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Intra-annual variability of wood formation and $\delta^{13}C$ in tree-rings at Hyytiälä, Finland

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ABSTRACT

Investigation of the relationship between tree-ring stable carbon isotope composition ($\delta^{13}C$) and environmental variables at the intra-seasonal scale can inform on the understanding of the environmental forcing affecting trees during the active period of radial growth. Recent progress in the measurement techniques for assessing the $\delta^{13}C$ signature of tree rings at high spatial resolution provides an opportunity to derive tree physiological information at fine temporal scale, within a given year. Three $\delta^{13}C$ time series of resin-extracted wholewood from tree-rings of Scots pine trees (*Pinus sylvestris* L.) sampled at Hyytiälä (Finland) have been produced by using laser-ablation stable isotope mass spectrometry. These intra-seasonal stable isotope series exhibit a strong common signal (EPS = 0.96) demonstrating the capacity of trees within a stand to preserve a common intra-seasonal response to external controls in a similar manner as found with annual measurements. To estimate when wood cells are active and responsive to environmental information, a Gompertz approach, assessed against microcore data, was adopted to model the timing of wood formation. The addition of a cell lifetime function into environment-growth models may evaluate more completely, the environmental effect on intra-annual tree-ring $\delta^{13}C$ values and that during the growing season. Statistical analysis of the resulting tree-ring $\delta^{13}C$ intra-annual signal implies a shift in importance from the influence of the environmental variables throughout the growing season.

1. Introduction

The use of isotopic time series to investigate the relationship between varying environmental factors and tree growth processes has been widely investigated at different time resolutions: by sampling one isotopic measurement representative of the full tree-ring (i.e. inter-annual resolution) or by sampling many isotopic measurements per tree-ring (i.e. intra-annual resolution) (Wilson and Grinsted, 1975, 1977; Leavitt and Long, 1982, 1991; Ogle and McCormac, 1994; Loader and Switsur, 1995; Robertson et al., 1997; Schleser et al., 1999). However, these dendroclimatological studies were limited by a lack of suitable methods for a precise and straightforward dissection of tree-rings with curved and non-parallel tree-ring boundaries which typically permitted only a few wide tree-rings to be analysed per study (Helle and Schleser, 2004). A significant improvement in high-resolution isotope analysis of tree-rings lies in the development of on-line methods for wood sampling, combustion and mass spectrometry (Matthews and Hayes, 1978; Preston and Owens, 1983, 1985) to allow larger number of samples to be analysed with improved time and cost efficiency. The current study has benefited from these developments to measure the $\delta^{13}C$ by UV laser ablation to build a 13 years long intra-annual time series. Considering the potentially high number of measurements resulting from such an approach, a standard methodology to analyse the environmental signal in current intra-seasonal $\delta^{13}C$ time series is desirable.

Early observation of covariance between air temperature and carbon stable isotope ratio in wood material by Urey (1947) initiated the use of this technique in climate reconstruction. Carbon fixation in plant metabolism has since been intensively studied to improve understanding of the relationship between plants and carbon isotopes (Farquhar et al., 1982, 1989). The relationship between the atmospheric $\delta^{13}C$ and the $\delta^{13}C$ of resulting plant cellulose has been described by Farquhar et al. (1982) as given in Equation 1:

$$\delta^{13}C_p = \delta^{13}C_a - a - (b - a)c_i/c_a \qquad (1)$$

Where $\delta^{13}C_p$ is the organic $\delta^{13}C$, $\delta^{13}C_a$ is the atmospheric $\delta^{13}C$, a is the discrimination against $^{13}CO_2$ during diffusion through the stomata (≈ 4.4 ‰), b is the net discrimination due to carboxylation (≈ 27 ‰) and c_i and c_a are intercellular and ambient CO_2 concentrations.

The organic carbon isotopic value ($\delta^{13}C_p$) is controlled by the $\delta^{13}C$ of the atmosphere ($\delta^{13}C_a$), the degree of conductance of carbon via diffusion through the stomata and the rate of photosynthesis. These factors affect the ratio of CO_2 concentration and isotope composition between the atmosphere and the stomatal chamber, often expressed as the ratio c_i/c_a (Farquhar et al., 1982).

Early process-based studies, conducted under controlled conditions, identified the role of air temperature and light intensity on plant $\delta^{13}C$ through the modulation of the stomatal conductance at different stages of carbon fixation (Smith et al., 1976). Subsequent research has investigated photosynthetic activity in plants in relation to environmental factors such as air temperature, precipitation, relative humidity (or vapour pressure deficit, VPD), irradiance, soil water availability, cloud cover and fog, air pollution, latitude and altitude with the primary aim of reconstructing the climate of the past and plant-environment relationships (Wilson and Grinsted, 1978; Leavitt and Long, 1991; Lipp et al., 1991; Loader et al., 1995; Panek and Waring, 1995; Saurer et al., 1995; Schleser, 1995; Switsur et al., 1996; Hemming et al., 1998; Barbour et al., 2002).

However, assuming that the seasonal δ^{13}C variability induced by environmental forcing at the leaf level is directly transcribed in tree-rings can be misleading. The tree-rings δ^{13}C measurements may include a signal reflecting storage processes and non-linear carbon allocation which may cause the resulting δ^{13}C signal to diverge from co-occurring environmental forcing. Therefore, Helle and Schleser (2004) attempted to represent intra-annual δ^{13}C variation through a recurring tri-phase pattern in tree-rings from broadleaf deciduous tree species characterised by the switch between the storage-dependent growth of the current year and the use of new (i.e. non-stored) photosynthates. The use of storage carbohydrate and its impact upon seasonal (i.e. intra-annual) δ^{13}C has also been investigated for conifer species by Vaganov et al. (2009) who suggest an indirect link between climate and δ^{13}C.

When evaluating environmental forcing on intra-annual δ^{13}C time series from tree-rings, it is necessary to understand the temporal dynamics of cell development requiring specific investigations on wood formation (Wimmer, 2002). In temperate climates, the cambial activity responsible for the radial growth increment of trees is characterised by an active period during summer and a dormant period in winter (Iqbal, 1994; Fujii et al., 1999). Therefore, the modelling of cambial dynamics may be restricted to the active period alone (Dufour & Morin, 2007). During the active period, the growth of xylem cells can be subdivided into three phases; cell division, enlargement, and secondary wall thickening (i.e. maturation) which are separated temporally across the developing tree-ring (Rossi et al., 2006). The formation and development phases of cell formation have been found to be independent and their reaction to environmental factors can differ (Antonova and Shebeko, 1981; Antonova et al., 1983) due to their different physiological controls (Larson, 1960; Richardson and Dinwoodie, 1960; Wodzicki, 1964; Zahner et al., 1964).

The present investigation explores the possibility of building a standard methodology to assess the effect of temperature, photosynthetically active radiation (PAR), precipitation and vapour pressure deficit (VPD) on the intra-annual carbon isotope signal in tree rings of *Pinus sylvestris* in Finland. Furthermore, the influence of stem growth dynamics are assessed and incorporated within the statistical relationship of high-resolution isotope signal and environmental variables.

2. Materials and methods

2.1. Study site

The SMEAR II site at Hyytiälä, 200 km north of Helsinki in Finland (61°51'N, 24°17'E), is an experimental forest research station (Station for Measuring Forest Ecosystem-Atmosphere Relations) operated by the University of Helsinki. From 1997 to 2009, the annual mean air temperature at the study site was 4.31 °C and annual mean precipitation was 498.25 mm (Pirinen et al., 2012). The parent material of the soil is coarse, silty, glacial till and the soil is a haplic podzol. The site has an average elevation of 170 m above sea level with a flat topography and a maximum of 10 m variation in altitude (Vesala et al., 1998).

At the time of sampling in 2011, Scots pines were the dominant tree species at the site (60%), approximately 50 years old and evenly distributed for about 200 m in all directions from the measurement site (Ilvesniemi et al., 2009; Williams et al., 2011). Species other than Scots pine present at the site include Norway spruce (*Picea abies*), downy birch (*Betula pubescens*), grey alder (*Alnus incana*) and aspen (*Populus tremula*). The SMEAR II infrastructures monitor the ecosystem-atmosphere fluxes to determine and understand relationships between flux emissions and environmental variation. This station includes an instrumented 73 m tall mast monitoring CO_2, H_2O, CO, O_3, SO_2, NO and NO_2 concentrations, temperature, wind speed profiles, solar and thermal radiation, and the fluxes of CO_2, H_2O and O_3 aerosols between the ecosystem and the atmosphere (Hari and Kulmala, 2005; Hari et al., 2013). Mast measurements are reported as half-hourly means (details in Vesala et al., 1998; Kulmala et al., 2001). Micrometeorological methods are used to record the ecosystem-atmosphere fluxes. With the eddy-covariance method, a frequency of 10 Hz or higher (e.g. Rannik et al., 2003) is used to measure CO_2, H_2O and O_3 concentrations into a three dimensional wind speed profile. This SMEAR II station is part of EUROFLUX and FLUXNET networks (details in Valentini et al., 2000).

2.2. Core sampling and preparation

Three Scots pines older than 40 years without any visible damage or disease were identified and selected for sampling. These trees were all located within the closed canopy rather than in open spaces that could affect the light availability and atypically modify $\delta^{13}C$ values (Gessler et al., 2001). Each tree sampled was cored once, with ring age established by simple count (i.e. no cross dating) as only recent years coincided with flux-tower measurements (i.e. 1997 to 2009). In addition to the tree cores, four microcore time series counting cambial cells were available from 2007 to 2009 and provide supplemental data for the determination of the period and duration of the radial growing season.

