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Interrogating tree response to climate forcing via high resolution stable carbon isotope (delta13C) analysis of Pinus sylvestris L. and eddy covariance measurements.

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Interrogating tree response to climate forcing via high resolution stable carbon isotope ($\delta^{13}C$) analysis of *Pinus sylvestris* L. and eddy covariance measurements.

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Abstract

Tree-rings are natural archives of the climate variation experienced by trees during their life span. Because trees actively discriminate against ^{13}C versus ^{12}C in atmospheric carbon dioxide due to environmental forcing inducing higher assimilation of ^{12}C in optimal conditions for growth, the ratio between these two isotopes represents a record of climate variability occurring at the time of the wood formation. Therefore, the δ^{13}C can be used to reconstruct palaeoclimate from when the trees sampled were living. As the instrumental period from meteorological methods to measure climate is relatively short (last 150 years), the calibration between δ^{13}C time series and climatic data can be used to improve the understanding of climate variability through longer periods. The main objective of this study is to produce a consistent methodology for the reconstruction of climate and environmental forcing on trees from the high resolution δ^{13}C time series over the period 1997-2009 at three study sites in Europe where extensive eddy covariance measurements have been conducted. This atmospheric measurement technique permits a very fine resolution to observe the exchange of gases between the atmosphere and a land surface with additional applications in meteorology. At Hyytiälä, dendrometer and microcore measurements were used to test if a methodology can be developed to predict the occurrence of radial growth during years when dendrological data are missing. The modeling of the intra-annual rate of growth is then performed via the Gompertz equation. Integration of cell life time to match climate information with δ^{13}C time series is also assessed. The δ^{13}C signature from both inter- and intra-annual resolution are tested against three weather variables: photosynthetically active radiation, temperature and precipitation. The results show stronger linear responses from the δ^{13}C time series of the most northern site (Hyytiälä, Finland) to the weather variables while the two other study sites (Norunda, Sweden and Loobos, the Netherlands) did not show significant linear relationships at both annual and intra-annual resolution. The approach developed in this study represents a first step in developing a generic method accessible for non-specialists in dendroclimatology for the use of δ^{13}C time series as climate archives.

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Acknowledgements

Dedication

I dedicate my PhD thesis to my parents, Jeannine and Daniel Soudant, who encouraged me during all my life to achieve greater goals.

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Chapter I: Introduction

1.1 Climate investigation

Increasing concerns as to the impacts of climate change has highlighted the need for detection, modelling and prediction tools to assess climate variation. The development of remote sensing using satellite, airborne and ground instruments has provided high data quantity and quality concerning climate variations for numerous sites of study and climatic influences. However, for most parts of the world precise meteorological data are not available on a long time scale due to the equipment cost and complex handling (Baldocchi, 2003). Analysis of natural climate dependent phenomena can provide climatic indications by establishing the nature of the dependency to climate and its intensity (Bradley, 1999). Tree-rings from annual tree growth can be used as such. Although the signal from these records can be difficult to interpret in terms of climate. Investigations on how to combine dendrology and climatology for climate reconstruction purposes have become an increasingly important subject (Offermann *et al.*, 2011; Gessler *et al.*, 2009; King *et al.*, 2013). The high data coverage and long dendrochronologies could be synchronised with on-site high-resolution weather dataset over a common period to benefit from all advantages of these techniques without the drawbacks. Therefore, this work aims to establish a methodology to analyse the climatic signal of tree-rings by matching observations of climate factors with carbon isotope values on a realistic time scale of tree growth. This approach should open this field of study to non-specialist laboratories by the use of simple techniques demanding little knowledge of tree physiology.

1.2 Tree-rings as environmental archives

The use of tree-rings as climate archives is commonly called dendroclimatology. The first investigation over the potential of this technique was performed by Douglass (1919) during the early 20th century. The use of tree-ring patterns as a local record of the environment was then extensively described by Fritts (1976).

Tree radial growth occurs each year by the initiation of cell division in the cambium. The timing of radial wood formation depends on tree species, latitude, altitude and climatic influences. In Europe, radial growth usually begins in April-May while the peak in growth occurs in the summer months and can last until October-November.

To form new cells, the cambium relies on soluble sugars brought by the phloem tissues. Their composition and proportion is variable through the growing season and can be either compounds stored from the previous year of growth or newly formed assimilates via photosynthesis at leaf level. As local weather conditions influence this process, trees record a climatic signal in tree-rings. Therefore, measuring tree-rings characteristics such as ring width, isotopic composition for carbon (δ^{13}C), oxygen (δ^{18}O), hydrogen (δ^{2}H or δD) or density can provide information about climate and are usually referred as proxies. Different time spans have been used to study these features: decadal, annual or even intra-annual. Tree-ring properties can then serve to understand tree physiology, build chronologies of past climatic variation or date wood material.

The use of trees as climate records benefits from their wide distribution over the globe which permits a more extensive sampling compared to other techniques using ice or sediments (Cook *et al.*, 1994). In temperate regions, tree species selected for dendroclimatology show definable annual growth increments such as *Pinus* (pine) or *Quercus* (oak) genera growing in environments with marked seasonal climatic variation. This technique provides a clearer climate signal when trees are growing towards the limit of their ecological range where only one climatic factor is the main limiting resource for tree growth (LaMarche Jr., 1974; Schweingruber, 1996). When more than one climatic factor is limiting growth, the climate signal is more difficult to extract due to the interaction of the climatic factors. Additionally, long records of tree-rings are influenced by the historic evolution of the atmospheric δ^{13}C towards more isotopically depleted values in the post-industrial period due to the release of CO_2 from fossil fuels to the atmosphere. Hence, the post-industrial age is naturally depleted in ^{13}C compared to the atmosphere of the pre-industrial period. This artificial trend is necessary to be removed from δ^{13}C time series before analysing the climate signal (Briffa, 2000; Hughes, 2002; Freyer & Belacy, 1983).

One of the developments in dendrology techniques consists of analysing the composition of the main elements in the wood. Trees actively sample carbon dioxide

and water from their direct environment and modify the source isotopic ratio via physiological processes in response to environmental stress. The use of the main wood elements isotopic composition in dendroclimatology was initiated by Urey (1947) who first observed the covariance of carbon stable isotope ratio in wood material and temperature. However, it is only by an intensive study of the plant metabolism processes that the relationship between tree physiology and carbon isotopes was clearly established (Farquhar *et al.*, 1982, 1989).

Previous studies using isotopes as proxys identified the main climate drivers in a wide range of environments and tree species (Saurer *et al.*, 1995; Krishnamurthy, 1996; Robertson *et al.*, 1997a). These investigations showed that the climate forcing differs from site locations depending on the local conditions and the global climatic system. Assimilation of CO_2 from the atmosphere occurs at the leaf level and is regulated by the intervention of two processes: the stomatal conductance and the photosynthetic rate. At dry sites, relative humidity and soil water status are dominant controls over these processes while at moist sites, the dominant controls are summer irradiance and temperature. Soil water transported by the xylem tissues to the leaves provides the H_2O molecules necessary to the photosynthesis process. Evaporation, leaf transpiration driven by temperature and vapour pressure deficit will modify the signature of source water and therefore the isotopic ratio (Buhay *et al.*, 1996; Craig & Gordon, 1965; Dongmann *et al.*, 1974; Barbour *et al.*, 2001, 2002).

While an annual resolution is desirable for climate reconstruction purposes, it is not always achieved for long tree-ring chronologies due to the time consuming procedures to build isotope series (Kress *et al.*, 2009; Young *et al.*, 2010; Treydte *et al.*, 2009; Loader *et al.*, 2003). To better understand tree physiology, some studies have initiated the use of isotopes at the intra-annual resolution and investigated how well the information contained in the tree-rings is linked to the seasonal climatic variation during the tree growth processes (Wilson & Grinsted, 1975, 1977; Leavitt & Long, 1982, 1991; Leavitt, 1993; Ogle & McCormac, 1994; Loader & Switsur, 1995; Robertson *et al.*, 1997b; Sheu *et al.*, 1996; Walcroft *et al.*, 1997; Schleser *et al.*, 1999; Porté & Loustau, 2001; Warren *et al.*, 2001; Leavitt, 2002; Leavitt *et al.*, 2003; Helle & Schleser, 2004). However, these studies were limited by the non automation of isotope extraction techniques and the lack of suitable methods for a precise dissection of tree-rings with curved and non-parallel tree-ring boundaries which permitted only few tree-rings to be analysed.

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1.3 δ^{13}C time series from tree-rings at the annual resolution

Analysis of the δ^{13}C variation at the annual resolution can inform about the tree response to climate between successive growing seasons. Climate factors such as temperature, light and precipitation have been identified to co-vary with the annual values of δ^{13}C. These analysis are mainly carried out on cellulose as the wholewood can be altered through time when using multi-centennial samples (Wilson & Grinsted, 1975). As earlywood can contain an isotope signal from storage compounds, latewood can be isolated to obtain annual resolution (Lipp *et al.*, 1991; Sheu *et al.*, 1996).

1.4 δ^{13}C time series from tree-rings at the intra-annual resolution

By dividing each tree-ring into smaller sections, Leavitt & Long (1991) initiated the investigations over the climate signal in δ^{13}C at the intra-annual resolution. Material to carry δ^{13}C seasonal analysis can be from wholewood, cellulose or organic matter as their seasonal variation is similar despite possible offsets (Warren *et al.*, 2001; Skomarkova *et al.*, 2006; Helle & Schleser, 2004). The influence of temperature and precipitation have been investigated at this resolution. However, the link between the δ^{13}C at the leaf level and in the tree-rings is indirect. Post-photosynthetic processes can modify the δ^{13}C signature of the sugars used to build the tree-ring during their transportation by the phloem and their redistribution in the different tree organs (Gessler *et al.*, 2009). Another effect mitigating the δ^{13}C amplitude in tree-rings comes from the mixing of phloem sugars both temporally and spacially before their use in tree-ring formation (Pate & Arthur, 1998; Kagawa *et al.*, 2006). The use of stored carbon compounds during seasonal growth can also be a source of uncertainty when evaluating the climate signal. Drew *et al.* (2009) suggest that the occurrence of a water stress during tree radial growth can trigger the storage of carbon compounds that will be used only after the release of the water stress. High values of δ^{13}C when co-occurring with precipitation may be an indication of such effects (Chapin *et al.*, 1990). Despite the identification that climate is not the main driver of the seasonal δ^{13}C variation due to the post-photosynthetic effects, accurately matching δ^{13}C values with climate factors by scaling their relationships with the timing of tree growth could improve the understanding of tree physiology processes and the estimate of the climate signal contained in tree-rings at the intra-annual resolution.

1.5 Temporal properties of wood growth

When evaluating the co-occurent weather forcing on intra-annual isotopic time series from tree-rings, it is necessary to understand the temporal dynamics of cell production and maturation. This step requires specific investigations on wood formation performed on developing cells during xylem expansion (Wimmer, 2002). In temperate and boreal regions, the cambial activity responsible for the radial growth of trees is periodic and characterised by an alternation between an active period during summer and a dormant period in winter (Iqbal, 1994; Fujii *et al.*, 1999). Therefore, the modelling of wood growth can be restricted to the active period alone (Dufour & Morin, 2007). During the active period, the growth of xylem cells can be subdivided to different phases from cell division, enlargement and secondary wall thickening which are separated in space and time (Rossi *et al.*, 2006a).

Consequent stages of formation and development of cells have been found to be independent processes and their reactions to environmental factors can be different (Antonova & Shebeko, 1981; Antonova *et al.*, 1983) due to different physiological controls (Larson, 1960; Richardson & Dinwoodie, 1960; Wodzicki, 1964; Zahner *et al.*, 1964). To allow non-specialist laboratories to carry out intra-annual studies on isotopic time series, the approach using S-shaped curves including the Gompertz curve can be performed on intra-annual cell counts without distinguishing the different tracheid development phases (Camarero *et al.*, 1998). Therefore, the use of the Gompertz equation developed by Rossi *et al.* (2003) to model cell number increase, rate of growth and periods of cell differentiation was adapted in this study to predict these dendrological features during years when dendrological information are unavailable.

A simple method to consider when wood cells can integrate climate information without an intensive study of wood formation is to add a period for cell activity corresponding to the extent of the cell phases from the date of cell formation estimated via the Gompertz equation. As earlywood cells live from a few days to several weeks while the latewood cells are able to stay alive months after their formation, this considerable difference induces that the climate information recorded in wood cells has a different integration period depending on the longevity of the cells during the growing season (Helle & Schleser, 2004; Schollaen *et al.*, 2014).

1.6 A comparative approach of three study sites in Europe

The evaluation of the climate impact on trees at the European scale cannot be based only on trees at the boundary of their geographic distribution as it will provide a false representation of the stress intensity experimented by the trees at different locations. Therefore, studies covering multiple study sites in Europe may permit to identify a gradient of climate responses depending on the site properties. Despite the evidence of a co-variance between different tree species in response to climate, study sites where a dominant species is present would provide the advantage of a homogenous landscape where each tree is equally impacted by the weather conditions. To record intra-annual climate variation, the presence of a flux-tower close to the trees sampled for $\delta^{13}C$ analysis provides the most accurate on-site measurements at high temporal resolution. This current work has selected three study sites presenting dominant Scots pine at different locations in Europe and with the presence of flux-towers recording environmental changes for more than 10 years. The most southern site was the first to be sampled at Loobos (the Netherlands) in 2009, then Norunda (Sweden) in 2010 and finally the most northern site selected, Hyytiälä (Finland) in 2011. These three sites present different climate influences characterised by variations in temperature, light and precipitation. The sites should still present similar types of response to climate as they are all in northern Europe with however, an increase in the response intensity to climate forcing where the conditions are the most limiting to growth.

1.7 Objectives and principal investigations

The present study aims at setting a simple procedure to compare inter-annual and intra-annual $\delta^{13}C$ time series with environmental variables for non-specialist laboratories. Secondly, assessment of the addition of cell longevity to the integration period between $\delta^{13}C$ values and co-occurrent environmental factors is carried out. This study profits from the improvements in laser sampling and mass spectrometry techniques to produce relatively long $\delta^{13}C$ time series on *Pinus sylvestris* to assess how the climate signal could be extracted with simple statistical tools after applying $\delta^{13}C$ corrections due to atmospheric changes. The Gompertz curve is then used at the intra-annual resolution to time the cell formation process with the addition of cell longevity integrating environmental factors on a realistic time scale corresponding to the time when radial cells are alive and active.

1.8 Research aims

This thesis focuses on two research aims in the dendroclimatology field:

- to build a simple methodology from isotope extraction to climate correlation applicable to the European scale;

- to improve the current knowledge on the complex relationship between the $\delta^{13}C$ and the climate factors partially driving its variation at both inter-annual and intra-annual resolution at different study sites.

1.9 Thesis structure

The thesis is organised as the following:

1.9.1 Chapter II: Literature review

An extensive bibliography on what has been achieved so far in tree-ring research with a particular focus on extracting intra-annual variability of $\delta^{13}C$ is presented in Chapter II. The theory and techniques to produce flux-tower measurements is also briefly described.

1.9.2 Chapter III: Data acquisition and collection

All datasets used for this study are presented in Chapter III with sections for tree-ring data, flux-tower data, dendrological information and isotopic measurements. A brief discussion shows how the data quality will impact the final results of this study.

1.9.3 Chapter IV: Investigation of wood growth properties and their modelling via the Gompertz equation.

Chapter IV focuses on how the growing season is defined by the methodology developed in this study. Three alternative methods are discussed with consideration of the uncertainties over the determination of the onset, cessation of radial growth and the attribution of dates to each isotope value at the intra-annual resolution. The method providing the most accurate dates compared to dendrological measurements at the study sites is selected after discussion of criteria to characterise the performance of each method to predict growth. The impact of this final method on the intra-annual correlation with climate is also assessed here.

