{yr} and DR_{yr} was expected to disappear with shorter integration times as a result of the increasing weight of water-related changes of DR. However, this was not the case (Table 1). Our analyses have clearly shown that the relationship remained close from annual to half-hourly time scales, yet with a switch of the algebraic sign for the regression from positive to negative. This switch can be attributed to the changing weights of growth-related (positive regression) and water-related (negative regression) contributions to DR from long (annual) to short (half-hourly) integration times.

Approaching causalities on different time scales

On annual time scales, wood growth – known as the main carbon sink of a forest ecosystem (Barford *et al.*, 2001; Rocha *et al.*, 2006) – is a main driver of DR_{yr} and NEP_{yr}, and therefore responsible for close relationships between the two measures (Fig. 5). However, the correlation between the two measures was closer than that reported in a tree ring study by Rocha *et al.* (2006), and was also closer than that

found in own preliminary tree ring data (data not shown). As DR includes not only woody growth but also 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 speculative because there are few data available on inter-annual phloem size changes (Gricar & Cufar, 2008; Gricar *et al.*, 2009). It is interesting that neither GPP_{yr} nor TER_{yr} showed a similar close relationship to DR_{yr} at this time scale (Table 1). This supports recent findings that wood growth is not controlled directly 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 occur 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 different ratios in summer and winter. The combination of these two processes was therefore also responsible for close relationships between DR_m, on the one hand, and NEP_m, GPP_m and TER_m, on the other (Table 1). Only on this time scale did all three EC-based measures show significant correlations with DR. The reason for this is not completely clear, but might be explained by split contributions of growth and tree water relations to DR_m. During the summer, DR_m increased up to 750 $\mu\text{m month}^{-1}$ (Fig. 4), about two-thirds of which was attributable to radial growth and one-third to water-related fluctuations (Zweifel & Häsler, 2001). Positive NEP_m in summer is 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, but in a ratio that favours assimilation over respiration, as shown by the positive NEP_m values (Fig. 4).

In winter, DR_m decreased with a rate of 400 $\mu\text{m month}^{-1}$ (averages, Fig. 4) and even with > 1000 $\mu\text{m month}^{-1}$ for individual trees (Zweifel & Häsler, 2000, 2001). There was no growth at this time of the season and such shrinkage is mainly attributable to freezing processes in the stem which lead to very rapid dehydration of elastic bark tissue with a consequent decrease in DR (Zweifel & Häsler, 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 previously by, for example, Monson *et al.* (2006) or Lipson *et al.* (2009), was not expected *a priori* to be so closely linked to negative DR_m, as lower temperatures should also lead to decreasing respiration (Schwalm *et al.*, 2010). However, this was not the case, as shown by our results

(Fig. 3). Furthermore, our finding at monthly scales produces an apparent discrepancy with winter findings at shorter time scales, as discussed below. As a synthesis of our results at monthly resolution, we conclude that growth- and water-related processes of trees in summer and temperature-induced, water-related processes in winter contribute to the close relationships observed. A clear mechanism, however, explaining these correlative findings, with physiological causes and effects, awaits further research.

On half-hourly time scales, the relationship between DR_{hh} and NEP_{hh} is highly water-related because of the influence of changing water contents on mainly bark and thus DR (Steppe *et al.*, 2006; Zweifel *et al.*, 2007). In contrast with the longer integration times investigated, the linear regression was found to be negative (Fig. 3), which is not surprising when considering the dominant physiological processes at this temporal scale. The sunnier the conditions, the more trees transpire and, consequently, the more depleted is tree internal water storage, for example in the bark (Steppe *et al.*, 2006). The same conditions also lead to higher assimilation rates by photosynthesis and, consequently, an increased ecosystem CO_2 uptake in parallel with 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 has been reported for trees at our site (Zweifel *et al.*, 2002), it apparently did not reduce NEP_{hh} to an extent that would have forced the discussed relationship to disappear. Overall, the longer and more pronounced the shrinking of stems over a day, the larger the assimilation and therefore NEP_{hh} (Figs 3, 6). Thus, any causal link between DR_{hh} and NEP_{hh} must relate to biotic and physical conditions (Stoy *et al.*, 2009) that induce large diurnal stem radius fluctuations which do not represent tree net assimilation only, but also the productivity of the entire forest ecosystem. Such a general relationship between DR_{hh} and NEP_{hh} has been found for days with temperatures above the freezing point, and is further supported by the close correlation between DR and GPP at half-hourly scales (Table 1).

Exceptions and anomalies

There are also exceptions from this general relationship between DR and NEP. Such anomalies indicate that, although the two measures have similar drivers, they may be linked only indirectly to each other. One such exception was present during May, the month with the highest NEP_m on average, but with little change in DR_m (Fig. 4). Wood growth had not yet started, but stem rehydration of winter shrinkage, mostly occurring in April at this site, had nearly finished. This succession of stem rehydration followed by initial wood growth has also been found in other studies (Larcher, 2003; Monson *et al.*, 2005; Zweifel *et al.*, 2006), and shows the importance of balanced tree water relations

for the initiation of wood growth (Lockhart, 1965; Steppe *et al.*, 2006, 2008; Turcotte *et al.*, 2009), in addition to the well-known limitations by temperature (Rossi *et al.*, 2008). The relationships of DR_m to GPP_m and TER_m were much less affected by the month of May (data not shown). However, increased GPP_m , together with slightly decreased TER_m , led to over-proportionally large NEP_m in relation to DR_m . This delay in RWG after NEP_m explains, at least partially, the somewhat disturbed relationship between DR_m and NEP_m in May (Fig. 3, Table 1), and is a strong indication for two, at least partially decoupled, mechanisms determining DR_m and NEP_m based on the same climatic drivers.

In contrast with that discussed for monthly values in wintertime, half-hourly DR_{hh} and NEP_{hh} values were found to be uncorrelated on days with freezing conditions (Fig. 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* as 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 & Häslér, 2000). However, despite this short-term decoupling of DR_{hh} from NEP_{hh} , it is surprising that dehydrated stems at cold temperatures tend to lead to higher winter ecosystem respiration on a monthly scale. In this case, increased ecosystem respiration might not be functionally linked to stem physiological processes.

The ecological relevance of DR measurements for NEP

In summary, DR is, with some exceptions, closely correlated with NEP at all time scales investigated. This has not been explained mechanistically in full yet and was not expected beforehand. However, it raises the question of why NEP measured by EC over this ecosystem seems to be driven mostly by tree metabolism. Other ecosystem components, namely heterotrophic (soil) respiration and understorey vegetation carbon turnover, 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 changes in stem radius, either contributing very little to NEP or, more likely, being in phase with the mature trees measured. Similar close relationships between wood growth and NEP have been found in a boreal forest in central Manitoba, Canada (Rocha *et al.*, 2006). On the one hand, this may be a coincidence and, on the other, might be a characteristic of subalpine (Davos) and boreal (Manitoba) regions, clearly differing from lowland deciduous forests where spring ephemerals can be a relevant short-term carbon sink which is not synchronous with the dominant tree species (Knohl *et al.*, 2003). In particular, freezing conditions in winter and spring seem to

play an important role for annual DR_{yr} and NEP_{yr} , as indicated by the high predictive power of the compensation day of the cumulative WRES (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 DR, a measure from individual trees (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. Both fractions of DR, tree water relations and stem growth, have considerable explanatory power for NEP. Furthermore, 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 with the pure wood-related tree ring widths. The relationships between DR and NEP, however, are a function of the time scale 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 time scales.

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

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