The three Scot pines trees were sampled non-destructively by removing a single increment core using 10 mm diameter increment borer at $\approx$ 1.2 m above ground (Mantgem and Stephenson, 2004). The samples were allowed to air dry prior to the sectioning of the sampled cores into smaller laths of 3 mm thickness using a Walesch twin-bladed saw. To permit a better observation of annual tree-rings, cuts were made transversely perpendicular to the fibre orientation. As the cores are from conifer wood, mobile resin and extractives were removed using pure ethanol in a Soxhlet extractor for a duration of 48 hours (Loader et al., 1997). Remaining ethanol in the laths was first removed by bathing the samples in boiling distilled water in the Soxhlet extractor and then by drying the laths in an oven at 40 ^{o}C for 12 hours. No further treatment was applied to the samples.

2.3. Description of laser procedure

A sample resolution of 80 microns was selected to obtain a fine enough resolution while at the same time collecting enough material for the spectrometry analysis. At high resolution, the quantity of wood material ablated per sample is very small and can be at the limit of confidence for the mass spectrometry equipment. To preserve high sampling resolution and to maximise the quantity of material available for each analysis, direct analysis of wholewood is favoured after extractives (i.e. resins) have been removed (Schulze et al., 2004). This approach represents an appropriate compromise, for carbon isotopes at least, where studies have shown similar signals to be preserved within the wholewood, cellulose and lignin components of the tree-ring (Borella et al., 1998; Helle and Schleser, 2004; Loader et al., 2003).

Laser ablation permits direct analyses of wholewood material at the micro-scale. With the ESI/New Wave system, the wood lath is positioned in an atmosphere-isolated sample chamber purged with helium. The sample is ablated by focusing the stationary laser beam on the desired area with a setting laser power and resolution of 80 μm. The ablated wood is transferred using helium carrier gas from the sample chamber to a furnace containing chrome (III) oxide where it is combusted at 600 °C. The gases produced during the combustion are passed through a Nafion trap to remove traces of water and the remaining CO_2 is cryogenically trapped using liquid nitrogen to separate the analyte from other non-condensable gases. As the amount of gas coming from the combustion is close to the lower limit for a mass spectrometer. The cryo-focusing step is essential to provide good chromatography of the resulting CO_2 during the analysis. At the start and end of each sample run (≈ 100 samples per batch), ten IAEA cellulose standards are analysed to yield a range of sample sizes equivalent to those obtained from the wood sample analysed. These standards permit calculation of the precision in the carbon stable isotope values produced and allow for the detection and to correct for possible sample size effects. Each sample analysis is measured against an injection of an in-house CO_2 reference gas. All samples were analysed on the same SERCON 20-20 mass spectrometer with an analytical precision calculated to be typically in a range of 0.1 to 0.2 ‰.

2.4. Standardisation of the δ^{13}C *time series*

Differences in annual tree-ring width mean that the resulting δ^{13}C time series developed from each of the three trees differ in the number of data points in each ring (Table 1). In this study, to aid comparison and combination of the intra-annual data from each of the trees, it was decided to express the inter-annual δ^{13}C data with common sampling resolution (i.e. number of analyses per ring). Rather than interpolation of multiple data points, standardisation between δ^{13}C time series with different number of measurements was conducted by first selecting the tree with the lowest number of analyses for any particular year and then in a second step, by reducing the number of measurements in the other series by mathematically combining multiple adjacent measurements into one value on the same position into the tree-ring. In doing so, the structure of the tree-ring data (i.e. its proportions in early-wood, middle-wood and late-wood) is preserved without increasing autocorrelation. The standardised time series may then be matched year by year and possess the same number of isotope measurements, this allows the series to be combined and the inter-series signal strength (i.e. the expressed population signal) to be calculated.

Table 1: *Number of carbon isotope measurements per sampled tree (i.e. Tree 1, Tree 2 and Tree 3) at Hyytiälä for the time period from 1997 to 2009. For comparison, the number of measurements for each ring are reduced to that of the lowest resolution (e.g. tree 1, 2009).*

Year	Tree 1	Tree 2	Tree 3
1997	27	17	17
1998	18	16	13
1999	14	16	12
2000	21	20	16
2001	21	18	14
2002	20	14	17
2003	14	15	11
2004	18	21	15
2005	18	16	17
2006	11	13	16
2007	10	19	19
2008	13	16	18
2009	17	18	22

2.5. Corrections of the δ^{13}C *time series*

Carbon isotope chronologies show a declining trend related to the emissions of isotopically depleted $^{13}CO_2$ since industrialisation (Epstein et al., 1990; Leavitt and Lara, 1994; Kitagawa and Matsumoto, 1995; Raffalli-Delerce et al., 2004; Feng and Epstein, 1995a,b; February and Stock, 1999; Treydte et al., 2001). To remove this non-climatic trend, a method based upon the mathematical correction of the series based on records from Antarctic ice cores was adopted (Saurer et al., 1997; Francey et al., 1999).

During the growing season, trees can deplete their local atmosphere in carbon dioxide, and as ^{12}C is preferred to ^{13}C during this process, the close surroundings of the forest can potentially become more depleted in ^{12}C through the course of the growing season. If δ^{13}C in the air is modified significantly then δ^{13}C assimilated by the trees is also influenced by this variation and may manifest in the resulting tissues (i.e. tree-ring). Further to this, δ^{13}C in the air is also affected by plant respiration which may also release CO_2 from the trees to the atmosphere with its own δ^{13}C signature. The re-use of respired CO_2 by the trees for photosynthesis would cause enrichment in leaf δ^{13}C values. However, Buchmann et al. (2002) found source air effects to be negligible at canopy heights greater than 1 m thus showing the δ^{13}C variation from the leaves to be primarily due to photosynthetic carbon isotope discrimination. To evaluate such source air effects at Hyytiälä, air δ^{13}C data from the Pallas-Sammaltunturi station available at the NOAA Earth System Research Laboratory (http://www.esrl.noaa.gov/) was selected for its similarity in terms of forest stand to Hyytiälä and the abundant flask data recorded from 2002 to 2009. If a significant seasonal pattern is detected during the active vegetation period, a correction matching this seasonal $\delta^{13}C$ variation will be added to the atmospheric correction.

No PIN correction for changes in atmospheric CO_2 concentration (McCarroll et al., 2009) was applied to the $\delta^{13}C$ time series due to the exploratory nature of this study and their relatively short length compared to traditional dendroclimatic studies that usually extend back to times before industrialisation.

2.6. Determination of radial wood growth

Due to limited availability of dendrological information for many study sites, it is necessary to develop a method capable of modelling wood growth when dendrological measurements are unavailable. Based on availability of carbon and water fluxes and meteorological measurements at Hyytiälä, a range of approaches was explored to determine whether the onset of and the cessation of wood growth could be modelled by these observations.

The net ecosystem production (NEP) as defined by Woodwell & Whittaker (1968), is the difference between the gross primary production (i.e. the amount of organic carbon fixed by photosynthesis in an ecosystem) and the total ecosystem respiration (i.e. the sum of autotrophic and heterotrophic respiration). However, eddy covariance measurements estimate the net ecosystem exchange (i.e. the total exchange of carbon dioxide above the ecosystem) which is equal to -NEP plus inorganic sources and sinks (e.g. weathering reactions, precipitation or dissolution of carbonates, and atmosphere–water equilibrations) that are considered negligible in this forest ecosystem. Our first approach uses the net ecosystem exchange (NEE) to characterise the period for carbon fixation at the leaf level and see if it relates to wood growth. A second similar approach using evapotranspiration as described in Cocozza et al. (2012) was also explored. Finally, a third approach based on recurrent environmental conditions was tested to determine whether meteorological observations could be used to model wood formation.

Onset and cessation of the production of new cambial cells were determined from the four microcore time series collected during 2007 to 2009. Using these, a period of time for cambial activity could be determined and used to evaluate if thresholds values of either NEE, evapotranspiration or meteorological observations could be linked to the onset of radial wood growth (Figure 1). However, NEE and evapotranspiration cumulated over the growing season only presented a weak correlation with cambial activity mainly due to the large variation of the fluxes between years. It hence is not feasible using these limited data, to predict wood growth onset or cessation on the basis of ecosystem fluxes.

Previous studies strongly suggest the determinant influence of temperature over the onset of cambial activity (Oribe and Kubo 1997, Oribe et al. 2001, 2003, Gričar et al. 2006, Begum et al. 2007, 2008, 2010, 2013). A widely tested approach is to select threshold values of temperature to predict the onset of cambial activity (Schmitt et al., 2004; Rossi et al., 2007; Deslauriers et al., 2008). However, investigation of a relationship with daily minimum and maximum temperature did not succeed in setting thresholds holding similar values during the three years when the microcores have been sampled (Figure 1). In parallel, analysis over day length was also conducted due to its determinant influence over the growth rate of tree-ring formation (Rossi et al., 2006) but did not provide a reliable threshold.

By smoothing measurements of photosynthetically active radiation (PAR) using smoothing splines (span = 0.8), a threshold set to 435 µmol m^{-2} s^{-1} provides a closer (visual) match to the dates for growth onset estimated by the microcore measurements. While growth onset is well predicted based on this correlation, predictions of cessation of cambial cell production are still poor (Figure 2).

Another approach to the prediction of cambial activity consists in using heat accumulation above a threshold temperature often expressed as degree-days (e.g. Sarvas 1972, Kramer 1994, Karlsson et al. 2003). Therefore, We further assessed the capacity of cumulative air temperature and cumulative PAR measured after the onset of cambial cells expansion to predict growth cessation. The convention used for this study is to cumulate air temperatures only above 5 ^{o}C which represents a theoretical lower limit for the onset of xylogenesis (Rossi et al., 2007). No restrictions were applied to the cumulated PAR values. Predictions of wood growth using cumulated PAR and air temperature only show poor correlation with microcore measurements and differ significantly from results of the smoothing splines method (Wilcoxon rank-sum test, $p < 0.01$).