1.9.4 Chapter V: Linear relationships between weather and isotope measurements at the inter-annual resolution

Inter-annual $\delta^{13}C$ variability between sites and the amplitude of the $\delta^{13}C$ signal are analysed in Chapter V. The common signal from the $\delta^{13}C$ measurements of three trees at each site is matched with weather variables over the growing season calculated in Chapter IV for the period 1997-2009. The temperature, light and precipitation influences on the $\delta^{13}C$ values are then evaluated by using simple linear regressions. The combined influence of the weather variables is assessed by a multiple linear regression model to inform how well the $\delta^{13}C$ values can record a climate signal on the selected time period at the inter-annual resolution.

1.9.5 Chapter VI: Linear relationships between weather and isotope measurements at the intra-annual resolution

The outputs from the methodology produced in Chapter IV provide the information necessary to model tree radial growth variation during the years studied (1997-2009) and permit to investigate the seasonal response of trees to climate forcing. Intra-annual $\delta^{13}C$ time series are then matched with weather variables at this finer resolution at the three study sites and these relationships are evaluated by means of simple linear regressions. As for Chapter V, a multiple regression linear model is applied to evaluate the combined interaction of the weather variables on the intra-annual $\delta^{13}C$ values.

1.9.6 Chapter VII: Discussion

Chapter VII discusses the results and their significance through the spectrum of the literature review. A particular attention is carried on the meaning of the results concerning the interaction between intra-annual time series and climate. Other points of discussion are the importance of physiological effects such as carbon pool limitation in the $\delta^{13}C$ signal, assessment of the methodology to reproduce the wood growth dynamics, the validity of the model using flux-tower data to predict isotope values, the implications and further investigations that need to be carried to improve the use of $\delta^{13}C$ as climate archives at the intra-annual resolution.

A flow chart of the work carried out during the thesis is presented in Figure 1.1.

Wood growth

Data collection

Dendrometers :
2 years Loobos (2009-2010)
2 years Norunda (2010-2011)
3 years Hyytiälä (2007-2009)
Microcores :
3 years Hyytiälä (2007-2009)

Determination of wood growth

by the net ecosystem exchange
by the evapotranspiration
by co-occuring environmental variables
by cumulated environmental variables

Wood growth modeling

Gompertz approach using estimated onset and cessation dates

Comparison with dendrological data

Integration of cell life time

Tree-rings

Core sampling

3 trees sampled at each site

Laser analysis

Preparation for laser procedure (drying, cutting, microtome)

Mobile resin extraction (Soxhlet extractor)

Laser ablation / microdissection

Production of the intra-annual $\delta^{13}C$ time series

Analysis of $\delta^{13}C$

Raw intra-annual $\delta^{13}C$
EPS calculation
Standardisation
Atmospheric correction
Seasonal correction

Flux-tower data

Site visits

Loobos (2009, 2010)
Norunda (2010)
Hyytiälä (2011)

Data treatment

Rename variables
Outliers / NA
Discard unwanted observations
Gapfilling

Climate analysis

Subsets
Statistical properties
New variables

Output

Time series / Graphics

Climate forcing analysis on $\delta^{13}C$ from wholewood

Annual $\delta^{13}C$ time series vs climate variables
Intra-annual $\delta^{13}C$ time series vs climate variables
Modeling the $\delta^{13}C$ variability by using linear regression

Figure 1.1: *Flow chart of the work carried out during the PhD. Labwork has been both conducted at Swansea University and at GFZ Potsdam, Germany.*

Chapter II: Literature review

2.1 Introduction

The purpose of this literature review is to present the previous work that has been carried out in tree-ring research to predict climate with a particular focus on isotope studies in dendroclimatology. The first section will briefly present the recent reasons for climate studies to be carried out. The use of tree-rings as climate archives will be then described from the first studies using tree-ring width to the more recent isotope theory and their applications. Finally, the flux-tower theory and its development will be briefly presented to explain how climate information is being recorded at the study sites.

2.2 The recent anthropogenic climate change and the need for understanding carbon and climate interactions

The past millennium has experienced various climatic events from cold to warmer periods (Williams & Wigley, 1983). However for the last century, Humanity by its industrial activities at an unprecedented scale has interfered with the global climate system. With the industrial revolution start dated at year AD 1850, the impact of human activities in climate records is clearly identifiable (Oldfield & Alverson, 2003). By releasing greenhouse gases such as carbon dioxide that can trap infrared radiation in the atmosphere and transforming landscapes, the industrial age is characterized by the increase of the globally averaged temperature and contributed to the greenhouse effect.

If we consider only the period between AD 1956 and 2005, mean global temperature rose by $0.13 \pm 0.30°C$ per decade. This is nearly twice the rate of increase than when including the 50 previous years to the record (AD 1906 to 2005) (Pachauri & Reisinger, 2007). The warmest period of the millennium is considered to be the

20th century (Jones *et al.*, 2001; Bradley *et al.*, 2003) due to the anthropogenic impact (Mann *et al.*, 2003).

The increasing volume of scientific literature and growing public opinion made clear human induced climate is a complex issue needing the involvement of governments and experts to better understand climate processes (Pachauri & Reisinger, 2007). In this context, current uncertainties relating to human activities impacting environmental processes and the possible consequences on the climate system represent important scientific challenges to be addressed in the coming decades.

2.3 Tree-ring research

2.3.1 Structure of the tree-ring

The tree-ring width of a single year of growth for tree species in Europe can be visually appreciated as each annual ring is formed by the succession of two constituents: earlywood and latewood. Earlywood can be described as soft and light coloured. Tree cells are formed rapidly during the early period of the growing season and are large and thin walled, they can allow great quantity of water to flow from roots to leaves but are poorly protected against desiccation. However, latewood cells growing during the summer during the year are dense and darker coloured due to a denser concentration of cells which are smaller and thick walled to resist water shortages (Domec & Gartner, 2002). Another feature varying in these two wood components is the shorter longevity of the earlywood cells that live from a few days to several weeks while the latewood cells are able to stay alive months after their formation. This considerable difference induces that the climate information recorded into wood cells has a different integration period depending on the longevity of the cells during the growing season (Helle & Schleser, 2004).

2.3.2 Climatic and non-climatic influences

As the tree-ring width varies from a year to another, investigation of the dominant drivers of this variation has been carried out. In cold and wet conditions such as in the northern latitudes, trees were found to be limited by temperature (Briffa *et al.*, 1988) and day length (Rossi *et al.*, 2006b). Whereas in warmer and drier conditions, the limitation seems to be primarily coming from precipitation (Hughes & Funkhouser, 1998). Despite intra-site variation, width sequences in the tree-rings indicating climate influence at a same site are conserved. Although, this variation is also the consequence of other influences than climate. Therefore, the

determination of individual tree growth and tree-rings presents a non-climatic component in ring width time series. To access only climatic information when considering using tree-ring width data, it is then necessary to remove the unwanted variability from these series. Equation 2.1 shows all components contained in tree-ring width series (R_t) (Cook & Kairiukstis, 1990).

$$R_t = A_t + C_t + \delta D1_t + \delta D2_t + E_t \qquad (2.1)$$

Where R_t is the tree-ring width series, A_t is the age trend, C_t is the climate signal, $\delta D1_t$ is the endogenous disturbances, $\delta D2_t$ is the stand wide disturbance and E_t is the unexplained variability. By increasing the number of trees investigated by site, the noise coming from endogenous disturbances ($\delta D1_t$) and unexplained variability (E_t) can be reduced. It is then possible to average these series and produce a mean value function that is representative of the tree signal at a site (Frank et al., 2006). By selecting trees without evident signs of injuries due to fire or pathogenic attacks, the stand wide disturbance ($\delta D2_t$) can be considered as null. Finally, the most constraining element in the above equation is the removal of age trend (A_t) from the individual ring width series. However when using isotopes extraction techniques from the tree-rings, this correction seems unnecessary beyond the initial juvenile effect of approximately 50 years (Gagen et al., 2007; Young et al., 2010; Esper et al., 2002). The climate signal (C_t) should then be the main explanatory factor in tree-ring width series (R_t).

2.3.3 Wood composition

Wood composition includes primarily carbon, oxygen and hydrogen (Griffiths, 1998). These three elements are common in living tissues. For trees, carbon atoms originate from the atmospheric CO_2 whilst oxygen and hydrogen originate from the soil water. The collection of these atoms and transformation to living tissue is made in the tree itself by different biochemical pathways explained in the next sections.

2.4 Stable isotopes

2.4.1 Introduction

The main atomic elements present in organic matter of trees exist naturally in different forms that are called isotopes. Isotopes from an element differ in the number of neutrons composing the atom of this same element. Carbon has two stable isotopes, ^{12}C and ^{13}C, twelve and thirteen representing the mass number of the carbon atom. It also possesses one naturally occurring unstable isotope, ^{14}C, being a radioactive form with a half life of 5,730±40 years. The relative natural abundance of the ^{12}C and ^{13}C are 98.93% and 1.07% respectively (De Laeter *et al.*, 2000). As plants, and therefore trees, do not assimilate these elements passively, the relative abundance of the ^{12}C and ^{13}C in plant organs differs from the natural atmospheric abundance.

Covariance between temperature and carbon stable isotope ratio in wood material was first observed by Urey (1947) which initiated the potential to use this relationship in climate reconstruction. Carbon fixation in plants metabolism has been now intensively studied for over 30 years and permits a deep understanding of the relationship between plants and carbon isotopes (Farquhar *et al.*, 1982, 1989).

2.4.2 Stable isotope ratio

To measure the difference in isotope ratio, scientists set an international standard value named the Vienna Pee Dee Belemnite (VPDB) (Gonfiantini, 1984; Coplen, 1995, 2006). The measurement of the ratio ^{13}C/^{12}C can be made by using an isotope ratio mass spectrometer. To express this ratio the notation delta (δ) is used with values being dimensionless. To calculate the sample value relative to the standard, Equation 2.2 is used:

$$\delta_{sample} = \left(\frac{R_{sample}}{R_{standard}} - 1 \right) 1000 \qquad (2.2)$$

Where δ_{sample} is the isotope fractionation of the analysed sample for a specific atomic element, R_{sample} is the ratio between two isotopes of the element in the sample and $R_{standard}$ is the equivalent ratio in the standard sample.

2.4.3 Carbon uptake by trees

To explain the meaning of the sample value, it is necessary to understand how the δ^{13}C varies in plants and what the metabolic processes involved are. Three

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photosynthetic pathways exist depending on plant species. They are described as C_3, C_4 or CAM options and constitute the largest factor affecting carbon isotopic composition (O'Leary, 1981). However, the C_3 pathway is the most widespread for trees (95%) and therefore most of dendroclimatology studies focused on trees with this photosynthetic mechanism.

Troughton & Card (1975) reported a mean $\delta^{13}C$ value for C_3 plants of -28.1 $\pm$ 2.5 ‰. As the $\delta^{13}C$ ratio for the atmosphere is currently close to -8 ‰ , we can assume organic matter will always be more depleted in ^{13}C compared to air (McCarroll & Loader, 2004). C_3 plants incorporate CO_2 from the atmosphere by carboxylation of ribulose bisphosphate (O'Leary, 1981). Both enzymatic and physical processes contribute to discriminate against the heavier stable isotope (^{13}C) in favour of the lighter one (^{12}C) (Farquhar et al., 1982).

The variations around the mean $\delta^{13}C$ value are due to differences at the stages of diffusion, dissolution and carboxylation in the Calvin cycle used by C_3 plants (O'Leary, 1981). This biochemical cycle permits the production of organic compounds by the fixation of carbon coming from atmospheric CO_2 to form a first photosynthetic product, the 3-phosphoglycerate (Roeske & O'Leary, 1984; Mauseth, 2003).

The key enzyme in this cycle is called RubisCO (Ribulose-1,5-bisphosphate carboxylase). Despite being light independent, this cycle requires the use of energy carriers ATP and NADPH which are produced by photophosphorylation in the thylakoid membrane of the chloroplast during the light dependent reactions of photosynthesis (Noctor & Foyer, 1998).

2.4.4   Carbon isotope theory

As the CO_2 enters the photosynthetic reaction by diffusion, it gets through small openings situated underneath plant leaves called stomata. By this mean, gases and water vapour are exchanged with the environment. These pores can modulate the flow of gases by controlling their aperture according to the metabolic needs of the plant. There is a first isotope fractionation of 4.4 ‰ occurring due to the microscopic size of the stomatal aperture (Hesterberg & Siegenthaler, 1991).

The first reaction, the carbon fixation, is catalysed by the RubisCO by incorporating a molecule of CO_2 in a C5 compound called ribulose-1,5-bisphosphate to form two C3 molecules of 3-phosphoglycerate as shown in Equation 2.3 (Rice &

Tenore, 1981).

$$CO_2 + RuBP \rightarrow 2,3 - PGA \qquad (2.3)$$

Where RuBP is the ribulose-1,5-bisphosphate and 2,3-PGA are the two C3 molecules of 3-phosphoglycerate. This reaction is followed by the carbon reduction which is a two-step reaction where the 3-phosphoglycerate is transformed into 1,3-disphosphoglycerate by an enzyme called phosphoglycerokinase (PGK) and by the use of ATP energy carriers. Then these molecules are transformed into glyceraldehyde-3-phosphate by the glyceraldehyde phosphodeshydrogenase (GAPDH) and the use of NADPH energy carriers. Finally, the last reaction is the regeneration of the ribulose. This reaction occurs also in different steps, the main ones being the re-utilisation of the glyceraldehyde-3-phosphate to form a ribulose-5-phosphate and then finally a ribulose-1,5-bisphosphate which can be used again for the carbon fixation reaction.

Not all glyceraldehyde-3-phosphate molecules are re-used in the process and are used by the plant to produce organic material. This reaction sequence discriminates against the heavier isotope of carbon and can modify the $\delta^{13}C$ in plants up to about 27 ‰ (Vogel, 1980). The relationship between the atmospheric $\delta^{13}C$ and the organic $\delta^{13}C$ has been compiled by (Francey & Farquhar, 1982) in Equation 2.4:

$$\delta^{13}C_p = \delta^{13}C_a - x - (y - x)c_i/c_a \qquad (2.4)$$

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

Therefore, the speed of the reaction sequence is controlled by two phenomena: the degree of conductance of carbon via diffusion through the stomata and the rate of photosynthesis by the enzymes during the Calvin cycle. This is affecting 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.*, 1989).

Water being the essential substrate for life and therefore a limiting factor for plant growth, the water loss during photosynthesis must be kept to a minimum while holding the highest carbon gain (Cowan, 1982). At a daily scale, stomata open and close in response to environmental conditions such as the light intensity, soil water content (SWC), the vapour pressure deficit (VPD), carbon dioxide and

ozone concentration in the atmosphere. This mechanism is controlled by the osmotic pressure in the guard cells surrounding the stomata. When the conditions inducing high water losses are present, the gas exchange is reduced via stomatal control. During the stomatal closure, the discrimination of $^{13}CO_2$ reduces as the lighter $^{12}CO_2$ molecules becomes depleted in the stomatal chamber. The stomatal conductance to environmental variations has been described by Jarvis et al. (1976) in Equation 2.5:

$$g_s = f(Q_o)f(VPD)f(T_a)f(\psi_L) \tag{2.5}$$

where g_s is the stomatal conductance, Q_o is the photosynthetic photon flux density, T_a is the air temperature and ψ_L is the leaf water potential.

Photosynthetic enzymes are dependent on temperature, therefore the photosynthetic rate is directly influenced by temperature with slower biochemical reactions when the temperature is lower than optimal (Kramer & Kozlowski, 1960). This relationship may be a significant limiting factor in leaf photosynthesis, even when the light dependent process of photosynthesis is at its maximum rate (Treharne & Cooper, 1969). However, when the light becomes the limiting factor it is the amount of RubisCO and its regeneration rate that may lower the photosynthesis rate (Scheidegger et al., 2000). Therefore, stomatal conductance and photosynthetic rate being both involved in the carbon discrimination, it is the balance between the two processes that should be considered to understand the carbon ratio in plant photosynthesis (Farquhar et al., 1982, 1989).

Environmental factors have been studied to estimate their influences on these processes as well as tree physiology (Stuiver & Braziunas, 1987). Early studies under controlled conditions have shown temperature and light intensity to correlate with the $\delta^{13}C$ (Smith et al., 1976) by modulating the stomatal conductance and the different stages of the carbon fixation. As many sites have been investigated, it seems the limiting environmental factors hold the majority of the explained variation in $\delta^{13}C$. For wet and cold sites at northern latitude, the environmental controls seem to be sunshine (McCarroll et al., 2003; Leavitt & Long, 1991; Young et al., 2010) and temperature (Wilson & Grinsted, 1977). Although on dry and warmer sites, it seems relative humidity (Saurer & Siegenthaler, 1989) and vapour pressure deficit (Ogle & McCormac, 1994) are explaining the $\delta^{13}C$. However, all these climatic variables are highly correlated (Walcroft et al., 1997) which can lead to inaccurate results when considering only one climatic parameter as driver of the $\delta^{13}C$ variation.

The overall range for $\delta^{13}C$ values in leaves and wood typically ranges from -20‰ to -30‰ (McCarroll & Loader, 2004). However, within this range, leaves are usually more depleted in ^{13}C than the wood and therefore present a higher value for $\delta^{13}C$ by 2 to 3 ‰ (Feng, 1998). Additionally, the $\delta^{13}C$ of wood may be affected by the use of reserves and respiration. Woody tissue respiration is a major component of the carbon balance of temperate forests. If the CO_2 from the stem respiration has the same $\delta^{13}C$ values as the organic matter from which it was lost, this loss of carbon would not have an impact on the isotope content of the stem (Damesin & Lelarge, 2003).

2.4.5 Investigation of the relationship with environmental variables

Stomatal control over the photosynthesis process is partially dependent on the environmental conditions (Brodribb & McAdam, 2011). Therefore, considerable research has been carried out to establish the link between the $\delta^{13}C$ in leaves and environmental information. Multiple studies have shown a significant effect of relative humidity, temperature, light, and the atmospheric concentration of CO_2 on the $\delta^{13}C$ composition of plant tissues (Ehleringer et al., 1986; Ehleringer & Cooper, 1988; Farquhar et al., 1989; Toft et al., 1989; Zimmerman & Ehleringer, 1990; Körner et al., 1991; Van de Water et al., 2002; Feng & Epstein, 1995a; Kelly & Woodward, 1995; Arens et al., 2009; Bowling et al., 2002; Yin et al., 2005, 2009; Aranda et al., 2007; Cernusak et al., 2009; Treydte et al., 2009; Kranabetter et al., 2010). However, as mentioned above, due to fractionation processes after the assimilation of CO_2 in the leaves, the $\delta^{13}C$ variation in the tree-rings differs significantly from the $\delta^{13}C$ in leaves. Thus, research has also been carried out to observe if the environmental signal was transmitted into the annually formed tree-ring $\delta^{13}C$ composition (Craig, 1954).

The range of environmental variables tested covers meteorological data such as temperature, precipitation, relative humidity and irradiance (Wilson & Grinsted, 1978; Mazany et al., 1980; Stuiver & Braziunas, 1987; Leavitt & Long, 1991; Lipp et al., 1991; Leavitt & Newberry, 1992; Yakir et al., 1994; Kitagawa & Matsumoto, 1995; Panek & Waring, 1995; Schleser, 1995; Lipp et al., 1996; Liu et al., 1996; Switsur et al., 1996; Panek & Waring, 1997; Robertson et al., 1997b,a; Zimmermann et al., 1997; Hemming et al., 1998; Edwards et al., 2000; Barbour et al., 2002; Geßler et al., 2001) but also soil water content (Dupouey et al., 1993; Walcroft et al., 1997; Panek & Goldstein, 2001; Leavitt, 2002; Högberg et al., 1995), water use efficiency (Bert et al., 1997; Walcroft et al., 1997; Duquesnay et al., 1998;

Tang *et al.*, 1999; Matzner *et al.*, 2001; Ponton *et al.*, 2001; Livingston *et al.*, 1999), cloud cover and fog (Young *et al.*, 2010; Roden *et al.*, 2009), pollution (Peng *et al.*, 1983; Martin & Sutherland, 1990), latitude and altitude (Stuiver & Braziunas, 1987; Kitagawa & Matsumoto, 1995). Results from these studies show no consensus over the main drivers of $\delta^{13}C$ variation in trees and over the intensity of the relationship with $\delta^{13}C$ in tree-rings. Gagen *et al.* (2008) states that no single environmental variable can explain the entire $\delta^{13}C$ signal in tree-rings which points out why different results are obtained in the above studies. Therefore, the reconstruction of a single environmental signal using only the $\delta^{13}C$ composition is likely to be insufficient and could be enhanced by using a second environmental tracer (Gagen *et al.*, 2007).

2.4.6   Extraction of intra-annual isotope variability

The recent improvement of methods to sample subsection of tree-rings by hand-slicing (Leavitt & Long, 1991; Leavitt, 2002, 2007; Kagawa *et al.*, 2003; Jahren & Sternberg, 2008; Roden *et al.*, 2009), microtome sectioning (Barbour *et al.*, 2002; Helle & Schleser, 2004; Nakatsuka *et al.*, 2004), and laser ablation (Schulze *et al.*, 2004; Vaganov *et al.*, 2009; Battipaglia *et al.*, 2010) provided the means to analyse intra-annual wood samples from 10 to 240 microns and can reach up to 300 samples in a single tree-ring (Schubert & Jahren, 2011).

One concern when extracting isotope values at the intra-annual level is that the isotopic signature is the combination of climatic and non-climatic influences. Many studies found significant differences in isotope time series when separating early-wood and latewood for climate signal detection purposes (Wilson & Grinsted, 1978; Fraser *et al.*, 1978; Leavitt & Long, 1991, 1982, 1986; Lipp *et al.*, 1991; Leavitt & Newberry, 1992; Ogle & McCormac, 1994; Switsur *et al.*, 1995; Livingston & Spittlehouse, 1996; Sheu *et al.*, 1996; Pate & Arthur, 1998; Schleser *et al.*, 1999; Leavitt, 2002). One of the physiological reasons to keep only the latewood when testing the relationship with environmental factors is that the isotopic signal in earlywood can be altered by the remobilisation of previous years reserves (Hill *et al.*, 1995; Jordan & Mariotti, 1997; Jäggi *et al.*, 2002; Rebetez *et al.*, 2003; Saurer *et al.*, 2000). However, these results are not always verified as remobilised carbon has been traced to be used mainly for new roots (85 %) (Teng *et al.*, 1999) or to present no effect on the relationship with climate (Kress *et al.*, 2009; Eilmann *et al.*, 2010). Finally, Klein *et al.* (2005) shows encouraging results at the intra-annual resolution with $\delta^{13}C$ time series from Aleppo pines presenting significant correlation with photosynthetically active radiation, vapour pressure deficit, air

temperature, and soil water content.

A second concern to high-resolution isotopic analysis is that the quantity of wood material per sample is very small and can be at the limit of confidence from the mass spectrometry equipment. It was then necessary to assess the use of whole-wood instead of cellulose analysis to maximise the quantity of material for each sample (Schulze et al., 2004). One early study from Wilson & Grinsted (1977) found a common variation in cellulose and lignin in Pinus radiata analysed over two consecutive years with an offset of approximately 3‰. It was then demonstrated that this offset was consistent between wholewood and cellulose and therefore showing similar inter-annual and intra-annual patterns (Leavitt & Long, 1991; Verheyden et al., 2005; Pons & Helle, 2011; Borella et al., 1998; Schleser et al., 1999; Leavitt & Long, 1986; Schleser, 1990; Livingston & Spittlehouse, 1996). Similar results were found between cellulose and lignin (Wilson & Grinsted, 1977; Robertson et al., 2004; Loader et al., 2003) and between bulk wood and cellulose (Barbour et al., 2001; Verheyden et al., 2005; Harlow et al., 2006). Moreover, the use of wholewood to extract carbon isotope ratio seems to retain the strongest climate signal which validates its use for dendroclimatology purposes (Borella et al., 1998; Loader et al., 2003).

At high intra-annual resolution, the main interrogation is to quantify the influence of ambient environmental conditions or seasonal events on the isotope time series (Roden et al., 2009). For this purpose, Kress et al. (2009) found unnecessary to separate earlywood from latewood. However, some studies still found a possible influence of storage processes on $\delta^{13}C$ time series (Skomarkova et al., 2006; Vaganov et al., 2009). Helle & Schleser (2004) presented the $\delta^{13}C$ variation as a tri-phase pattern characterised by the switch between the storage dependent growth to the current year use of photosynthates. Other studies have shown that a different set of environmental variables to influence the $\delta^{13}C$ variation can be found depending on the study sites selected. McCarroll & Pawellek (2001) found summer sunshine, temperature and antecedent precipitation to be the main drivers in three study sites while the fourth site was more influenced by antecedent precipitation and relative humidity. Vaganov et al. (2009) found the $\delta^{13}C$ time series to correlate with vapour pressure deficit and net radiation but not temperature and precipitation. However, the variation of control factors between study sites seem not always to be detectable when investigated in a close geographic range (Brendel et al., 2002). When considering a large range of climatic influences and environmental properties, Schubert & Jahren (2011) found that a relationship with atmospheric CO_2 and precipitation variation between the dormant and active season could provide

a first modelling tool for a global approach at the seasonal resolution. Finally, an interesting hypothesis developed in Drew *et al.* (2009) present the possibility of an increase of $\delta^{13}C$ when the water stress is relieved and not necessarily during the peak of water stress. This would suggest that trees store intra-annually carbon reserves when the water stress does not permit wood formation and use these reserves when the new water supplies are available later during the same growing season.

2.5 Mass spectrometry on-line methods

A major improvement in analysing high-resolution isotope time series lies in the development of on-line methods for mass spectrometry. On-line mass spectrometry also described as the continuous flow IRMS method has been developed by interfacing an elemental analyser with a mass spectrometer (Matthews & Hayes, 1978; Preston & Owens, 1983, 1985). This evolution in carbon isotope analysis enables the sample to be prepared, purified and transferred to the mass spectrometer all in one manipulation by the use of a continuous flow of gas carrying the sample through the procedure. This automation allows a large number of samples to be analysed with time and cost efficiencies. However, precautions have to be observed concerning this specific method to obtain reliable results (McCarroll & Loader, 2004). The run of samples for many hours can co-occur with variations in the flow of carrier gas and in the combustion efficiency that can lead to a drift in the isotopic measurements. By regularly running standard cellulose samples between a number of real samples, this possible trend can be corrected afterwards, when all samples have been analysed. Another precaution to take is to keep a relatively low variation in the sample size during a same run such that the relation between the reference gas pressure and the sample gas remains constant. Especially with small samples, a large weight variation can lead to inaccurate results. It would be then necessary to run test samples of different weights to match the range of analysed samples and possibly correct any effect of the sample size variation. When correctly identifying and correcting these possible effects in the isotope time series, the precision of this method is comparable to offline methods ($\simeq 0.1$ ‰) (McCarroll & Loader, 2004).

Concerning carbon isotopes, the analysis can be carried out on wholewood or cellulose and transformed into CO_2 for isotopic measurement. The preparation of the samples to be analysed consists in placing each sample in a tin capsule, to compress it, making it hermetic and removing trapped atmosphere to permit the sample measurement. When heated to 1000 °C with the contribution of ex-

ogenous helium gas, the combustion of the tin capsule will release sufficient heat to ensure the full combustion of the sample. To remove water traces in the combustion products, chemical traps can be used such that the final gas produced is only composed of CO_2 and N_2 that can be segregated by the occurrence of two different peaks through the gas chromatography procedure. Finally, the resulting gas is sent to the mass spectrometer for isotopic analysis of the CO_2. For samples weighted in a range of 100 to 200 μg of carbon, the full procedure takes approximately 8 minutes per sample and provides an analytical precision of 0.1 ‰. It is expected that smaller samples will slightly reduce this precision (McCarroll & Loader, 2004).

2.6 Isotope time series post-treatment

When using carbon isotope time series for climate reconstruction purposes, three non-climatic effects are to be considered before correlating isotope values to climatic data:

- the effect of the variation of atmospheric δ^{13}C during post industrial times on the final isotopic composition of tree material;

- the effect of tree age or 'juvenile effect' characterised by a depletion of approximately 1 ‰in the carbon isotope time series during the juvenile tree growth with a progressive enrichment for about 50 years (Gagen *et al.*, 2008; McCarroll & Loader, 2004);

- the intra-annual variation in the air δ^{13}C due to the ecosystem functioning during the growing season which can potentially affect the organic δ^{13}C variation Hemming *et al.* (2005).

2.6.1 Atmospheric δ^{13}C trend

The industrial age is characterised by the release of carbon dioxide into the atmosphere by the combustion of fossil fuels. In addition to increasing the concentration of carbon in the atmosphere, the δ^{13}C signature in fossil fuels is lower than the natural CO_2 from the pre-industrial age δ^{13}C (Freyer & Belacy, 1983). Therefore, carbon isotope chronologies show an increasingly declining trend related to this artificial CO_2 addition by about 1.5 ‰ since industrialisation (Epstein *et al.*, 1990; Leavitt & Lara, 1994; Kitagawa & Matsumoto, 1995; Raffalli-Delerce *et al.*, 2004; Feng & Epstein, 1995a,b; February & Stock, 1999; Treydte *et al.*, 2001). To remove this atmospheric trend in δ^{13}C time series, Saurer *et al.* (1997) proposed

a simple solution using straight segments of correction values for different time spans. This method does not change pre-industrial values and can be amended segment by segment rather than changing the overall method if a particular time period diverges significantly from the proposed correction values. Francey *et al.* (1999) used only two segments from 1850 to 1961 and 1962 to 1980 with different declining trends based on records from Antarctic ice cores. Correction values to add during the more recent period (1981 to 2003) can be extrapolated with confidence as proposed in McCarroll & Loader (2004).

2.6.2 Effect of tree age

When building $\delta^{13}C$ time series, previous studies have observed a marked period during the early stages of growth where the carbon isotope values yield lower values than in the mature stage (Gagen *et al.*, 2008; Duquesnay *et al.*, 1998). Trees from different sites seem to display a comparable pattern which can last from 20 to 50 years of growth. Gagen *et al.* (2008) has detected a rate of change from 0.002 to 0.053 ‰ per year during the juvenile stage. The maximum rate has been recorded by Li *et al.* (2005) with a value of 4 ‰ in Chinese pine trees. Four interpretations have been proposed to explain this juvenile effect: 1) the recycling of respired air by young trees closer to the forest floor from the canopy (Schleser & Jayasekera, 1985). However, for study sites at altitude or in tropical dense forests, this hypothesis does not provide an explanation for the variation in $\delta^{13}C$ in the juvenile stage (van der Merwe & Medina, 1991). 2) Cernusak *et al.* (2001) suggests that the contribution of the bark to photosynthesis declines with its hardening in the mature stage. 3) Donovan & Ehleringer (1992) suggest that the intercellular CO_2 concentration varies differently in response to environmental changes during the lifetime of a plant. This effect could account for a variation of 3 ‰ when studying a tall shrub species from seedling to large adult. 4) the last hypothesis is linked to the observations that the increase of tree height with age induces changes in the hydraulic conductivity of trees (Ryan & Yoder, 1997; McDowell *et al.*, 2002). Due to these juvenile effects, a simple solution is to use only tree-rings formed during the mature stage of trees and avoid using the first 50 years of growth when it is possible (Gagen *et al.*, 2008; McCarroll & Loader, 2004).