The method selected to predict the onset dates of radial growth in this study relies on using a threshold of smoothed PAR (435 µmol m^{-2} s^{-1}) as it predicted the best the onset of cambial activity determined by the microcore measurements for the tested three years. Based on observations from Gričar et al. (2007) and Rossi et al. (2007), the cessation of xylogenesis was set to an arbitrary threshold of smoothed air temperature at 10 ^{o}C (Figure 2). Dates selected for onset and cessation of cambial activity are shown in Table 2.

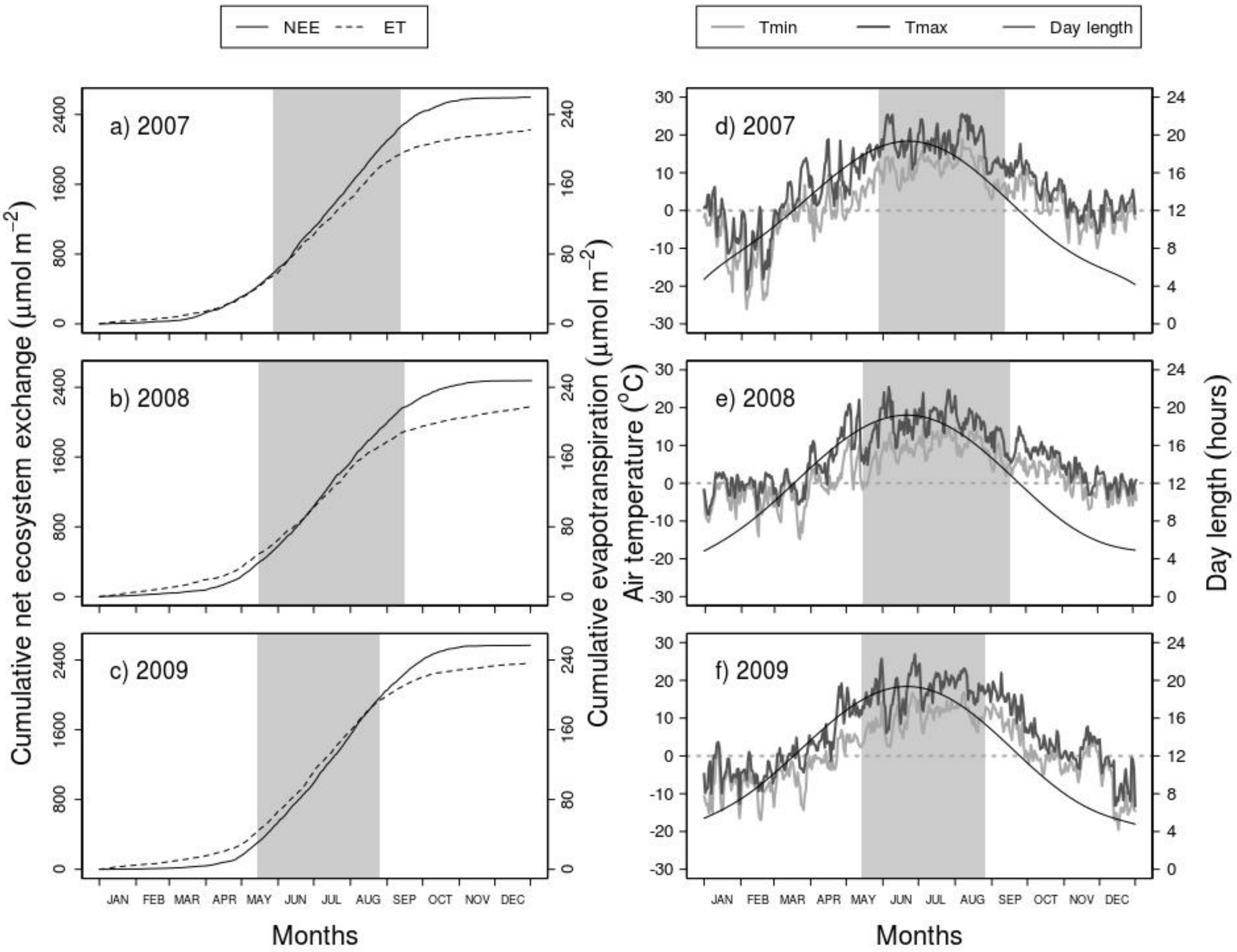

Figure 1: *Investigation of the correlation between cumulated net ecosystem exchange (i.e. NEE, continuous line) and evapotranspiration (i.e. ET, dashed line) for years a) 2007, b) 2008 and c) 2009. Daily values of minimum (i.e. Tmin, light grey line) and maximum air temperature (i.e. Tmax, dark grey line) and day length (black line) are presented for years d) 2007, e) 2008 and f) 2009. is The light grey area in all panels represents the time period for cambial cell formation evaluated by microcore measurements.*

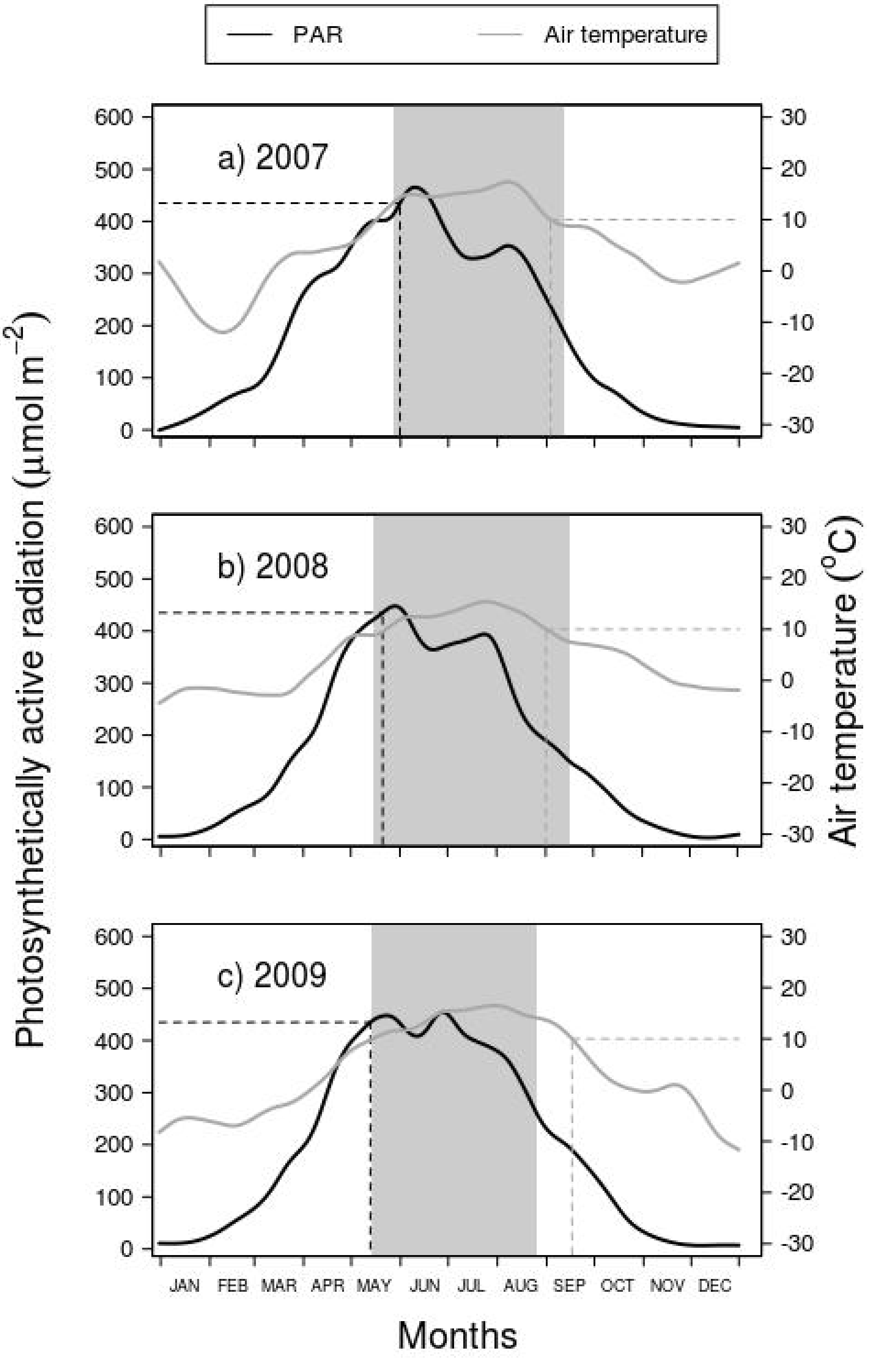

Figure 2: *Determination of thresholds (black and grey dashed lines) to characterise the onset of radial wood growth with smoothed photosynthetically active radiation values (PAR, black line) and to characterise the cessation of radial wood growth with smoothed air temperature (grey line) using smoothing splines (span = 0.8) for a) years 2007, b) 2008 and c) 2009. The light grey area in all panels represents the time period for cambial cell formation evaluated by microcore measurements.*

Table 2: *Estimated onset, cessation and duration of cambial cells formation at Hyytiälä in days of the year for the time period from 1997 to 2009 (e.g. January the first is day 1).*

Year	Onset	Cessation	Duration
1997	145	256	111
1998	154	238	84
1999	148	265	117
2000	138	247	109
2001	156	263	107
2002	134	255	121
2003	138	233	95
2004	156	261	105
2005	160	266	106
2006	156	271	115
2007	151	246	95
2008	141	244	103
2009	132	259	127

2.7. Modelling of cambial cells formation

Although desirable, it is not practical to conduct detailed cambial investigations for each intra-annual study. Therefore, an approach using S-shaped curves as Gompertz functions has been developed to assign chronology and to model the cell number increase, the rate of growth and periods of cell differentiation (Camarero et al., 1998).