2.6.3 Seasonal variation

During the photosynthesis activity, trees deplete isotopically the atmosphere in CO_2 gas to be transformed in organic matter. As ^{12}C is preferred to ^{13}C during this process, the close surroundings of the forest can possibly get more depleted in

^{12}C than in ^{13}C. Therefore, if the air δ^{13}C is modified during the growing season, the δ^{13}C in the trees can also be influenced by this variation in its CO_2 supply. Another cause of variation in air δ^{13}C is that the respiration process releases CO_2 from the trees to the atmosphere with a different δ^{13}C signature. The re-use of respired CO_2 by the trees for photosynthesis would cause an enrichment in organic δ^{13}C that was prominent for angiosperms species but not for gymnosperms (Hemming *et al.*, 2005). During 2001 and 2002, Hemming *et al.* (2005) investigated the seasonal variation of air δ^{13}C at 16 study sites mainly in Europe with a wide range of climatic influences, tree species and site characteristics. All these sites were equipped with flux-towers permitting eddy covariance measurements. During 2001, a global trend was detected for a seasonal variation in air δ^{13}C showing an enrichment from 26 ‰ to 24.5 ‰ between July and September followed by a depletion to 30 ‰ in November. However, this pattern was not verified during 2002.

2.7 Inter-tree variability

2.7.1 Characteristics of the variability between trees

Despite studying trees in a close range, previous studies observed a significant difference in growth and isotope values measured in trees that present similar characteristics (age, position in the canopy, competition). Reasons for such differences between adjacent trees remain uncertain. However, McCarroll & Pawellek (1998) suggest that these differences remain stable over time causing an offset in isotope time series coming from different trees. For tree-ring width records, the difference between trees seem to be more variable from a year to another than for isotope time series. It is hence necessary to characterise inter-tree variability so a common response from trees can be extracted and assimilated to the mean response of trees to climate forcing (Leavitt & Long, 1984). An adequate method to fulfill this objective is to use statistical tools such as confidence intervals that define a range of values where the true mean is located. However, when an offset is present between time series, it is necessary to standardise the dataset to a common mean level that will allow the characterisation of a representative standard deviation from the common signal (McCarroll & Loader, 2004).

Another consequence of using different trees to build a consistent common signal is that the maximum number of isotope measurements in one tree-ring vary from a tree to another due to the inter-tree variation in tree-ring width. Therefore, when comparing long isotope time series from different trees, the ring boundaries

will be non matching causing a time offset in the isotope signal. A simple solution to resolve this issue is to standardise the isotope series for each tree-ring between the different trees so that the same number of isotope observations is matched to contribute to the common signal calculation.

2.7.2   Expressed population signal (EPS)

Due to differences in inter-tree variation, the strength of the common signal needs to be assessed in a way that it is possible to see the contribution of additional time series to the quality of the signal. The expressed population signal is a statistic tool used to estimate the uncertainties in the mean of a set of correlated time series (Wigley *et al.*, 1984). Therefore, this tool can help understanding the isotopic common signal at a study site. The equation of the EPS is as follows:

$$EPS = \left(\frac{n\bar{r}}{1 + (n-1)\bar{r}} \right) \tag{2.6}$$

where n is the total number of tree series and $\bar{r}$ is the mean inter-tree correlation coefficient. Addition of trees increases dramatically the variation in the EPS values up to a limit of ten trees where the benefit from adding new trees diminishes (Briffa & Jones, 1990). Despite the lack of minimum EPS threshold of acceptability, values superior or equal to 0.85 have been suggested as reasonable for a high common signal (Wigley *et al.*, 1984). The EPS is usually applied at the annual resolution, but can be tested for intra-annual time series. However, intra-annual analyses are quite new in dendroclimatology and the EPS values are to be interpreted with caution as intra-annual $\delta^{13}C$ time series from different trees can show high auto-correlation patterns that will increase greatly the EPS score. Moreover, the EPS calculation is usually applied to annual $\delta^{13}C$ time series on periods from a few hundreds of years to a thousand which is considerably greater than the time series developed in this study. When the EPS shows a good common signal at a study site, the averaged time series from the different trees can be considered to represent a significant common climatic signal at the study site.

2.8   Impact of tree species physiology in isotopic studies

The choice of which tree species to study influences greatly the isotope time series mean level and variability due to the physiological differences in tree species. As many species have been studied for isotopic analysis (McCarroll & Loader, 2004; Ramesh *et al.*, 1986; Hemming *et al.*, 1995), there is a solid literature for

new isotope time series to be analysed in respect of previously published datasets. Conifers have shown to hold higher carbon isotope values than angiosperms (Stuiver & Braziunas, 1987; Leavitt & Newberry, 1992; Leavitt, 2002). This observation can be explained by the difference in the water transport system of the ring-porous broadleaved angiosperms that permits greater amounts of water to flow from the roots to the leaves but also a greater sensitivity to dessication. Therefore, as the hydraulic conductivity affects stomatal conductance, the isotope ratio in the leaves will be also affected. Other differences such as leaf morphology (Barbour *et al.*, 2002), rooting system (Warren *et al.*, 2001) and position in the canopy (Livingston *et al.*, 1998) have been suggested to also modify photosynthetic processes and hence isotope ratio. However, the isotope signal coming from different trees from the same species seems to be at least as variable as inter species variation (Leavitt & Long, 1984; Leavitt & Lara, 1994; McCarroll & Pawellek, 1998; Brendel *et al.*, 2002). Moreover, different species when their isotope time series are standardised, can show high similarities in terms of climatic signal (Warren *et al.*, 2001; Gagen *et al.*, 2004) despite holding large differences in ring width chronologies.

2.9 Flux-tower background

2.9.1 Why flux-tower measurements / data coverage

flux-towers are usually identifiable as metal scaffolding towers where mounted instruments are measuring the gas exchanges between the land surface and the atmosphere. The number of instruments and height of the towers can vary depending on the research interests and the type of vegetation cover. The potential of this technique stands in its precision to measure exchanges between the atmosphere and the vegetation such as fluxes of carbon, water and heat while recording meteorological information to a high temporal resolution (20 to 1 Hz). Therefore, it is possible to access the dynamic variations of the ecosystem gas exchanges recorded continuously during all year with good confidence (Baldocchi *et al.*, 2001). This technique can permit the measurement of fluxes from a relatively small surface area (100 metres to 2 kilometres). This feature can be an advantage when studying the direct impact of climate at the tree level. Nowadays scientific investigations are conducted in forests, bogs, urban areas and agricultural areas all over the world on more than 500 flux-towers (Luyssaert *et al.*, 2009).

2.9.2 Flux measurements / eddy covariance method

Fluxes are defined as the measurements of an inert substance moving through a unit area per unit of time (Equation 2.7).

$$F = \overline{\rho_a} \cdot \overline{\omega' s'}$$ (2.7)

Where F is the fluctuation of the vertical velocity, $\overline{\rho_a}$ is the density of dry air and $\overline{\omega' s'}$ is the fluctuation of the mixing ratio (c/a) with c the density of the gas of interest on a, the air density. Only vertical fluxes are considered and result from the covariance of vertical velocity and gas concentration while horizontal fluxes are considered to be negligible. Flux measurements are widely used to estimate heat, water and CO_2 exchange in climatic studies or ecophysiological studies. Flux densities are generally considered to be positive for fluxes from the surface to the atmosphere (the atmosphere gain material or energy). High-frequency measurements are needed in order to quantify the turbulence. The flux-tower data are usually obtained by the eddy covariance method. As fluxes are considered to be horizontally constant in the surface layer, proceeding to measurements in this layer will give a good representativeness of the exchanges between the underlying surface (the vegetation) and the atmosphere. This surface layer varies in height depending on the atmospheric conditions. It can vary from approximately 10 m during a stable stratification while it can rise to 20 to 50 m when the stratification is unstable (Stull, 1988; Garratt, 1992; Foken, 2006). As the dominant transport mechanism in this layer is atmospheric turbulence, the application of the eddy covariance has been justified and is currently the most widespread method to derive turbulent fluxes (Rosenberg *et al.*, 1983; Baldocchi *et al.*, 1988; Verma *et al.*, 1989). The general principle of the eddy covariance method is to obtain a covariance between the concentration of interest and the vertical wind speed of eddies (Burba & Anderson, 2007).

Sir Osborne Reynolds conceptualised the Reynolds averaging which is essential to provide a statistical representation of turbulent wind, its non-Gaussian attributes and turbulent fluxes (Reynolds, 1895). The motion of a turbulent fluid, like air, can be defined at any instant in time as being equal to the sum of its mean state ($\overline{x}$) and is fluctuation from the mean (x'). Other important properties associated with Reynolds' averaging rules include:

- the mean product of two fluctuating variables is a function of the product of the individual means plus a covariance, $xy = \overline{xy} + \overline{x'y'}$;

- the average of any fluctuating component is zero, $\overline{x'} = 0$;

- the average of the sum of two components is additive, $\overline{x+y} = \overline{x} + \overline{y}$.

However, these properties can only be used when many observations are done under identical conditions, also called ensemble averaging. As this condition cannot be satisfied with atmospheric measurements, the hypothesis stating that time averaging is equivalent to ensemble averaging can provide time averages instead of repetition averages (Kaimal & Finnigan, 1994). Therefore, the time frame for averaging has also to be statistically stationary. A definition of steadiness conditions is that none of the statistical parameters vary in time (Panofsky & Dutton, 1984). Drivers of this status can be:

- changes at a daily basis of climate variables such as temperature, sunshine and precipitation;

- meteorology changes at the mesoscale;

- changes in the areas influencing measurements;

- changes in the internal boundary layers (especially internal thermal boundary layers in the afternoon);

- presence of gravity waves.

The theoretical principles for computing scalar and momentum gradients and fluxes in the surface layer have been conceived during the 1940s by Monin and Obukhov. These principles were then successfully tested on different surface roughnesses and thermal stratification and were determinant for later studies (Foken, 2006). However, the major advances in the field only occurred later in the 1950s by the improvement of the instrumentation, especially in fast responding hot-wire anemometry and thermometry able to record data at high-resolution with a small time of response.

2.9.3 Micrometeorological and ecosystem observations

Due to the advancement in available technology enabling continuous flux measurements, micrometeorologists have been able to measure carbon dioxide (CO_2) and water vapour (H_2O) exchange between vegetation and the atmosphere since the late 1950s and early 1960s (Baldocchi et al., 2001). The earliest reported micrometeorological measurements of CO_2 exchange were conducted by Inoue (1958), Lemon (1960), Monteith & Szeicz (1960) and Denmead (1969). These studies employed the flux-gradient method over agricultural crops during the growing season. By the late 1960s and early 1970s, a few scientists started applying the flux-gradient method over natural landscapes. Several flux-gradient studies of CO_2 exchange were conducted over forests (Denmead, 1969; Baumgartner, 1969; Jarvis

et al., 1976).

Routine application of the eddy covariance method was not possible until the 1980s, when technological advances in sonic anemometry, infrared spectrometry, and digital computers were made. Initial studies were conducted over crops (Anderson *et al.*, 1984; Desjardins *et al.*, 1984; Ohtaki, 1984), forests (Verma *et al.*, 1986), and native grasslands (Verma *et al.*, 1989) for short intense periods during the peak of the growing season. By the late 1980s and early 1990s, the further technological developments, such as larger data storage capacity and linear and nondrifting instruments, enabled scientists to make high standard measurements of eddy fluxes for extended periods (Baldocchi *et al.*, 2001). For over 40 years micrometeorologists focused their efforts on the development of theory, instrumentation and methods to measure trace gas, energy and momentum fluxes between the land surface and the atmosphere.

2.9.4 Derivation of the net ecosystem exchange (NEE), gross ecosystem production (GEP) and ecosystem respiration (Re)

Measurements from eddy covariance only record the net exchange of matter or energy between the atmosphere and the vegetation. It is essential to understand that these observations result from two fluxes of opposite direction: vegetation to atmosphere and its opposite, atmosphere to vegetation. In the case of the carbon exchange, the eddy covariance measurements record the net ecosystem exchange of CO_2 (NEE) which can be decomposed into CO_2 uptake by the vegetation from the atmosphere (gross ecosystem productivity - GEP) and ecosystem respiration (R_{eco}) releasing CO_2 from the ecosystem back to the atmosphere as shown in Equation 2.8.

$$NEE = GEP + R_{eco} \qquad (2.8)$$

where NEE is the net ecosystem exchange of CO_2, GEP the gross ecosystem productivity and R_{eco} the ecosystem respiration. Although NEE gives good indication of carbon sequestration, it is necessary to estimate its two components to understand the underlying processes responsible of the carbon exchange at the ecosystem level. One of the properties of GEP is to be zero during night conditions for C_3 and C_4 plants (San Jose *et al.*, 2007). Therefore, R_{eco} is the only contributor to NEE measurements during the night. Despite suboptimal conditions for the application of the eddy covariance theory due to often stable atmosphere with

insufficient turbulence, it is possible to extrapolate R_{eco} measured at night to day time R_{eco} and thus model GEP from Equation 2.8.

Besides studying the carbon exchange, another indication of the processes in an ecosystem relies on measuring the water fluxes from the vegetation. The evapotranspiration can be defined as the sum of transpiration by plants and the evaporation of the intercepted water on leaves and shoots and the ground surface. This relation is presented in Equation 2.9:

$$E_{tot} = E_{plant} + E_{int} + E_{soil} \tag{2.9}$$

where E_{tot} is the evapotranspiration, E_{plant} is the transpiration by plants, E_{int} is the evaporation of the intercepted water on leaves and shoots and E_{soil} is the evaporation of the intercepted water on ground surface. E_{plant} is usually estimated by using sapflow instruments on a sample of vegetation and scaling it to the density of vegetation present in the flux measurements area around the flux-tower.

2.10 Specific choices for isotope - flux-tower studies

2.10.1 Site selection

It is difficult to predict which study sites will hold the clearer climate signal. However, it is known that the water status in trees influences the stomatal conductance and therefore the isotope ratio. Soil water content and relative humidity are the two environmental factors causing variations in the stomatal conductance that can be measured at a study site. It is expected that sites with a low precipitation input will hold higher isotope values than moist sites. The response to climate variation from trees under a stronger stress from the environment is expected to offer a clearer relationship with isotope ratio. However, sampling solely sites experimenting important stress can lead to false interpretations of the impact of climate variation in less extreme conditions (McCarroll & Loader, 2004). Therefore, conducting an analysis on a range of stress régimes at different sites can give a more realistic representation of the relationship between isotope time series and climatic variation.

2.10.2 Tree selection for sampling

When selecting trees that will provide the material for isotope analysis, there

are three considerations to take into account: 1) the trees have to be positioned upwind of the main wind direction in a 200 m range distance from the flux-tower so their contribution to the flux-tower data is significant (Vesala, 1998; Dolman *et al.*, 2002; Lindroth *et al.*, 1998; Kljun *et al.*, 2004). 2) The selection should only concern living trees without any visible damage to obtain a comparable signal between trees showing no noise signal coming from an inferior performance due to a physiological diminution. 3) Finally, trees should all be in the same closed canopy situation rather than in open spaces that could affect the availability of light and modify $\delta^{13}C$ values (Geßler *et al.*, 2001).

2.11 Dendrological information availability

Wood formation onset and cessation are difficult to measure and different methods exist to estimate the growing period. The most wide spread method used is dendrometer records (Yoda *et al.*, 2000; Pesonen *et al.*, 2004). However they measure stem radius rather than wood formation which can introduce a bias when water movement occurs in trees (Mäkinen *et al.*, 2003). The second method microcoring (Bäucker *et al.*, 1998) involves the extraction of a very limited wood sample (microcore) from the tree to identify cell formation through time between two microcores taken at two different times during the probable onset and cessation of radial growth. A last technique known as the pinning method was first used by Wolter (1968). This method consists in provoking a local wound in the cambium tissue by the insertion of a pin in living wood. Xylem formation after the time of wounding can be then detected when extracting the surrounding wood tissue. These methods have been tested against each other and do not predict the same dates for the onset and cessation of radial growth. In general, the microcoring technique seems to start recording growth around two weeks before the pinning method does when studying Scots pine and also seems to notify a later cessation than pinning. Finally dendrometer records differ from both microcoring and pinning techniques with the earliest detection of growth (Mäkinen *et al.*, 2008). The causes of the differences between microcoring and pinning when these methods are used for Scots pine have not been identified. However, the difference from dendrometers may be explained by increasing temperature that can trigger transpiration from trees while the water loss cannot be replaced from soil water due to soil frost (Tardif *et al.*, 2001). When soil frost is later released, the water uptake by trees will then causes an increase in tree radius unrelated to wood growth (Kozlowski & Winget, 1964; Downes *et al.*, 1999; Herzog *et al.*, 1995; Zweifel *et al.*, 2001). Due to the differences in the growth determination from these methods, a theoretical approach to estimate onset and cessation dates of radial growth is

necessary to provide a consistent way to estimate the growth properties applicable during a period of time when dendrological data is possibly unavailable. One of the sites selected in this study (Hyytiälä) possesses both dendrometers and micro-core measurements. These records will be presented and compared in Chapter III Section 3.7. One application has been developed by Rossi *et al.* (2003) to calculate the tree cells number increase in wood and to estimate both the rates of growth and periods when the cells are maturing at a daily resolution during the growing season. This method is based solely on the Gompertz equation which facilitates its use for dendrological studies and its precision can be tested against dendrological records.

The Gompertz curve can be performed on intra-annual cell counts without distinguishing the different tracheid development phases (Camarero *et al.*, 1998) which is an advantage when predicting wood growth with limited dendrological information. However, the timing of each stage of wood formation for individual cells is poorly represented with this method Dufour & Morin (2007). A better approach would be to calculate the time spent in each phase by all the cells which demands a more precise knowledge in wood development than the evaluation of the general tendency for cell development via the Gompertz approach. A comparison between Gompertz modelling and dendrological data will be presented in Chapter IV Section 4.4.

2.12   Conclusion

Tree-rings can be used as archives to date climate events and conditions as they record the ambient environment trees have been living in via the structural and chemical variations of their wood properties. Multiple studies have shown that stable isotopes in plant material covaries with climate conditions at the annual resolution. However, there is no consensus on the intensity of this relationship within tree-rings when considering seasonal weather events. The recent development of methodology allowing high-resolution sampling in single tree-rings can provide the technical frame to produce stable isotope time series over decades at the intra-annual resolution. In parallel, the development of the flux-tower network at the European scale and the availability of high-resolution weather data for the recent twenty years provide the means to understand how climatic events are integrated into the tree-rings. The following chapter will present all datasets used during this study to achieve this goal.

Chapter III : Data

3.1 Introduction

This chapter presents the study sites characteristics and all collected data at these sites. The different datasets of tree-ring width (Section 3.5), carbon isotopes (Section 3.5), dendrological records (Section 3.6) and weather datasets (Section 3.7) will be presented separately and data quality will be discussed in each section. The first section of this chapter (Section 3.2) presents the three study sites: Hyytiälä, Norunda, Loobos and their characteristics. Section 3.3 describes the fieldwork chronology, the collection of the climate information and the sampling of the tree cores which will serve for the construction of the $\delta^{13}C$ time series (Section 3.4). Details on the laser procedure and descriptions of the two laser systems are given further in Section 3.4. Section 3.5 focuses on the analysis of the $\delta^{13}C$ time series, the standardisation and corrections procedures. The availability of dendrological information at the study sites is then discussed in Section 3.6. Finally, the weather datasets produced at each site by the local research team is detailed in Section 3.7. A brief data summary and their provenance are described in Table 3.1.

Table 3.1: *Data availability, origin and units at Hyytiälä, Norunda and Loobos. Abbreviations: NOAA ESRL (National Oceanic & Atmospheric Administration - Earth System Research Laboratory), EC (eddy covariance), PAR (Photosynthetically active radiation), NEE (net ecosystem exchange).*

			Availability		
	Origin	Units	Hyytiälä	Norunda	Loobos
Section 3.6					
Raw $\delta^{13}C$	Swansea University	‰	1991-2010	1991-2009	1996-2009
Atmospheric correction	McCarroll & Loader (2004)	‰	1991-2010	1991-2009	1996-2009
Seasonal correction	NOAA ESRL	‰	1991-2010	1991-2009	1996-2009
Section 3.7					
Dendrometers	local research teams	radial increment (mm)	2007-2009	2010-2011	2009-2010
Microcores	local research teams	cell counts	2007-2009	2010-2011	2009-2010
Section 3.8					
Temperature	on-site measurements	degree Celcius	1997-2009	1997-2009	1997-2009
PAR	on-site measurements	μmol m^{-2} s^{-1}	1997-2009	1997-2009	2002-2009
Precipitation	on-site measurements	millimetres	1997-2009	1997-1998, 2000-2002	1997-2009
Section 4.3					
NEE	on-site measurements	μmol m^{-2} s^{-1}	1997-2009	1997-2009	-
Evapotranspiration	on-site measurements	μmol m^{-2} s^{-1}	1997-2009	1997-2009	-

3.2 Site selection and characteristics

3.2.1 Selection of the sites

The main feature necessary to carry out intra-annual climate calibration with $\delta^{13}C$ values is the presence of on-site weather data at high resolution. Therefore, all three study sites selected for this study are characterised by the presence of a flux-tower recording carbon dioxide and water fluxes in addition to weather data such as temperature, radiation and precipitation. As the $\delta^{13}C$ time series produced cover a common period from 1997 to 2009, the eddy covariance measurements carried out at the study sites should at least match this same period. Additionally, the average tree age at the selected study sites is superior or equal to 40 years to reduce a contribution of the juvenile effect to the $\delta^{13}C$ time series. The dominant tree species at the three selected sites is the Scots pine (*Pinus sylvestris* L.). The last characteristic is the presence of dendrological information to provide supporting data for determination of the period and duration of the growing season. However, this information is limited at the selected study sites with dendrological data only available for a few years. This section will present the three study sites, their characteristics such as location, annual weather values, soil properties, topography and elevation which are summarised in Table 3.2.

3.2.2 Hyytiälä

The Hyytiälä site (61°51'N, 24°17'E) in Finland is operated by the University of Helsinki (Figure 3.2). The flux-tower is part of the SMEAR field measurement station (Station for Measuring Forest Ecosystem-Atmosphere Relations). At the time of the sampling in 2011, the dominant Scots pines (*Pinus sylvestris*L.) were on average 40 years old and were homogeneous for about 200 m in all directions from the measurement site. Only 1% of species other than Scots pine were present at the site. The annual mean temperature is 4.31°C and average precipitation is 498.25 mm over the period 1997 to 2009 at the study site. 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 globally flat topography and a maximum of 10 m variation in altitude (Vesala, 1998).

Figure 3.2: *Study site at Hyytiälä, Finland.*

3.2.3   Norunda

The Norunda site (60°05'N, 17°29'E) in Sweden is operated by the University of Lund (Figure 3.3). The flux-tower has been recording data for almost 20 years with continuous activity. The forest composition is dominated by 50 to 70 years old Scots pines (65%, *Pinus sylvestris* L.), Norway spruce (33%, *Picea abies* L.) and other tree species in minor proportions (2%). The site has an elevation of 70 m above sea level with a flat topography spreading at least one kilometre in each direction from the flux-tower. Due to evenly-aged trees, the canopy height only varies slightly within a range of 24 to 28 m. The soil is a sandy glacial till with moderate to high occurrence of large boulders and is covered with mosses and stands of dwarf shrubs. A detailed description of the vegetation and soil properties can be found in Lagergren *et al.* (2008). The mean annual temperature is 6.40°C and the mean annual precipitation is 416.73 mm over the period 1997 to 2009 at the study site (Lindroth *et al.*, 1998).

Figure 3.3: *Study site at Norunda, Sweden (Craig Mahoney).*

3.2.4 Loobos

The Loobos site (52°10'N, 05°44'E) in the Netherlands is operated by the University of Wageningen (Figure 3.4). The forest was planted on sand dunes in the beginning of the 1900's and is now almost 100 years of age with a dominant height of about 15 to 17 m. The dominant species is the Scots pine (*Pinus sylvestris* L.). The soil is a sandy soil (humus podzol) with a 10 cm top layer of organic material (Dolman *et al.*, 2002). Mean annual temperature is 10.23°C and mean annual precipitation is 895.15 mm over the period 1997 to 2009 at the study site. The site has an average elevation of 52 m above sea level with a maximum altitude difference across the site of 10 m (Schelhaas *et al.*, 2004).

Figure 3.4: *Study site at Loobos, the Netherlands.*

Table 3.2: *Location, annual weather means, soil properties, topography and elevation of the study sites at Hyytiälä, Norunda and Loobos.*

	Study sites		
Characteristics	Hyytiälä	Norunda	Loobos
Location	Finland	Sweden	The Netherlands
Coordinates	61°51'N, 24°17'E	60°05'N,17°29'E	52°10'N, 05°44'E
Average temperature	4.31°C	6.40°C	10.23°C
Precipitation sum	498.25 mm	416.73 mm	895.15 mm
Soil properties	haplic podzol	sandy glacial	humus podzol
Topography	flat	flat (boulders)	hilly
Elevation	170 m	70 m	52 m

3.3 Fieldwork

3.3.1 Chronology of the site visits and collection of the tree material

The first site to be visited was Loobos in 2009 and 2010 then Norunda in 2010 and 2011 and finally Hyytiälä in 2011. All trees have been sampled during the growing season period (April-September). The flux-tower datasets were provided by the local teams and covered the period of 13 years (1997-2009) necessary to achieve the climate analysis at the three study sites. Finally, dendrological data was also collected by the local teams with three years of dendrometers and microcores at Hyytiälä (2007-2009), two years of dendrometers at Norunda (2010-2011) and two years of dendrometers at Loobos (2009-2010). This dendrological information will be further presented in Section 3.7.

3.3.2 Core sampling and preparation

Tree cores were taken using increment borers 10 and 12 mm diameter at breast height ($\approx$ 1.2 m) (Figure 3.5). This method is non-destructive for trees (Mantgem & Stephenson, 2004). The location of sampled trees was recorded using a high-precision GPS system (Leica GX1230) (Figure 3.6) and compared with the flux-tower position and the main wind direction. To protect cores during transit from the study site to the laboratory in Swansea University, they were stored in sealed plastic tubes of a diameter of 14 mm to avoid damage during transportation. On arrival at Swansea University, cores were removed from the tubes, attached to wooden mounts and left drying at room temperature (20°C) for 2 weeks (Figure 3.7). A typical wooden core from a Scots pine is shown in Figure 3.8. The surface of the sampled cores is sanded to permit a better observation of tree-rings and the determination of ring width. However, this surface is not used for laser ablation / microdissection to avoid contamination from aluminium oxide traces left by the sand paper on the core surface.

Figure 3.5: *Coring process on a Scots pine tree by using a 12 mm borer in Finland.*

Figure 3.6: *Leica GX1230 GPS base system while Natascha Kljun and Craig Mahoney are operating it (left). Leica GX1230 GPS Rover taking the tree position relative to the base while Craig Mahoney is taking a core from a tree (right).*
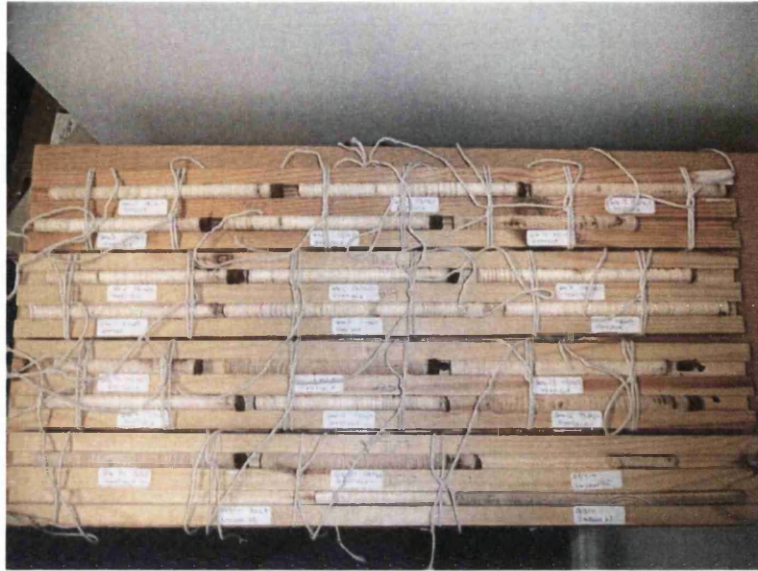
Figure 3.7: *Woodblock holding cores during the drying process.*

Figure 3.8: *Scanned image of a Scots pine tree core after drying.*

3.4 Carbon isotope time series production

3.4.1 Introduction

The procedure to build the carbon isotope time series from the sample preparation through laser sampling and the corrections to apply to the $\delta^{13}C$ time series are detailed in this section. Two laser systems were used to produce the raw $\delta^{13}C$ time series demanding a different sample preparation. The procedure to perform the $\delta^{13}C$ analysis with each system is described in Section 3.5.3. The resulting $\delta^{13}C$ time series (Section 3.5.4) differs in length from each other due to the inter-tree variability in ring width causing more $\delta^{13}C$ measurements in wider rings. The total number of measurements and each ring width is presented in Table 3.3 and table 3.4 respectively.

3.4.2 Sample preparation for laser procedure

To obtain high resolution stable carbon isotope series via laser sampling, the final step for sample preparation was to cut the cores into smaller laths that could fit the laser chamber. This preparation was dependent on which laser system the samples were supposed to be sent through and will be detailed in this section.

Two different laser systems have been used for this study. A Leica LMD7000 system developed at GFZ Potsdam (Germany) and an ESI/New Wave system developed at Swansea University (UK). For the Leica LMD7000, the cores have been cut into laths by microtomy to obtain subsamples of 300 microns to 500 microns thickness. This thickness was recommended by the Potsdam research team so the laser could cut quickly through the sample using low power settings and therefore avoiding burn traces on the edge of the cutting area. For the ESI/New Wave system, the cores have been cut into laths of wood of 3 mm using a double bladed automatic saw. As the tracheids are the dominant element in tree-rings of pine trees and are vertically oriented cells, vertical cuts were performed to permit a better observation of the annual rings. Cores are destroyed in this process when cutting out one or two laths. As the cores come from conifer wood, mobile resin and possible handling contamination were removed by an extraction using pure ethanol in a Soxhlet extractor for a duration of 24 hours (Loader et al., 1997). Remaining ethanol in the laths was first removed by bathing the samples in boiling distilled water in the Sohxlet extractor and then by drying the laths in an oven at 40°C for 12 hours. No further treatment was applied to the samples. A sample resolution of 80 microns was selected for both systems for comparable results. Moreover, 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 ‰ (Loader, 2013).