As only three years of microcore measurements were available at the time of the study, the Gompertz model for the years 1997 to 2009 was constrained using annual tree-ring width as the maximum annual growth while estimated onset and cessation dates were used to delimit the radial growth period. Therefore, the Gompertz equation produces a growth curve that can be used to match isotope values with a date of estimated new cambial cells formation (Figure 3). The rate of formation for new cells is slower at the beginning and at the end of the growing season while the central part is characterised by rapid growth. Therefore, when matching environmental data and $\delta^{13}C$ time series on the same temporal scale, the integration of environmental information will differ depending on the position of the isotope measurements within the tree-rings.

The Gompertz curves resulting from the covariance of cambial cells formation with meteorological conditions, compared with the mean signal calculated over the four available microcore time series of cambial cell measurements during 2007 to 2009 shows that the Gompertz method does not always fit perfectly the dendrological data (Figure 4). Therefore, as a consequence of the inevitable deviation between modelled cells growth and microcore measurements, environmental variables and $\delta^{13}C$ measurements may be partially mismatched during the analysis of the environmental forcing and may cause a weaker, or less clear, signal than expected.

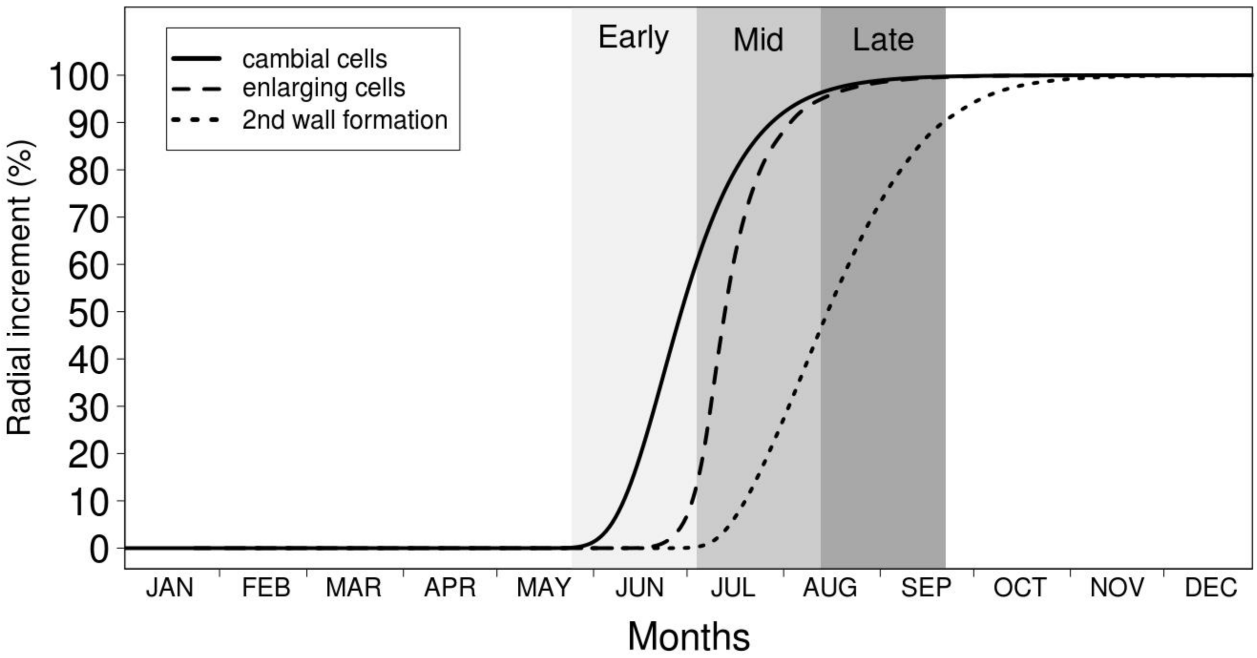

Figure 3: *Evolution of the duration of the modelled wood cells growth phases by the Gompertz approach (i.e. cambial cells, enlarging cells and secondary wall formation) during an example of active growth period for Scots pines at Hyytiälä against radial increment expressed as a percentage of tree-ring width. The division into three equal tree-ring sections are represented in light to dark grey (i.e. Early, Mid, Late).*

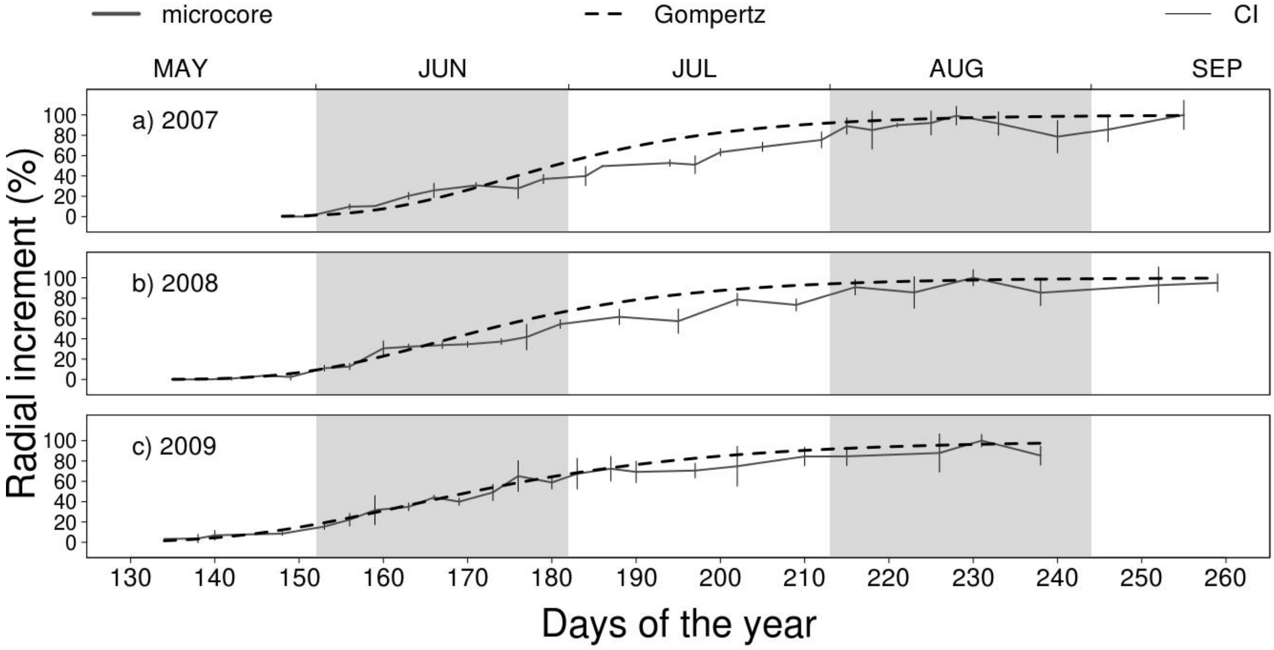

Figure 4: *Comparison of the mean signal from four microcore time series (i.e. microcore, solid black lines), its confidence intervals (i.e. CI, solid vertical lines) and the Gompertz curves (i.e. Gompertz, dashed lines) for the years a) 2007, b) 2008 and c) 2009 at Hyytiälä against radial increment expressed as a percentage of tree-ring width.*

2.8. Implementation of cell longevity

A simple method for determining when wood cells can integrate environmental information without an intensive study of wood formation consists in adding a period for cell activity corresponding to the duration of the cell phases starting from the date of cell formation estimated by the Gompertz equation. Earlywood cells can live from a few days to several weeks while the latewood cells are able to stay alive months after their formation (Schweingruber and Briffa, 1996). This difference means that the environmental information recorded within wood cells has a different integration period depending on the longevity of the cells during the growing season (Helle and Schleser, 2004; Schollaen et al., 2014; Wimmer, 2002). Therefore, a theoretical longevity can be added to the tree radial growth model in the form of additional Gompertz curves. Based on cell phases timing estimation for Scots pines (Wodzicki, 1971), this current study will use a linear decrease from 23 to 5 days to characterise the cell enlargement evolution during the growing season and a linear increase from 15 to 51 days for secondary wall thickening. Figure 3 shows the resulting evolution of these two additional cell phases during a year of growth. Although, it is anticipated that the incorporation of cell lifetime improves the capacity of modelling of intra-annual carbon isotope variability, it is recognised that the allocation of carbon to the tree-ring varies during the different phases of its development and will likely not contribute equally to the overall carbon isotope signature of the ring. In an attempt to better understand physiological activities modifying the δ^{13}C signature (e.g. release of storage carbon compounds), the δ^{13}C measurements can be segregated into three equal sections of tree-rings that will be referred to as early-, middle- and late-wood.

2.9. Statistical approach

2.9.1 Expressed population signal

The expressed population signal (EPS, Wigley et al., 1984) assesses the common signal expressed between the individual δ^{13}C time series. Where the EPS is deemed to be sufficiently high (i.e. typically greater than 0.85), the individual trees may be regarded as sharing a common environmental signal and may therefore be suitable for combination into a representative average time series for palaeoenvironmental analyses.