3.4.3 Laser system description

3.4.3.1 Laser microdissection

The Leica LMD7000 (Figure 3.9) is a microdissection system interfaced via a software controlling both the microscope and the laser system. The microscope allows the user to observe and identify which areas to cut on the sample. Then the laser will cut from above following the patterns identified by the user and the selected area will fall into a cup tray beneath the microscope sample platform. By setting the focus of the laser accurately, the laser beam should not damage the wood surrounding the defined pattern. A continuous sample cutting through the wood lath can be obtained by setting the software to cut through a succession of patterns.
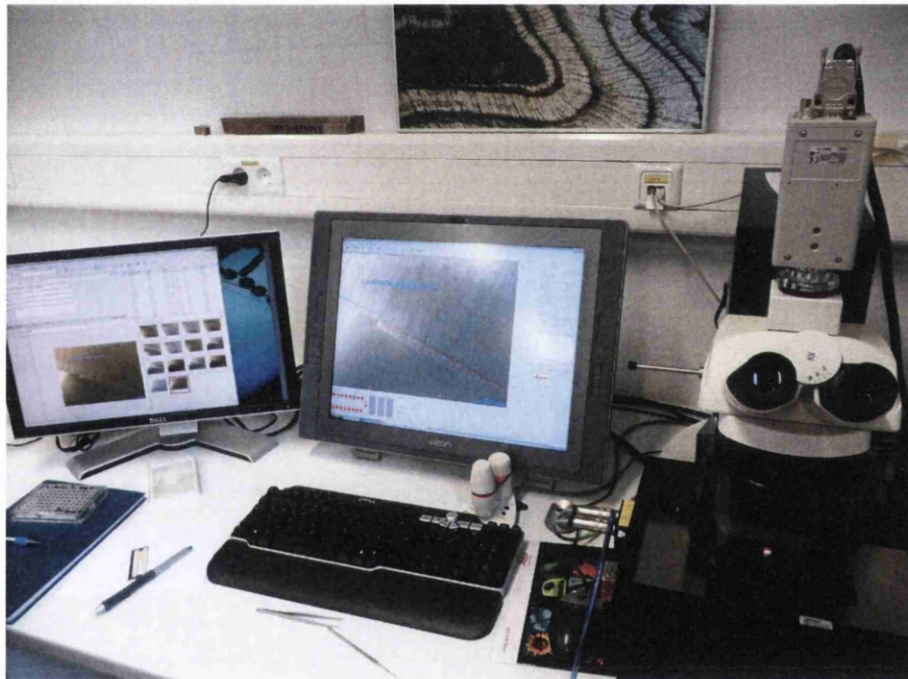
Figure 3.9: *Leica LMD7000 system at GFZ Potsdam.*

3.4.3.2 Laser ablation

The ESI/New Wave system (Figure 3.10) has a moving sample platform which present the selected ablation area to the stationary laser for ablation. The ablation of wood sample takes place directly on the wood lath and will leave distinctive traces of where the laser ablated through the wood (Figure 3.11). As the sample chamber is isolated from the atmosphere, the wood coming from the combustion is sent into the mass spectrometry system without contamination. Each sample run ($\approx$ 100 samples per batch) sent through on-line mass spectrometry starts and ends with ten C_3 cellulose (IAEA) test samples that have similar weight to the wholewood samples and have a constant ^{13}C signature. These standards permit calculation of the precision in the determination of the carbon stable isotope values and allow to correct for a possible sample size effect due to the choice of high resolution in laser sampling (80 μm) which lead to a large number of small size samples within a single tree-ring. Moreover, before the combustion of the ablated wood in the furnace, each sample analysis is calibrated by the injection of a CO_2 reference gas in the mass spectrometer. After combustion, the resulting sample gas is first sent through a Nafion water trap to eliminate water trace coming from the wood combustion. Finally, the gas is sent to a liquid nitrogen bath trapping the gas into the capillary for a short period of time. As the quantity of gas coming from the combustion is small and at the lower limit of the recommendations for mass spectrometry, this step is essential for a good recovery and chromatography of the resulting CO_2 during the analysis.
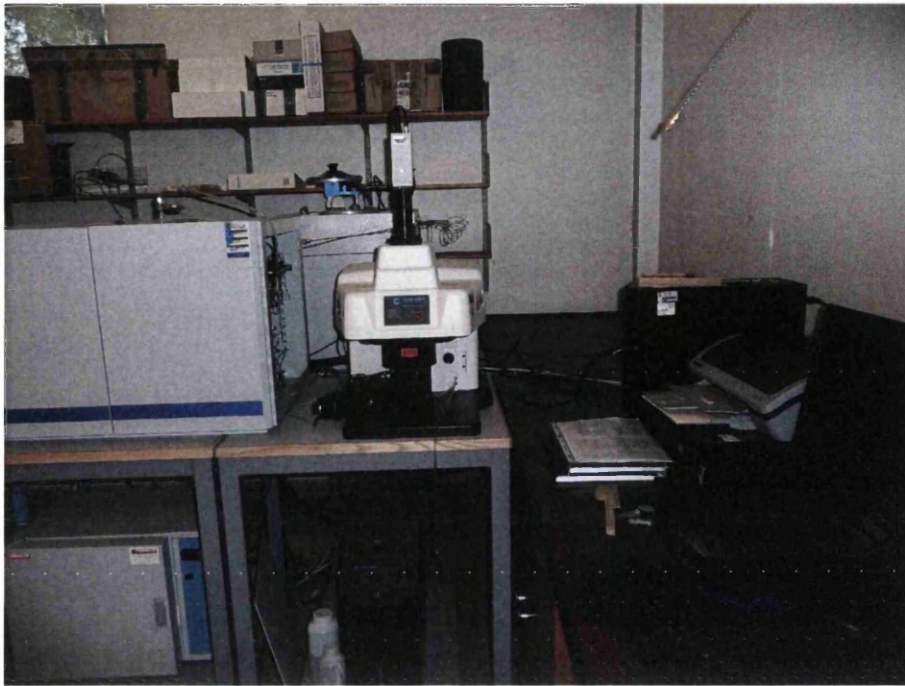
Figure 3.10: *ESI/New Wave system at Swansea University.*
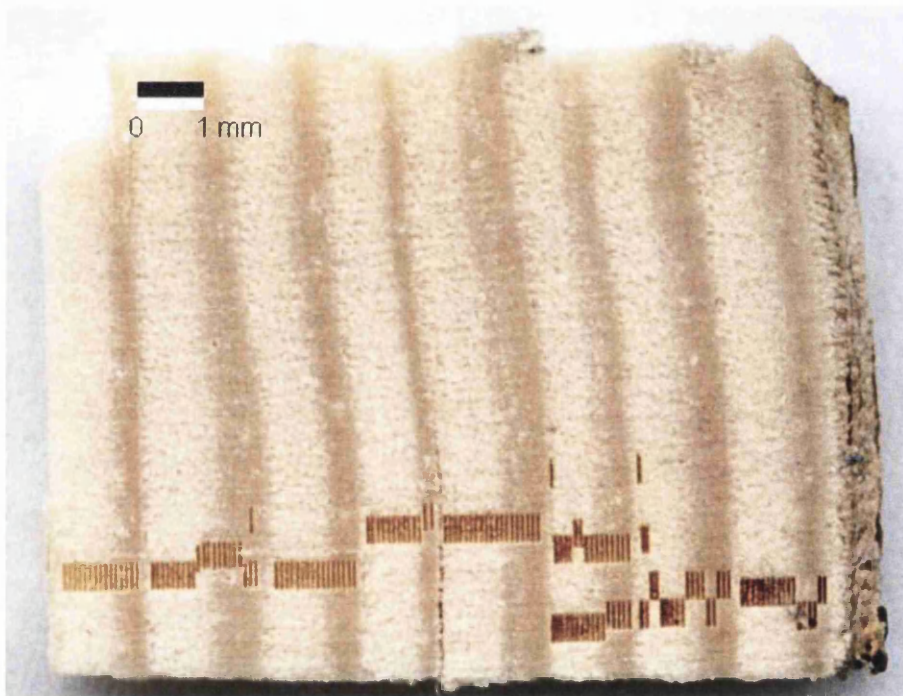
Figure 3.11: *Sample after ultraviolet laser ablation. The straight lines show where the laser has been sampling through the tree-rings.*

3.4.4 Production of the δ^{13}C time series

The laser procedure to ensure confidence in the carbon isotope values can be time consuming and resulted in the production of a total of nine raw δ^{13}C time series. By keeping the same settings on laser and spectrometry during the carbon stable isotope procedure, no noticeable change in the carbon stable isotope time series was detected to be provoked by artefacts. Therefore, producing resin extracted wholewood and whole ring carbon stable isotope time series at the intra-annual resolution by laser sampling represent a reliable method.

When sampling each tree-ring for δ^{13}C analysis, a different number of isotope measurements were obtained due to inter-tree variability in ring width. The wider the tree-ring is, the greater the number of isotope measurements. Table 3.3 shows the total number of δ^{13}C measurements per tree and per site. However, at Hyytiälä δ^{13}C time series are longer (1991 to 2010) than at Norunda (1991 to 2009) and Loobos (1996 to 2009). When considering the common period for the three sites (1991 to 2009), the trees sampled at Hyytiälä show a greater number of measurements and thus wider rings than the two other sites. This is surprising as Hyytiälä is the most Northern site out of the three study sites. However, a possible explanation could be that the age of the trees as Hyytiälä is populated by the youngest trees ($\approx$ 40 years) while trees were older at Norunda ($\approx$ 50-70 years) and Loobos ($\approx$ 100 years). Therefore, it is very probable that the difference in ring width depends mainly on a tree age effect rather than on an environmental influence.

In parallel to the carbon isotope analysis, measurements of the ring width were made. Each tree-ring width is presented in Table 3.4 for the three study sites. These measurements can be compared to inter-annual isotope values and evaluate if a common signal can be detected.

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Table 3.3: *Total number of $\delta^{13}C$ measurements for each tree at Hyytiälä, Norunda and Loobos. The value in brackets is the number of measurements for the common period 1996 to 2009.*

Tree analysed	Hyytiälä	Norunda	Loobos
Tree 1	385 (245)	206 (146)	194
Tree 2	359 (236)	262 (175)	213
Tree 3	335 (225)	271 (167)	266

Table 3.4: *Tree-ring width (mm) at Hyytiälä, Norunda and Loobos for the period 1991-2010.*

Year	Hyytiälä			Norunda			Loobos		
	Tree 1	Tree 2	Tree 3	Tree 1	Tree 2	Tree 3	Tree 1	Tree 2	Tree 3
1991	1.62	1.80	0.84	0.84	1.08	1.14	NA	NA	NA
1992	1.14	0.90	0.96	0.72	0.9	0.96	NA	NA	NA
1993	1.68	1.62	1.44	.066	1.20	0.66	NA	NA	NA
1994	1.86	1.32	1.50	0.90	1.14	0.72	NA	NA	NA
1995	1.14	0.72	0.90	0.48	0.72	0.72	NA	NA	NA
1996	1.38	1.02	1.08	0.48	0.96	1.08	0.78	0.54	1.32
1997	1.62	1.02	1.02	1.44	0.96	0.78	1.02	0.48	1.62
1998	1.08	0.96	0.78	1.20	1.02	0.84	0.78	0.72	1.50
1999	0.84	0.96	0.72	0.3	0.84	0.78	0.72	0.90	2.34
2000	1.26	1.20	0.96	0.6	0.78	0.78	1.08	1.02	0.96
2001	1.26	1.08	0.84	0.6	0.66	0.48	0.54	0.72	0.54
2002	1.20	0.84	1.02	0.48	0.54	0.36	0.54	0.78	1.08
2003	0.84	0.90	0.66	0.6	0.48	0.72	1.32	1.02	1.02
2004	1.08	1.26	0.90	0.42	0.84	0.48	0.78	0.78	0.84
2005	1.08	0.96	1.02	0.54	0.60	0.78	0.60	0.36	0.84
2006	0.66	0.78	0.96	0.72	0.84	0.84	0.96	1.56	0.90
2007	0.60	1.14	1.14	0.36	0.72	0.66	0.54	1.14	0.90
2008	0.78	0.96	1.08	0.6	0.78	0.66	0.66	0.84	0.84
2009	1.02	1.08	1.32	0.42	0.48	0.48	0.78	0.94	1.26
2010	0.96	1.02	0.96	NA	NA	NA	0.54	0.96	NA
Average	1.16	1.08	1.01	0.62	0.82	0.73	0.78	0.85	1.14

3.5 Analysis of carbon stable isotope

3.5.1 Introduction

This section details the processing steps necessary to obtain a stable carbon isotope dataset for comparison with local weather data at Hyytiälä, Norunda and Loobos. Exploration of individual δ^{13}C time series to characterise their properties is made at both intra-annual and inter-annual resolution. The use of the expressed population signal (Wigley *et al.*, 1984) assesses the appropriateness of the common signal between the individual δ^{13}C time series. The averaged δ^{13}C time series can then be interpreted as the mean response of the forest to climate influences. Trend analysis is performed to detect if non-climatic trends, such as the industrial effect (Freyer & Belacy, 1983), are present in the dataset. These trends should be removed via correction from the atmospheric δ^{13}C values to allow comparison with local climate data. The location of the three study sites presented in this study is covering a wide geographic range in Northern Europe. Therefore, inter-site comparison can bring insight on the difference of variation in climate response from interpreting the δ^{13}C time series depending on the latitude.

3.5.2 Intra-annual raw time series of δ^{13}C at each study site for the period 1991-2010

The raw series of δ^{13}C are examined in order to characterise the individual tree signal and patterns of variation through time. The length of the δ^{13}C time series differs depending on the study site: 19 years for Hyytiälä (from 1991 to 2010), 18 years for Norunda (from 1991 to 2009) and 14 years for Loobos (from 1996 to 2010). For each site, three δ^{13}C series have been produced from three different trees. The δ^{13}C raw time series of each tree are presented in Figure 3.12 for Hyytiälä, Figure 3.13 for Norunda and Figure 3.14 for Loobos. Each year in the δ^{13}C time series represents a single tree-ring formation. At the intra-annual resolution, each stable carbon isotope value represents 80 μm of ring width. Therefore, the δ^{13}C time series can be both represented against a time axis and a width scale where tree-rings with a small number of δ^{13}C measurements also represent a short width for the tree-rings.

The general pattern observable on the δ^{13}C time series is to have the most negative (depleted) values of δ^{13}C close to the rings boundaries (beginning and end of each year of growth) and having the less negative values (enriched) at the middle of the tree-rings. However, the amplitude of the δ^{13}C variation during a year can differ greatly in each individual δ^{13}C time series. The maximum range of amplitude is

found at Hyytiälä on the tree 1 time series between year 1992 and 2008. During year 1992, the amplitude is 3.81 ‰ while during year 2008 the amplitude is only 0.74 ‰ which may indicate a large spread of responses to climate forcing or a larger climate variability during a year of growth at this study site.

For the period 1997-2009, the inter-tree standard deviation is small and can be an indication of a high common δ^{13}C signal between the trees at each site. At Hyytiälä, the inter-tree standard deviation is 0.795 ‰ ranging from 0.709 to 0.838 ‰. At Norunda, it is equal to 0.654 ‰ ranging from 0.558 to 0.739 ‰. At Loobos it is equal to 0.837 ‰ ranging from 0.684 to 1.097 ‰. However, the individual δ^{13}C time series need to be standardised to accurately quantify the δ^{13}C common signal. The significance of the trends into the δ^{13}C time series are tested with the Fisher test with a significance level of $p \leq 0.05$. This test concludes that at Hyytiälä, only one time series has a weak significant negative trend (Tree 3). At Norunda, two time series have a weak significant negative trend. At Loobos all three individual δ^{13}C time series have a weak significant negative trend.

The theoretical annual bell shape pattern for evergreen species (Schubert & Jahren, 2011) is not always present in the δ^{13}C time series at the three study sites. It is expected that the weather variations and the tree physiology status from one year to another will modify this theoretical pattern into a different shape that can be interpreted to be the consequence of the difference in the intensity of the stress factors driving the carbon stable isotope variation through the growing season. During a same period of time, the intensity and the nature of the stress endured by the trees can vary from one study site to another. Differences between the carbon stable isotope time series of each site can then be observed. Therefore, the characterisation of the weather variation at each site may help to understand the inter-site variation.
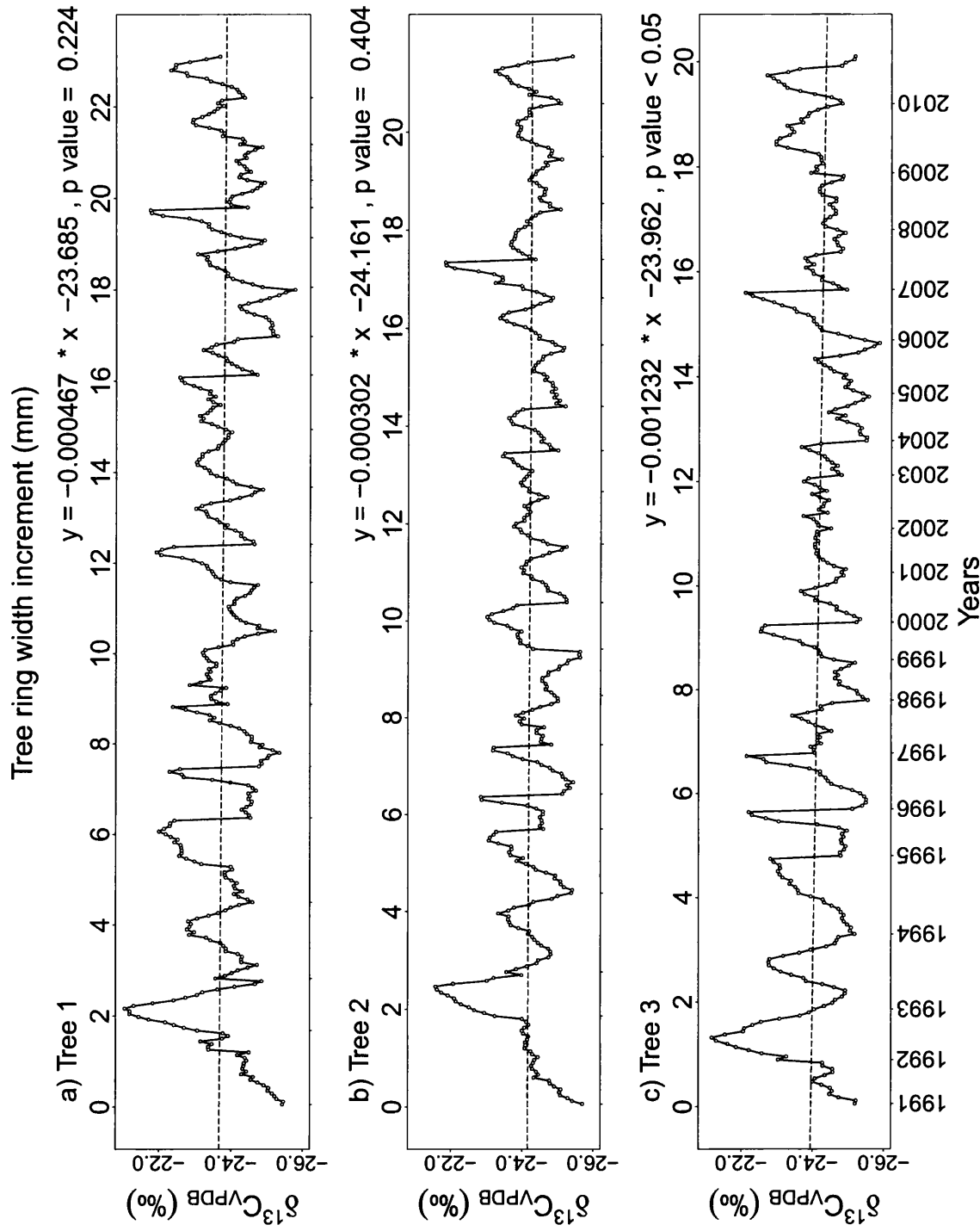
Figure 3.12: *Intra-annual variation of the stable carbon isotope composition at Hyytiälä (black open circles) of wholewood material from tree-rings with a sample resolution of 80 μm between 1991 and 2010 for three studied pines (a) for Tree 1 (b) for Tree 2 (c) for Tree 3. Each δ¹³C sample is represented against a time axis displaying the years sampled and against a tree-ring width scale (mm). The equation of the linear trend for the intra-annual time series is displayed at the topright corner of each tree sub-Figure where y is the δ¹³C trend value and x the position of the sampled value in the δ¹³C time series.*
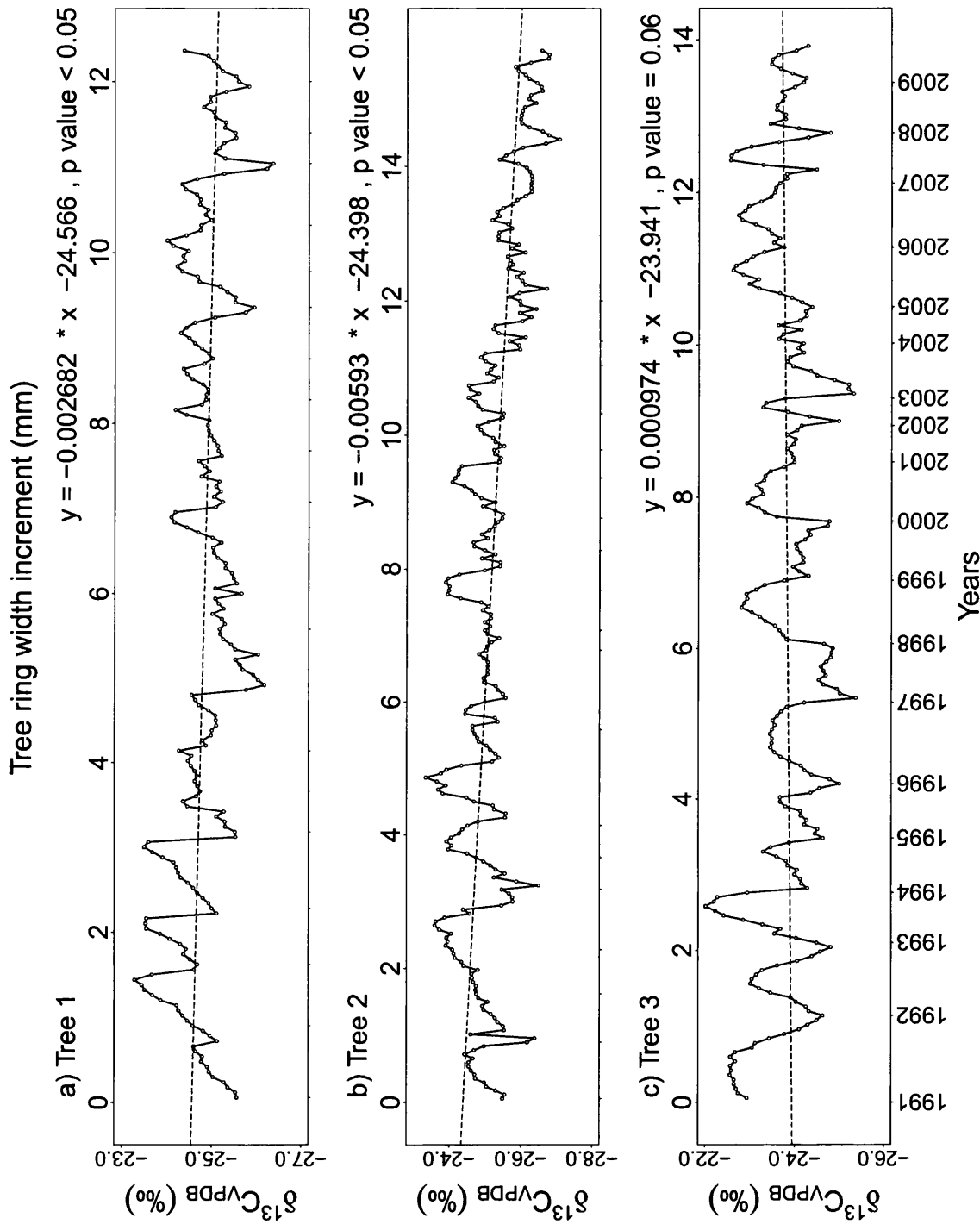
Figure 3.13: *Intra-annual variation of the stable carbon isotope composition at Norunda (black open circles) of wholewood material from tree-rings with a sample resolution of 80 μm between 1991 and 2009 for three studied pines (a) for Tree 1 (b) for Tree 2 (c) for Tree 3. Each δ¹³C sample is represented against a time axis displaying the years sampled and against a tree-ring width scale (mm). The equation of the linear trend for the intra-annual time series is displayed at the topright corner of each tree sub-Figure where y is the δ¹³C trend value and x the position of the sampled value in the δ¹³C time series.*

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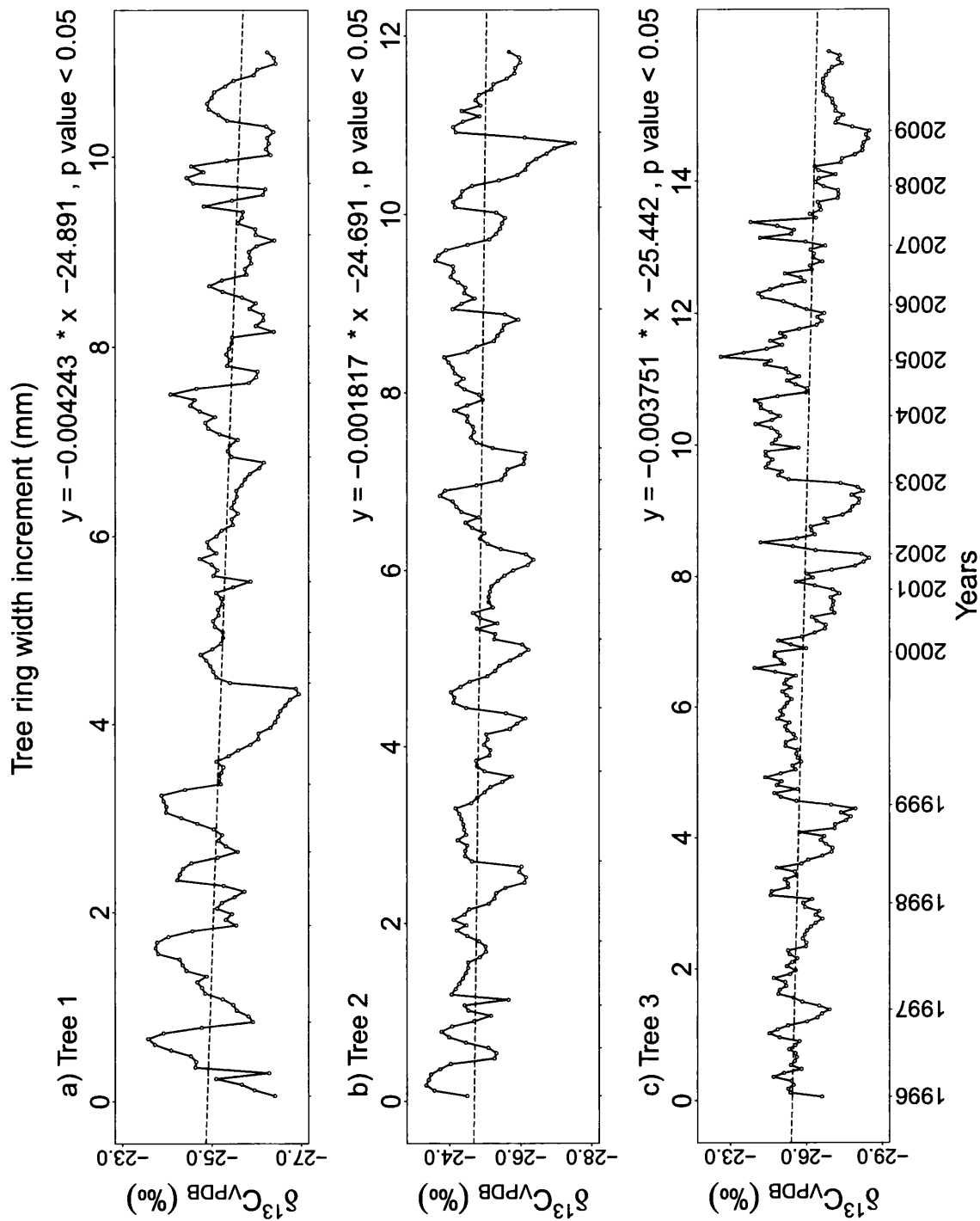
Figure 3.14: *Intra-annual variation of the stable carbon isotope composition at Loobos (black open circles) of wholewood material from tree-rings with a sample resolution of 80 μm between 1996 and 2009 for three studied pines (a) for Tree 1 (b) for Tree 2 (c) for Tree 3. Each δ¹³C sample is represented against a time axis displaying the years sampled and against a tree-ring width scale (mm). The equation of the linear trend for the intra-annual time series is displayed at the topright corner of each tree sub-Figure where y is the δ¹³C trend value and x the position of the sampled value in the δ¹³C time series.*

3.5.3 Raw inter-annual $\delta^{13}C$ and ring width time series

By degrading the high resolution isotope time series to obtain one average value per tree-ring, inter-annual time series for the sampled trees can be observed. These values can be compared with the variation in ring width to investigate if a co-variation exists between the two measurements in tree-rings. Inter-annual $\delta^{13}C$ and ring width time series are presented for each tree at Hyytiälä (Figure 3.15), Norunda (Figure 3.16) and Loobos (Figure 3.17). Despite using relatively short ring width time series, the expressed population signal is high and equivalent for Hyytiälä and Norunda (EPS = 0.89), but is below the threshold of a significant common signal for Loobos (EPS = 0.78). Therefore, at least for the period of time when isotope measurements have been produced, the two northern sites show a common signal in ring width time series which can be interpreted as a common response to environmental forcings at these sites. For the carbon isotope time series, the expressed population signal is high for Hyytiälä (EPS = 0.97) and below the threshold of 0.85 for Norunda (EPS = 0.81) and Loobos (EPS = 0.83). Therefore only at Hyytiälä presents a significant EPS values for both ring width and δ^{13} time series at the inter-annual resolution.