2.9.2 Simple linear correlation coefficients

To evaluate the quality of the environmental signal during an average year of growth, a correlation analysis is carried out between the inter-annual $\delta^{13}C$ measurements and simple environmental parameters (i.e. monthly mean values of air temperature, photosynthetically active radiation, precipitation and vapour pressure deficit). This step permits comparison with previous studies in northern latitudes and highlights the time period when a clear environmental signal from the $\delta^{13}C$ measurements can be extracted (McCarroll and Pawellek, 2001; Vaganov et al., 1999). To determine whether the use of stored carbon of a specific growing season can be detected, the corresponding correlation was tested from October to September of 1997 to 2009. The correlation is then assessed by a t test with a confidence level of 0.05 for a two-sided distribution.

2.9.3 Simple linear analysis

It is not expected that a single environmental driver can accurately explain the $\delta^{13}C$ variation (McCarroll and Loader, 2004). However, analysing each one of the selected local environmental variables separately can inform on the evolution of the environmental forcing on $\delta^{13}C$ measurements (i.e. assessed by R^2, $p < 0.05$). Although investigating only a short period of time (13 years), the environmental signal contained within the intra-annual data was analysed in parallel with similar investigations on annually averaged data. A "statistically optimised" fit is determined by progressively increasing the significant period of correlation determined by the monthly simple linear coefficients until the best linear fit for the four environmental variables is found. Then, the linear relationships are evaluated for the early-, middle- and late-wood tree-ring sections to gain information on the temporal occurrence of physiological events that may weaken the environmental signal.

The "realistic" period determined by the estimated onset and cessation dates for cambial cells formation and the integration of cell lifetime is also tested. This finding may help development of intra-annual models with improved understanding of the time period over which environmental information needs to be integrated. Here, we stress again the relatively short nature of the time series and that the correlations are not subject to an independent calibration and verification as is common practice in dendroclimatology (Fritts, 1976).

2.9.4 Multivariate linear analysis

Autocorrelation is an inherent property of environmental variables that can be detected either along time series or across a geographic distance (i.e. temporal or spatial autocorrelation). This feature impairs standard statistical tests due to the lack of independence of the variables (Anderson and Cribble, 1998). However, a general additive multiple regression approach can inform on the relationships between these variables (e.g. Whittaker, 1984).

When carrying the multiple regression analysis, this study adopted an operational approach consisting in selecting which explanatory variables are driving the process while reaching an optimised explanatory power to model the $\delta^{13}C$ variation (Newton and Spurrell, 1967).

The decision to include or exclude explanatory variables into the analysis can be based on prior knowledge on the process analysed (Cox and Snell, 1974). Two common procedures referred as stepwise methods are forward selection (FS) and backward elimination (BE). A basic description of these ideas is that forward selection starts with no variables in the equation and adds one variable at the time until a stopping criterion is satisfied or that all variables are already included, while backward elimination is the opposite process (i.e. all variables are first included and eliminated one at a time) (Hocking, 1976). As these two procedures can lead to different results to the determination of the final model, all combinations from the three environmental variables will be tested both from FS and BE. As a stopping criterion, both the Akaike information criterion and an ANOVA procedure will be conducted to test the significance of the addition or deletion from the tested environmental variables. In this study, both procedures resulted in the same variables being selected for multivariate linear analysis.

3. Results

3.1 δ^{13}C *time series*

The resolution standardisation procedure yields a total of 179 data points for each raw δ^{13}C time series for inter-tree comparison at Hyytiälä (Figure 5). The δ^{13}C time series span 13 years from 1997 to 2009. Each year represents a single tree-ring formation with each δ^{13}C value measured sequentially at 80 µm resolution.

The general pattern observed in the δ^{13}C time series shows the most negative (i.e. depleted) values of δ^{13}C close to the rings boundaries (i.e. early and late sections of tree-rings) and less negative (i.e. enriched) values towards the middle-section of the tree-rings. The amplitude of the δ^{13}C variation during a year can differ greatly in each individual δ^{13}C time series and in some cases, the expected pattern is not present. The maximum range of amplitude is found in the δ^{13}C time series of tree 1. In 1992, the amplitude is 3.81‰, while in 2008 the amplitude is only 0.74‰ which may reflect differences in the responses to or combination of environmental forcing or a larger environmental variability during a particular year of growth. For the period 1997 to 2009, the inter-tree standard deviation is small with 0.795‰. A slight declining trend is detected in the averaged series at Hyytiälä (F-test, $p < 0.05$). However, after mathematical correction for changes in atmospheric δ^{13}C, the corrected mean series exhibits no statistically significant trend (F-test, $p > 0.05$).

Profiles of air δ^{13}C over a canopy result from ecosystem-atmosphere exchanges. Photosynthesis and air turbulence tends to deplete the ambient CO_2 concentration and increase the air δ^{13}C values while soil microbial activity and plant respiration provoke an increase in ambient CO_2 and decrease in the air δ^{13}C values (e.g. Buchmann and Ehleringer 1998; Buchmann et al., 2002; Francey et al. 1985; Lloyd et al. 1996; Silveira et al., 1989). For dense canopies, the resulting daytime profile of air δ^{13}C can be increased significantly during summer compared to winter due to the photosynthesis activity. Analysis of air δ^{13}C values from the Pallas-Sammaltunturi station presents this cyclic seasonal pattern with more negative air δ^{13}C values during winter and spring followed by an increase in air δ^{13}C values from July to October. The average annual variation in air δ^{13}C values is 0.89‰. During the three summer months (i.e. June, July and August) when most of the tree growth occurs, the variation in air δ^{13}C is even smaller (0.26‰). The wholewood δ^{13}C seasonal amplitude at Hyytiälä is typically of 1.42 ± 0.59‰. It is hence assumed for the current study that the effect of seasonal air δ^{13}C variation on the intra-annual δ^{13}C time series of wholewood is negligible and no seasonal correction will be employed.

Although only three trees were studied, intra-annual EPS is high (n = 3 trees, 179 observations, EPS = 0.96), indicating a high common variability in δ^{13}C values from the three trees sampled. Hence, it is sufficient to express a high proportion of the common signal at the study site. Calculation of the EPS based upon annual averages of the dataset yields a similarly high value (n = 3 trees, 13 observations, EPS = 0.97) supporting preservation of an inter-annual common signal as well as an intra-annual signal.

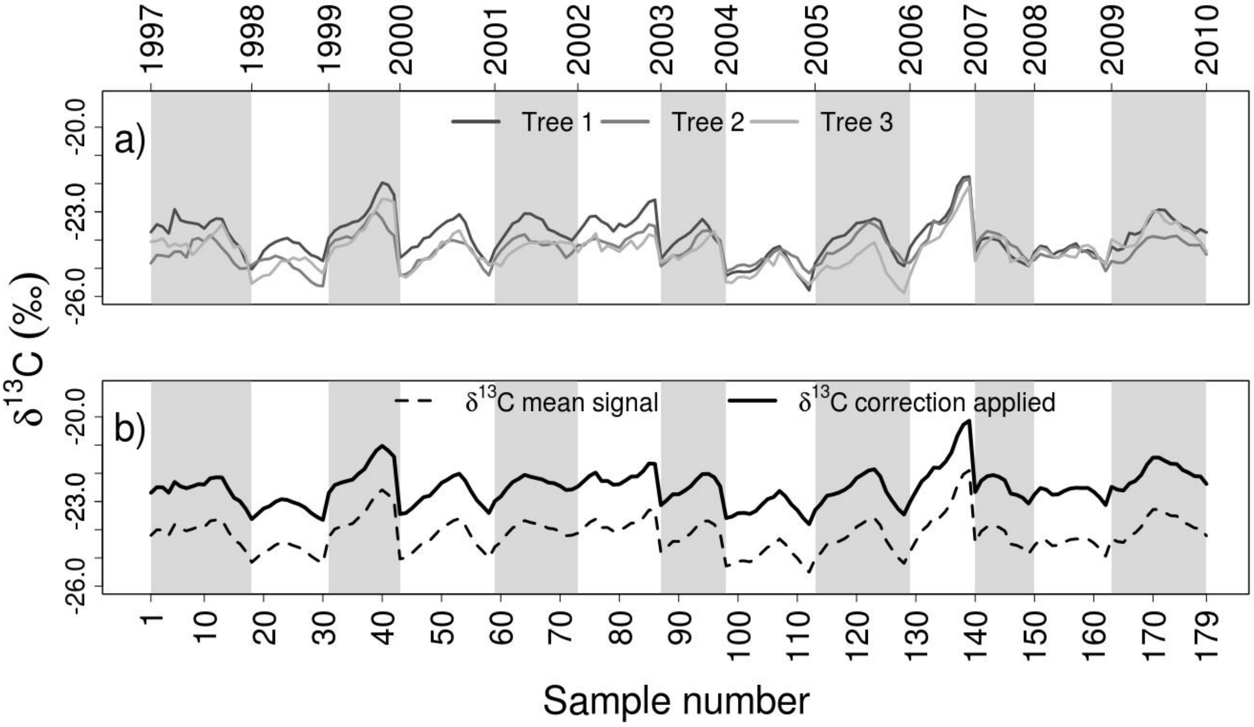

Figure 5: *a) standardised δ^{13}C time series for sampled tree 1 (dark grey line), tree 2 (grey line) and tree 3 (light grey line), b) mean signal calculated over the three δ^{13}C time series (dashed line) and atmospheric corrected δ^{13}C time series (solid line) at Hyytiälä. Shaded vertical sections indicate year boundaries; width is proportional to ring width.*

3.2 Inter-annual simple linear correlations between δ^{13}C values and environmental forcing

Figure 6 displays the simple linear correlation coefficients between the inter-annual atmospheric corrected δ^{13}C time series and the mean monthly air temperature (°C), the mean monthly photosynthetically active radiation (µmol m^{-2} s^{-1}), the monthly sums of precipitation (mm) and the mean monthly vapour pressure deficit (Pa) for the pooled period from 1997 to 2009. When estimating the significance of the correlations, only June is significant for air temperature, photosynthetically active radiation and precipitation coefficients are significant for June and July, vapour pressure deficit coefficients are significant for July and September. There is no significant influence of October to December parameters from the previous year in the current year environmental signal. These results suggest that the "realistic" period determined by the estimated onset and cessation dates for cambial cells formation is likely to provide a weaker relationship between local environmental variables and $\delta^{13}C$ time series due to the absence of significance during months like for example, August for air temperature, precipitation and vapour pressure deficit. The calculation of a "statistically optimised" period may then permit to observe when all four environmental variables present a stronger influence on the $\delta^{13}C$ time series.

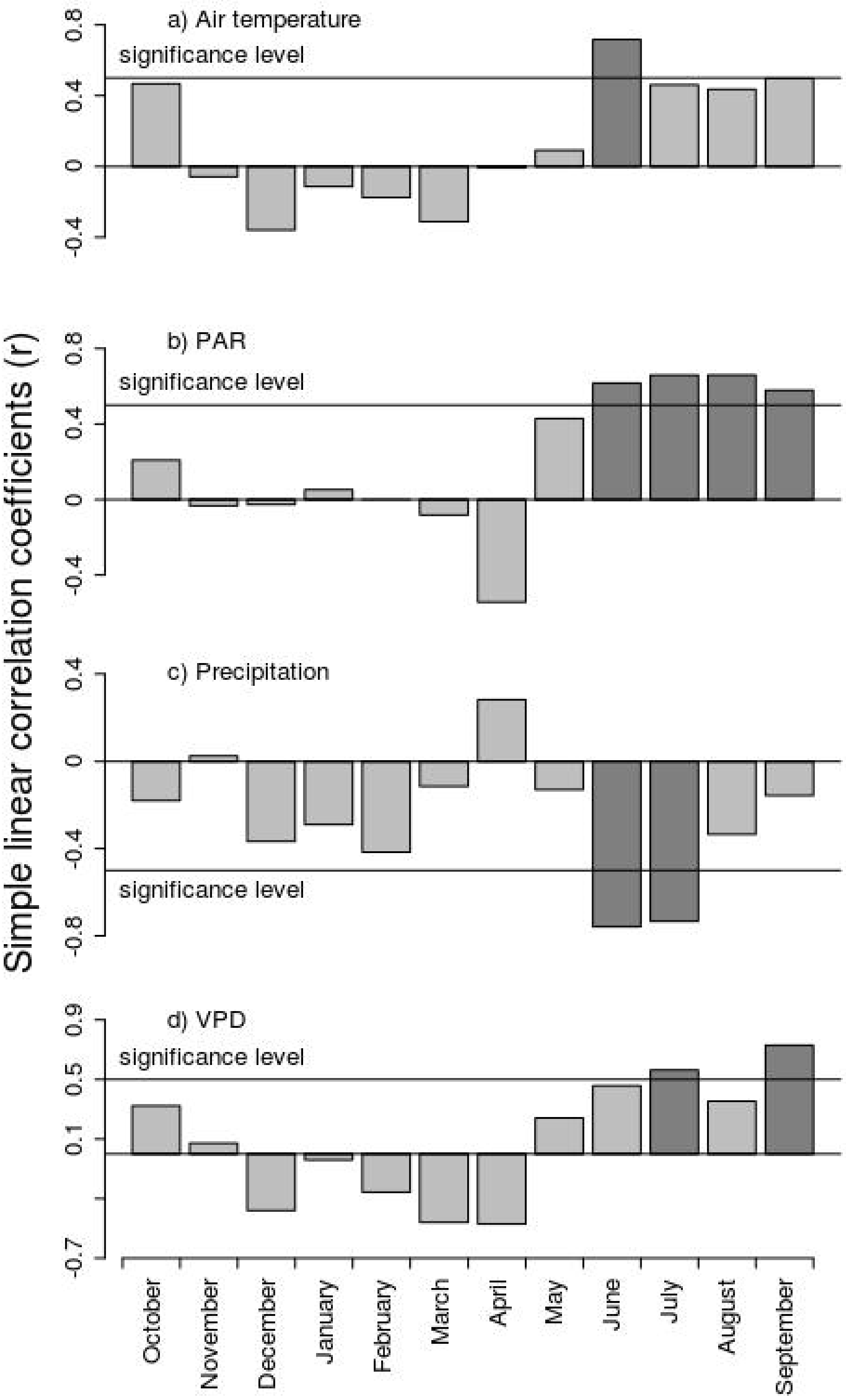

Figure 6: *Simple linear correlation coefficients (r) between monthly mean environmental variables (i.e. a) air temperature, b) photosynthetically active radiation (PAR) c) precipitation and d) vapour pressure deficit (VPD) and inter-annual* $\delta^{13}C$ *values. The significance level determined by t test is displayed as a solid black line (r = 0.50, p < 0.05), months that show a significant simple linear coefficient are displayed in darker grey. October to December data are from the year prior to ring formation while January to September are from the current year.*

3.3 Inter-annual δ^{13}C *variation and environmental forcing*

Considering only the production of new cambial cells (i.e. without cell longevity, Table 3) reveals that only the relationship with PAR presents a strong linear relationship with annual δ^{13}C values ($R^2 = 0.735$, $p < 0.05$), while correlations with air temperature, precipitation and vapour pressure deficit are not significant. However, when including cell lifetime (i.e. with cell longevity, Table 3), single linear regressions provide a significant relationship with air temperature ($R^2 = 0.448$, $p < 0.05$), with PAR ($R^2 = 0.683$, $p < 0.05$) and with vapour pressure deficit ($R^2 = 0.281$, $p < 0.05$). Although the precipitation linear fit increases ($R^2 = 0.182$, $p < 0.10$), it is less significant than for the other environmental variables. Therefore, without the inclusion of cell longevity, the δ^{13}C variation is mainly explained by PAR, while the other environmental variables have no statistically significant effect at the inter-annual level. However, when including an estimate of cell lifetime, the effect of air temperature, precipitation and vapour pressure deficit are revealed clearly. It appears important to consider the timing of cell phases to observe the different environmental influences on inter-annual δ^{13}C time series. The following sections will therefore describe the results including cell lifetime.

By adding days on both ends of June when the environmental forcing is found to be significantly correlated with δ^{13}C values for three out of four tested local environmental variables (i.e. air temperature, PAR and precipitation), an optimised period for the cell formation phase can be established from the 17th of May to the 30th of June (i.e. adding days before the 17th of May or after the 30th of June decreases the quality of the relationship). The two following cell phases (i.e. enlargement and secondary wall thickening) may then be added based on this time period. This final cell lifetime matches the best combination of linear regressions strength for all four local environmental variables and both inter- and intra-annual resolution. With this "statistically optimised" time period, linear regressions show an equivalent strength with the four relationships at the inter-annual resolution (i.e. air temperature: $R^2 = 0.559$, PAR: $R^2 = 0.527$, precipitation: $R^2 = 0.552$, at $p < 0.05$, vapou pressure deficit: $R^2 = 0.510$). Compared to the "realistic" radial growth period including cell longevity, the influence of PAR is decreased but the precipitation and the vapour pressure deficit signals becomes as strong as the two other variables (see Figure 7).

A multiple linear regression based on the four local environmental variables for a "realistic" period of growth demonstrates that a single linear regression with PAR provides the best model to predict δ^{13}C time series at the inter-annual resolution. However, for an optimised period of correlation, precipitation and vapour pressure present a significant combination which may be used to explain the δ^{13}C variation ($R^2 = 0.712$, $p < 0.05$).

Table 3: *Linear relationships between inter-annual $\delta^{13}C$ values and local environmental variables (determined by R^2, $p < 0.05$) with and without cell longevity or for a statistically optimised period at Hyytiälä. 'ns' stands for non-significant ($p > 0.05$).*

Variables	R^2 ($p < 0.05$) Without cell longevity	With cell longevity	With statistical optimal fit
Temperature	ns	0.448	0.559
PAR	0.735	0.683	0.527
Precipitation	ns	ns	0.552
VPD	ns	0.281	0.510

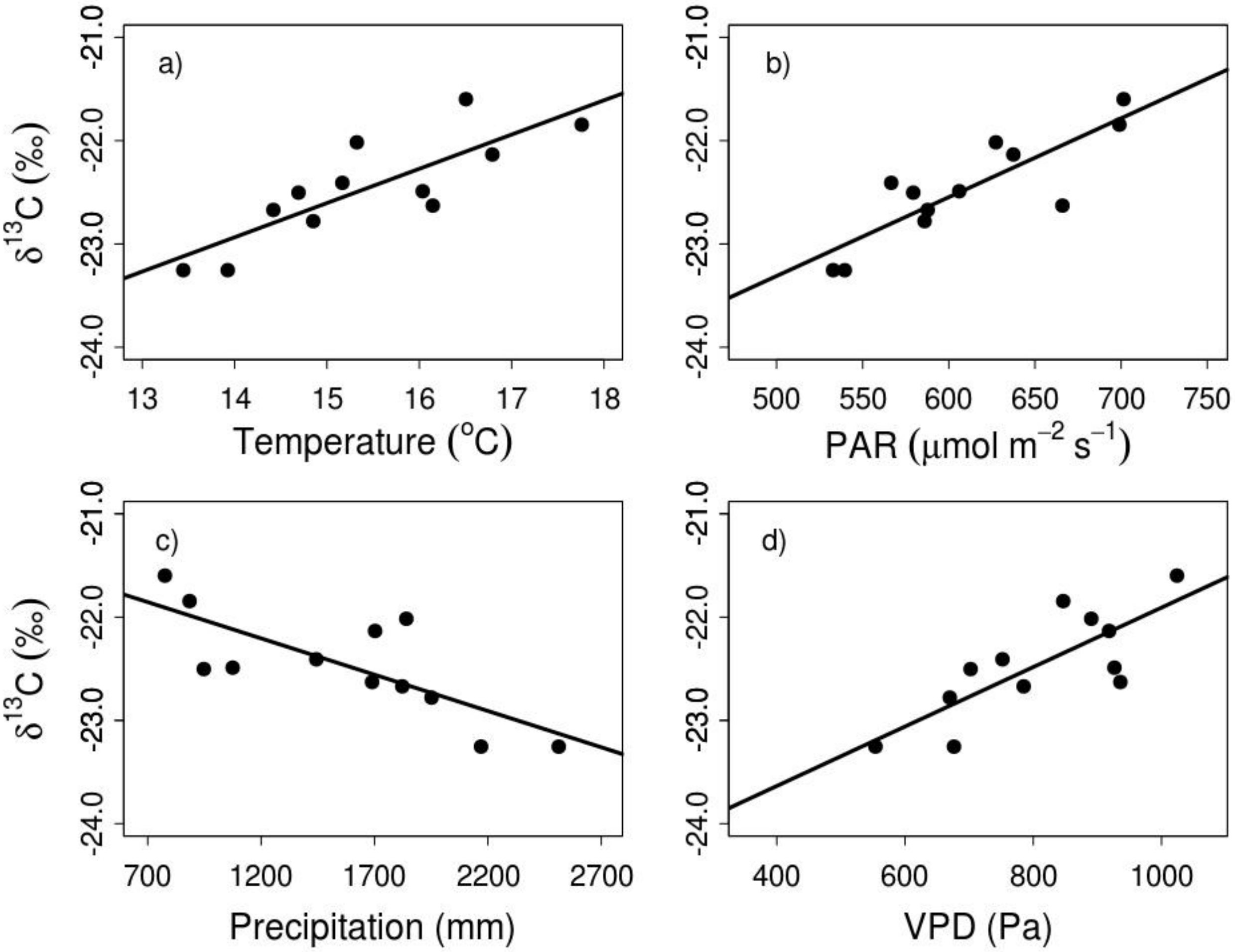

Figure 7: *Linear regressions between inter-annual $\delta^{13}C$ values calculated by averaging the measured intra-annual $\delta^{13}C$ values and local environmental variables, i.e. a) air temperature, b) photosynthetically active radiation (PAR), c) precipitation and d) vapour pressure deficit (VPD) at Hyytiälä with cell longevity and on the optimised statistical period established to provide the highest relationships.*

3.4 Seasonal δ^{13}C *variation and environmental forcing*

Linear regressions between δ^{13}C values and local environmental data at the intra-annual resolution for a "realistic" radial growth period (i.e. presented in table 2) present relatively weak relationships (see Table 4). During the early-wood tree-ring section, δ^{13}C values are similarly well explained by air temperature ($R^2 = 0.246$, $p < 0.05$) and PAR ($R^2 = 0.234$, $p < 0.05$), vapour pressure deficit presents a weaker relationship ($R^2 = 0.154$, $p < 0.05$) while precipitation is not influencing the δ^{13}C variation significantly (not significant, $p > 0.05$). For the middle-wood and the late-wood tree-ring sections, all four relationships with local environmental variables are significant with a slightly stronger influence by PAR. For the total tree-ring section, the air temperature relationship ($R^2 = 0.261$, $p < 0.05$) and vapour pressure deficit ($R^2 = 0.144$, $p < 0.05$) remains unchanged. However, the PAR relationship ($R^2 = 0.138$, $p < 0.05$) is largely decreased compared to the division into sections. Due to the absence of significance for precipitation in the early-wood section, the total wood relationship is weak but significant ($R^2 = 0.093$, $p < 0.05$). The combination of the local environmental variables into multiple linear regressions does not improve the explanation of the δ^{13}C variation both for tree-ring sections and total wood.

For a "statistically optimised" period of correlation, the linear regressions present stronger relationships than for the "realistic" time scale (see Table 4). When arranging the δ^{13}C values depending on the tree-ring sections, the δ^{13}C variation during the early-wood is primarily influenced by air temperature ($R^2 = 0.605$, $p < 0.05$) and vapour pressure deficit ($R^2 = 0.555$, $p < 0.05$) while PAR ($R^2 = 0.407$, $p < 0.05$) and precipitation ($R^2 = 0.307$, $p < 0.05$) present weaker relationships. The δ^{13}C variation during the middle-wood tree-ring section exhibit a more dominant influence from vapour pressure deficit ($R^2 = 0.465$, $p < 0.05$) than from the other environmental variables. During the late-wood section, the δ^{13}C values are mainly influenced by PAR ($R^2 = 0.501$, $p < 0.05$) and precipitation ($R^2 = 0.650$, $p < 0.05$), then by vapour pressure deficit ($R^2 = 0.448$, $p < 0.05$) while the air temperature relationship ($R^2 = 0.296$, $p < 0.05$) is weaker.

The influence of the local environmental variables on the total tree-ring for a "statistically optimised" period is not representative of the stronger relationships with air temperature in the early-wood section while PAR and precipitation relationships are stronger within the late-wood section. Therefore, considering only total growth could adversely impact the interpretation of the intra-annual environmental signal in δ^{13}C values. Combining the local environmental variables shows the early-wood section to be characterised by the significant influence from all four environmental variables, the middle-wood section from vapour pressure deficit only, while the late-wood section is significantly explained by PAR and precipitation. However, the increase in the proportion of variance explained is small compared to the single linear regressions. Therefore, finding the time period when the environmental signal is the clearest (i.e. the statistically optimised time period) to match δ^{13}C values with local environmental variables could provide a more powerful tool to study the strength of the environmental signal in intra-annual data than an attempt to combine local environmental variables into a multiple linear regression model.

Table 4: *Linear relationships between intra-annual $\delta^{13}C$ variation and local environmental variables (determined by R^2, $p < 0.05$) for each tree-ring section and total wood formation either for a 'realistic period' of radial growth or for a 'statistically optimised' period at Hyytiälä. 'Model' stands for the combination of the local environmental variables into a multiple linear regression while 'ns' stands for not significant.*

Variable	Ring section	R^2 ($p < 0.05$)	
		Realistic	Optimal
Temperature	early	0.246	0.605
	middle	0.269	0.289
	late	0.243	0.296
	total	0.261	0.334
PAR	early	0.234	0.407
	middle	0.342	0.300
	late	0.361	0.501
	total	0.138	0.341
Precipitation	early	ns	0.307
	middle	0.210	0.314
	late	0.262	0.650
	total	0.093	0.220
VPD	early	0.154	0.555
	middle	0.138	0.465
	late	0.215	0.448
	total	0.144	0.459
Model	early	0.307	0.664
	middle	0.362	0.465
	late	0.419	0.717
	total	0.271	0.561

3.5 Evolution of the environmental forcing during the growing season

It is evident from Figure 8 that the slope of the linear regressions varies between the tree-ring sections. By testing the significance of the difference between the slopes (t-test, $p < 0.05$), it appears that the slopes from early- and late-wood for PAR and precipitation differ significantly. Therefore, the relationship between $\delta^{13}C$ values and PAR or precipitation evolves during the growing season with an increase of the response from $\delta^{13}C$ values to the forcing induced from these variables towards the late-wood compared to the early-wood tree-ring sections.

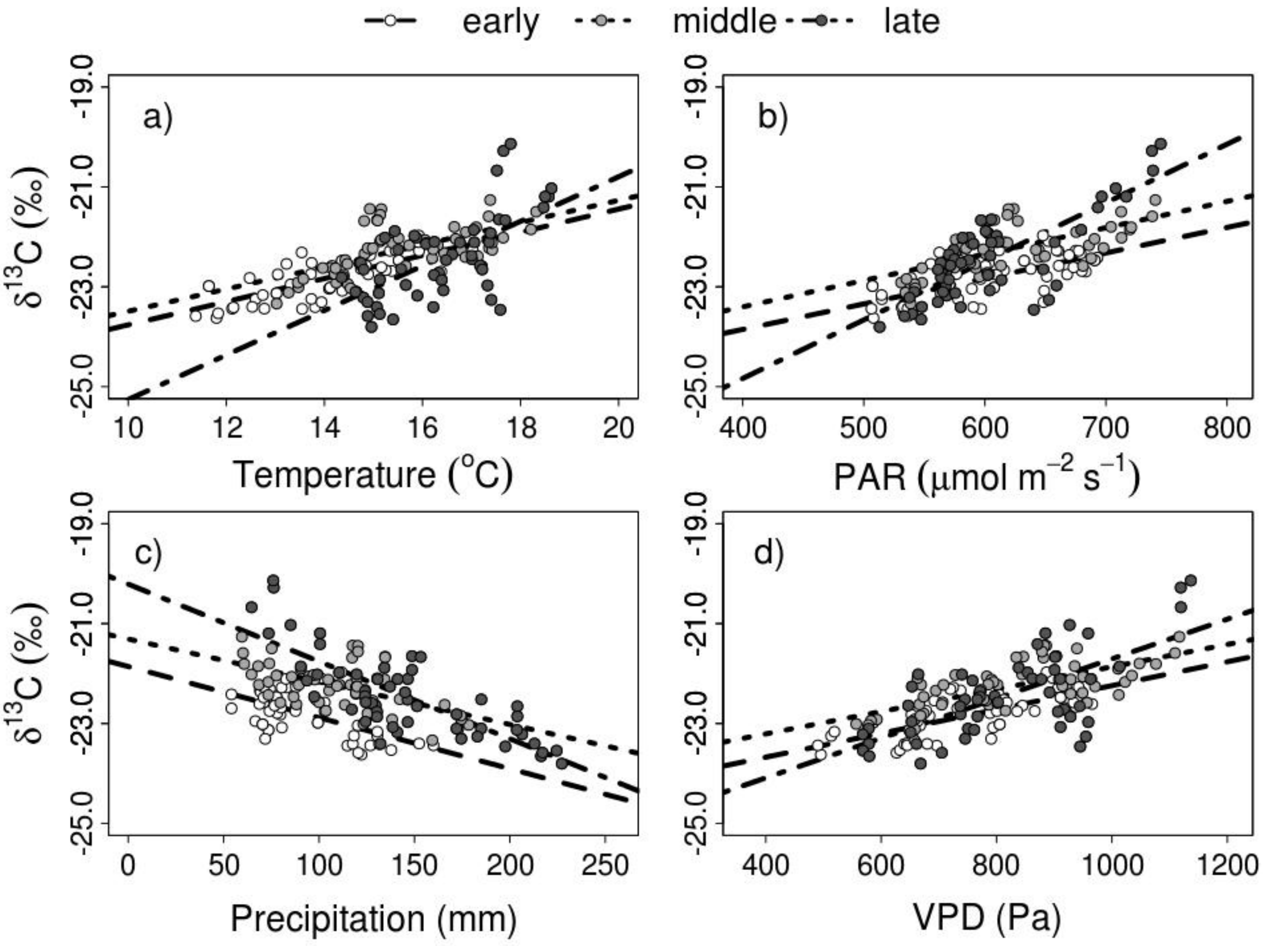

Figure 8: *Partial linear regressions on tree-rings sections (i.e. early: dashed line, white face; middle: dotted line, grey face; late: dash-dotted line, dark grey face) between mean intra-annual* $\delta^{13}C$ *values and local environmental variables, i.e. a) air temperature, b) photosynthetically active radiation (PAR) c) precipitation and d) vapour pressure deficit (VPD) at Hyytiälä.*

4. Discussion

4.1 Predicting wood radial growth

A possible explanation for the limited success in predicting wood growth based on ecosystem fluxes is that measured fluxes may include a contribution from other vegetation present at the study site, reducing the signal from the studied Scots pines. It is also likely that the limited wood growth information currently available for use in this study cannot be directly linked to net carbon and water fluxes and that additional observational data on cambial dynamics would be required to resolve these signals (Offermann et al., 2011). The robust determination of onset and cessation of wood growth remains a challenging topic for dendrology and phenology studies

(Menzel et al., 2006). However, recent progress in high resolution measurements of wood formation dynamics permits better estimation of radial wood growth and thus improve a realistic calibration between δ^{13}C time series and the time period for environmental integration (Cuny et al., 2015).

The Gompertz function can successfully reproduce cambial cell production when microcore data are available. However, due to the uncertainties in the determination of radial growth onset and cessation using thresholds of air temperature or PAR, the Gompertz curve may not adequately represent the period of radial growth when dendrological data are not available. Results of models such as the Vaganov-Shashkin model (Vaganov et al., 2006), a simple biosphere model (Sellers et al., 1986) or the TREERING model applied to isotopes (Hemming et al., 2001) may add valuable information.

Despite the clear advantage of using the Gompertz function to predict wood growth when only limited dendrological information is available (Rossi et al., 2003), the timing of wood formation phases of individual cells is poorly represented with this method (Dufour and Morin, 2007). However, deriving the time period of each cell phase demands a more precise knowledge of the cambial dynamics than the evaluation of the general trend for cell development modelled by the Gompertz approach. The difficulties of estimating wood cessation when dendrological information is sparse further justifies the preference of the Gompertz method over a more sophisticated approach.

4.2 Environmental controls on the inter-annual δ^{13}C *variation*

The observation of correlation between environmental variables (i.e. temperature, PAR, precipitation and VPD) and δ^{13}C time series is expected and physiologically justifiable. The general trend in inter-annual δ^{13}C time series presented here agrees well with findings of Young et al., (2010); Loader et al., (2013); McCarroll and Pawellek, (2001); and Seftigen et al., (2011), despite the difference of used material (i.e. wholewood versus cellulose). The dominance of the radiation control on annual δ^{13}C variation has been previously described across Fennoscandia; a region experiencing low moisture stress while air temperature may represent a secondary control (Young et al., 2010; McCarroll and Loader, 2004; McCarroll and Pawellek, 2001; Seftigen et al., 2011; Loader et al., 2013). A combined effect of water and radiation was also reported (Gessler et al., 2001; Farquhar et al., 1989). The relationship between PAR and δ^{13}C values for a "realistic" growth period at the inter-annual resolution presents a strong linear association both with and without the addition of cell lifetime. However, air temperature, precipitation and vapour pressure deficit only exhibit significant linear relationship when adding cell lifetime. Therefore, the main environmental influence on inter-annual δ^{13}C values can be detected in both cases but secondary controls (i.e. air temperature, precipitation and vapour pressure deficit) cannot. This suggests that the inclusion of cell lifetime is necessary to explain the environmental effect on intra-annual δ^{13}C values. Most of the variance in δ^{13}C values can be explained by PAR only, while the addition of secondary controls does not significantly improve the explanatory power. It is also likely that all modelled and observed correlations may include a degree of non-linearity or change in their relative importance through out the growing season.

When correlating the $\delta^{13}C$ values with local environmental variables over the "statistically optimised" period including cell lifetime, temperature, PAR, precipitation and vapour pressure deficit display statistically significant and similarly strong relationships. Therefore, when the environmental signal is relatively clear, a similar strength from each of the tested local environmental variables can be expected. However, the autocorrelation of these local environmental variables should be accounted for and may limit the capacity of a purely statistical model to predict the $\delta^{13}C$ variation. A more mechanistic approach to model $\delta^{13}C$ values beyond environmental variables alone is therefore more likely to explain a greater proportion of the variation of $\delta^{13}C$ measurements (McCarroll and Loader, 2004; Ogée et al., 2009).

4.3 Environmental controls on the intra-annual $\delta^{13}C$ *variation*

Linear relationships with local environmental variables are clearly stronger when including cell lifetime for a "realistic" period for radial growth. However, the derivation of a "statistically optimised" period of correlation between $\delta^{13}C$ values and local environmental data still provides a better prediction of intra-annual $\delta^{13}C$ variation. Therefore, care should be taken to ensure that the direct linking of $\delta^{13}C$ to realistic wood formation dynamics does not add unwanted noise to the environmental signal. Investigation of the influence of the environmental variables on intra-annual $\delta^{13}C$ time series supports previous observations made on wood formation (Antonova and Stasova, 1993; Rossi et al., 2006). Early wood production from pine trees is known to depend almost entirely on current photosynthates (Dickmann and Kozlowski, 1970; Glerum, 1980; Barbour et al., 2002; Kress et al., 2009). Therefore, matching co-occurrent environmental variables with $\delta^{13}C$ values in tree-ring sections was expected to improve the environmental signal at the intra-annual resolution.

This division into three tree-ring sections matches the pattern of $\delta^{13}C$ measurements with an increase in $\delta^{13}C$ values observed for the early-wood, a peak for the middle-wood in nine out of thirteen years, and finally a decline in $\delta^{13}C$ values in late-wood. Despite the high correlation between air temperature and PAR, our findings show a shift of importance from all tested environmental variables for the early-wood to vapour pressure deficit for the middle-wood and photosynthetically active radiation and precipitation for the late-wood. Moreover, it is noticeable that the variance explained by the linear regressions on $\delta^{13}C$ values by tree-ring sections is greater than when considering the whole tree-ring. Therefore, the shift of importance from the local environmental variables during the growing season is likely to be linked with the intra-annual pattern of $\delta^{13}C$. This fact may indicate changes in the allocation and usage of stored photosynthates as well as seasonal changes in moisture stress and could be used to identify which variable is significantly influencing the $\delta^{13}C$ values at a given time during the growing season.

5. Conclusions

The exploration of the relationship between wood radial growth and environmental variables such as temperature, photosynthetically active radiation, precipitation and vapour pressure deficit by a newly developed approach using environmental thresholds and Gompertz curves to predict cambial activity leads to evidence of a strong link between tree-ring sections and intra-annual $\delta^{13}C$ variation. However, extracting the environmental signal from seasonal $\delta^{13}C$ profiles suffers from the current lack in knowledge of post-photosynthesis fractionation processes. Therefore, matching local environmental variables directly with wholewood $\delta^{13}C$ measurements by linear regression alone can only explain a limited portion of the observed isotopic variation on a "realistic" time scale. PAR and precipitation influence the $\delta^{13}C$ values with a variable intensity through out the growing season. The increase in the gradient of the response of $\delta^{13}C$ values to environmental forcing may indicate an increasing demand on trees to maintain growth and metabolism towards the late growing season.

This study provides evidence that integration of environmental forcing on tree radial growth at the intra-annual resolution may vary through out the growing season. It further demonstrates how intra-annual $\delta^{13}C$ time series can now be produced for multiple years routinely. Such data are capable of preserving a high degree of common forcing (EPS) equivalent to annually-resolved data and have the potential to make significant contribution to plant physiology and palaeoclimatology. For this potential to be realised and the link between tree physiology and the environment to be more fully understood, complementary data from dendrometers, microcores, meteorological stations and ecosystem flux measurement stations are essential.

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