When comparing these two types of dendrochronological information for each tree, only one time series showed a significant relationship between $\delta^{13}C$ and ring width time series (tree 2 at Norunda) on the period considered. This time series is characterised by a clear decline in both the $\delta^{13}C$ and the ring width time series from 1991 to 2009. As this decline is not present in the other time series at the same study site, it is possible that this tree is experiencing a particular forcing causing a decrease in both measurements and increasing the correlation between the two time series. This effect is detrimental to the common signal at Norunda and can cause a lower EPS score than desired. At Loobos, tree 3 presents an increase in the annual $\delta^{13}C$ value for year 2003 which slowly decreases during the following years until 2008. This pattern is not seen in the other time series at the same site nor in the ring width time series. No satisfying explanation currently exists to justify this variability in this particular tree and similarly to Norunda, this individual behaviour will affect the common signal at the study site and will affect the results when establishing the link between $\delta^{13}C$ time series and environmental forcing. The absence of correlation between ring width and carbon isotope time series may indicate that the intra-site variation in carbon isotope series is not due to different growth performance during a same year.
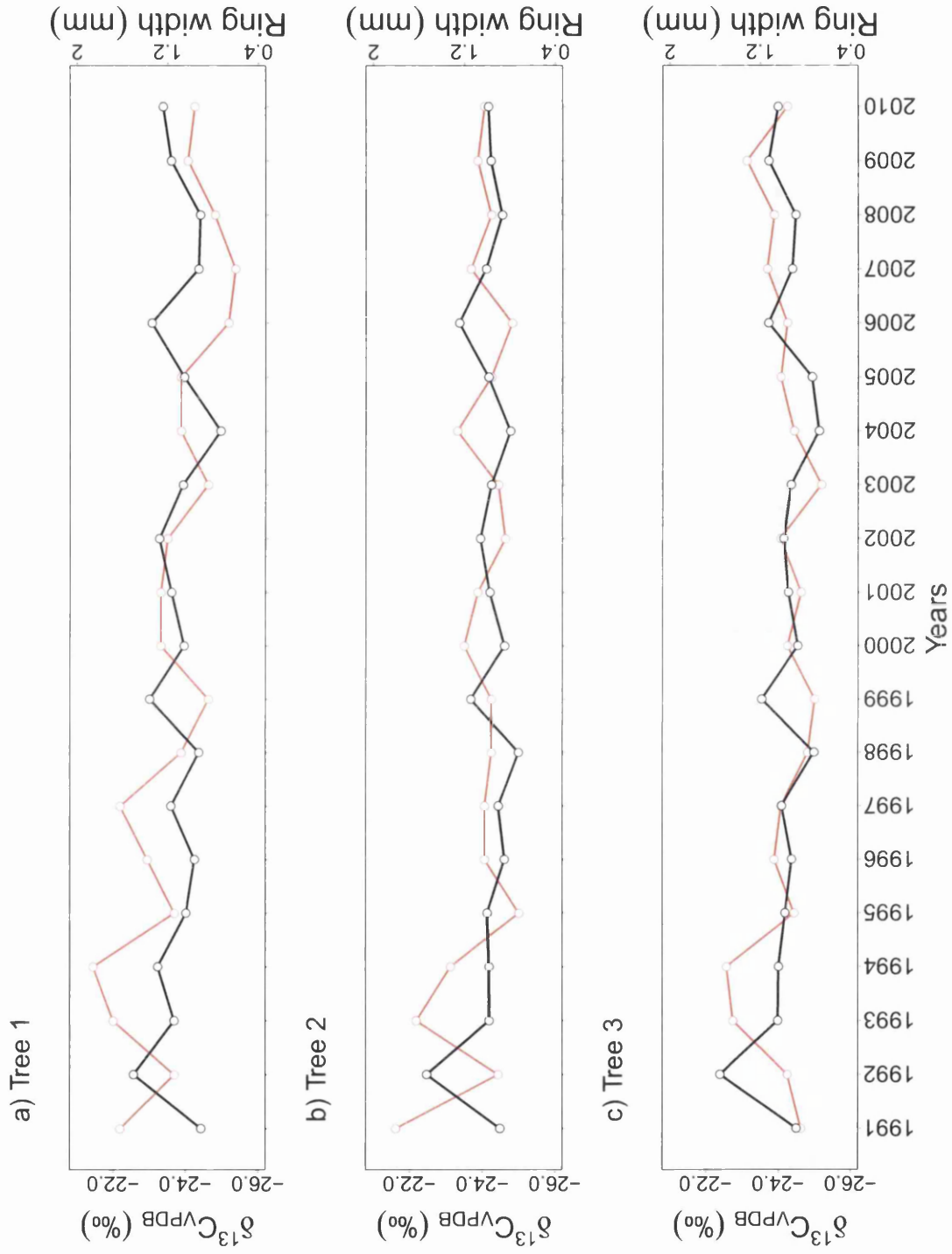
Figure 3.15: *Comparison between the inter-annual δ^{13}C time series (a) for Tree 1 (b) for Tree 2 (c) for Tree 3 (black open circles) and ring width (orange open circles) variation at the inter-annual resolution for the period 1991-2010 at Hyytiälä.*
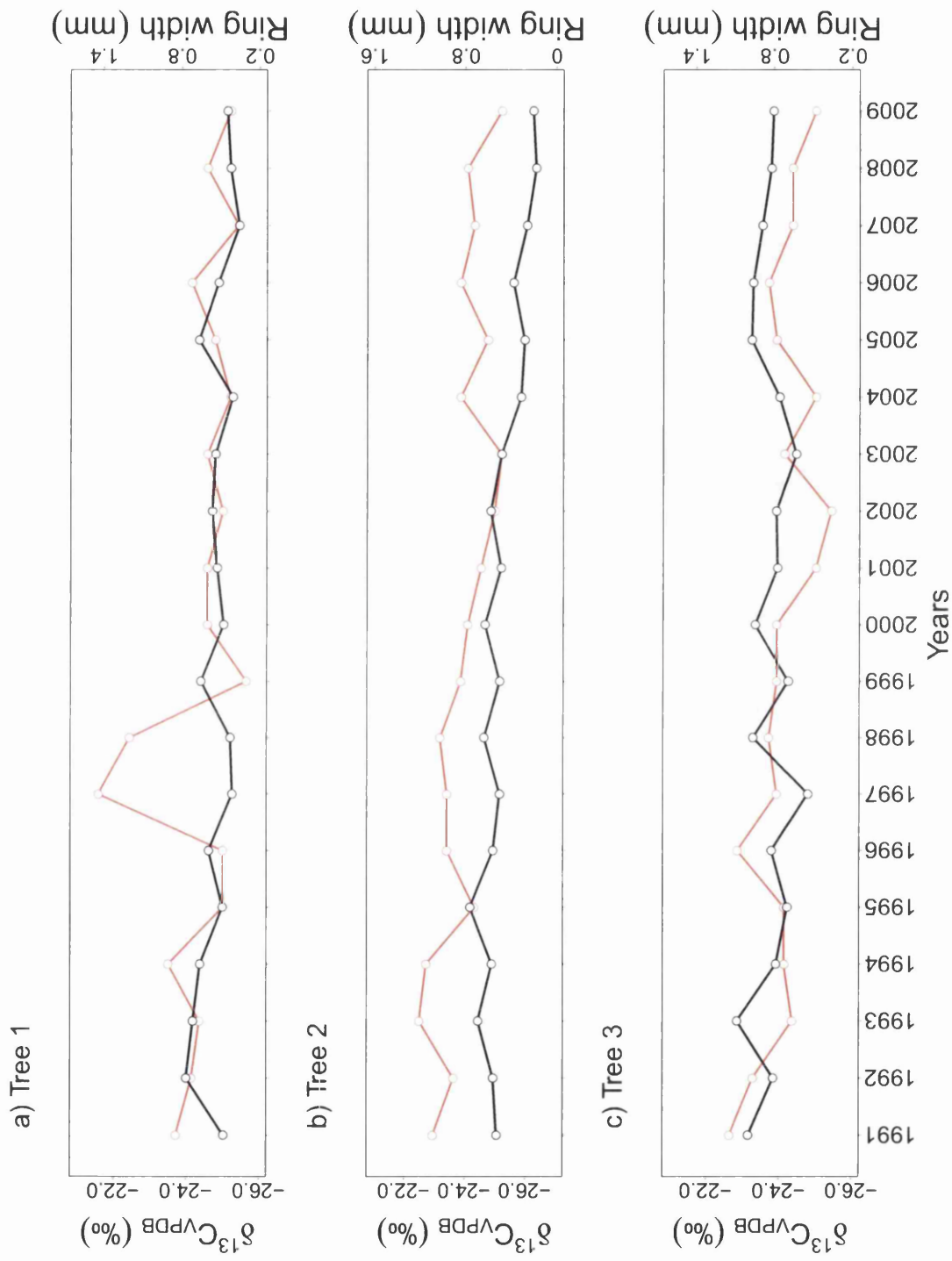
Figure 3.16: *Comparison between the inter-annual $\delta^{13}C$ time series(a) for Tree 1 (b) for Tree 2 (c) for Tree 3 (black open circles) and ring width (orange open circles) time series variation at the inter-annual resolution for the period 1991-2009 at Norunda.*
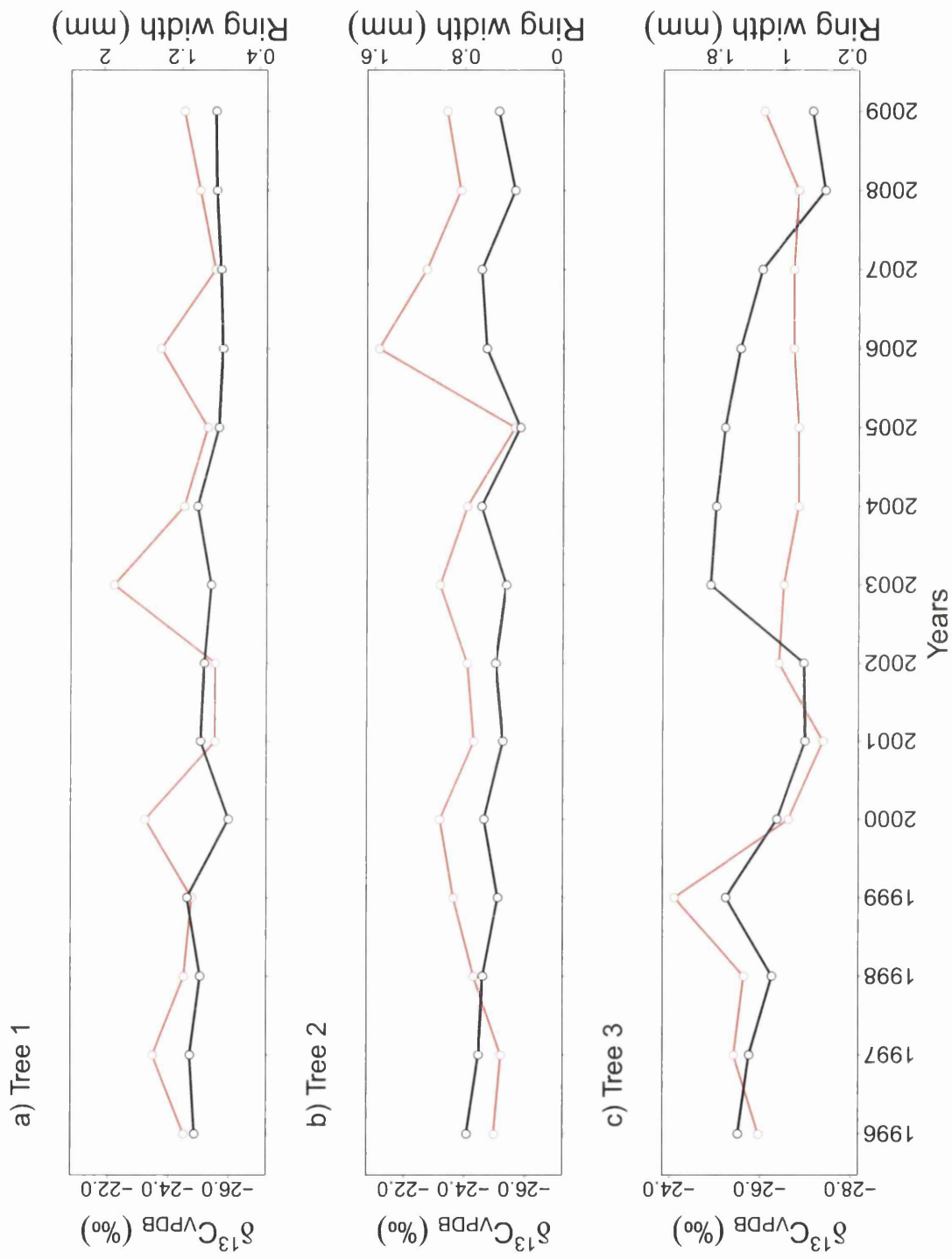
Figure 3.17: *Comparison between the inter-annual $\delta^{13}C$ time series (a) for Tree 1 (b) for Tree 2 (c) for Tree 3 (black open circles) and ring width (orange open circles) time series variation at the inter-annual resolution for the period 1996-2009 at Loobos.*

3.5.4 Standardisation of the stable carbon isotope series

In this study, the approach selected for standardisation is to degrade the number of isotope measurements in each tree-ring to match the minimum number of measurements from one of the three time series analysed. The percentage of ring formation is calculated for each tree and the interpolation of the isotope values can be made in accordance with the same relative position in each tree-ring. The standardised time series are then matched year by year and possess the same number of isotope measurements. The choice of matching each tree-ring to the minimum number of isotope measurements avoids the introduction of an auto-correlation component when one wants to match the shortest time series to the other time series as the additional isotope values need to be interpolated between two measured values and then producing an artificial linear pattern in the final interpolated time series.

The resulting standardised three individual raw δ^{13}C time series have the same number of measurements per tree: 300 measurements for Hyytiälä, 137 for Norunda and 159 for Loobos. Thus, it is possible to calculate the expressed population signal (EPS) to evaluate the common signal at each site at the intra-annual resolution. For Hyytiälä, the common variability is quite high (EPS = 0.96, Eq 2.6). However, for Norunda and Loobos, the EPS values are equal to 0.79 and 0.83 respectively which is below the threshold of acceptability equal to 0.85 (Wigley *et al.*, 1984). Therefore, three trees are enough to obtain a significant common signal at Hyytiälä for intra-annual δ^{13}C time series during the period considered but not for Norunda and Loobos. These time series are presented in Figure 3.18a for Hyytiälä, Figure 3.19a for Norunda and Figure 3.20a for Loobos.

3.5.5 Signal strength of the δ^{13}C time series at each study site for the period 1991-2010

By averaging the three standardised δ^{13}C time series into a unique and representative δ^{13}C time series, the common δ^{13}C signal at each site is observable. These series are presented in Figure 3.18b for Hyytiälä, Figure 3.19b for Norunda and Figure 3.20b for Loobos. The most δ^{13}C depleted mean value of -24.05 $\pm$ 0.754 ‰ is found at Hyytiälä, followed by Norunda with -24.564 $\pm$ 0.474 ‰ and Loobos with -25.419 $\pm$ 0.645 ‰. The standard deviation around the mean value shows the intensity of the intra-annual variation. Therefore, the maximum intra-annual variation is observable at Hyytiälä then at Loobos and Norunda. Trend analysis shows a significant slightly declining and trend for the averaged series at Hyytiälä, Norunda and Loobos (F-test, $p < 0.05$). As these declining trends are being provoked by non-climatic effects, it is necessary to remove them before climate

analysis.

3.5.6 Atmospheric correction for stable carbon isotope series applied to δ^{13}C time series at each study site for the period 1991-2010

The correction from McCarroll & Loader (2004) to compensate for the atmospheric change in δ^{13}C is the method selected and applied to the δ^{13}C time series produced in this study. This correction procedure adds an isotope correction value year by year. The correction procedure used is based on Francey *et al.* (1999) results over δ^{13}C CO_2 measurements in the Southern Hemisphere, see Table 3.5. By correcting δ^{13}C values year by year, we aim to remove post-industrial trends from the stable carbon isotope time series. This correction method produces an offset in the δ^{13}C time series as shown in Figure 3.18b for Hyytiälä, Figure 3.19b for Norunda and Figure 3.20b for Loobos. This offset affects the statistical properties of the δ^{13}C time series, the Hyytiälä mean value is changed to -22.460 $\pm$ 0.741 ‰, Norunda -23.009 $\pm$ 0.434 ‰ and Loobos -23.756 $\pm$ 0.615 ‰. However, as the same correction is applied to the three sites the most depleted series are still the ones at Hyytiälä followed by Loobos and Norunda. Trend analysis at Hyytiälä and Norunda shows that the negative trends previously found are now non-significant (F-test, $p > 0.05$). However Loobos still shows a weak negative and significant trend (F-test, $p < 0.05$). Because this site has the shortest δ^{13}C time series (1996-2010), the detection of a trend can be due to a local variation in the δ^{13}C time series which may be mitigated by a longer time series. Moreover, when fitting a trend over the same period at Hyytiälä, a significant slight positive trend is detectable, reinforcing this hypothesis.

Table 3.5: *Values for atmospheric corrections from McCarroll & Loader (2004) expressed in ‰ for the period 1991 to 2003, the corrections values from 2003 to 2010 are linearly extrapolated from the previous values.*

Year	atmospheric correction (‰)
1991	1.34
1992	1.37
1993	1.39
1994	1.42
1995	1.45
1996	1.48
1997	1.51
1998	1.53
1999	1.56
2000	1.59
2001	1.62
2002	1.65
2003	1.67
2004	1.70
2005	1.73
2006	1.76
2007	1.79
2008	1.81
2009	1.84
2010	1.87
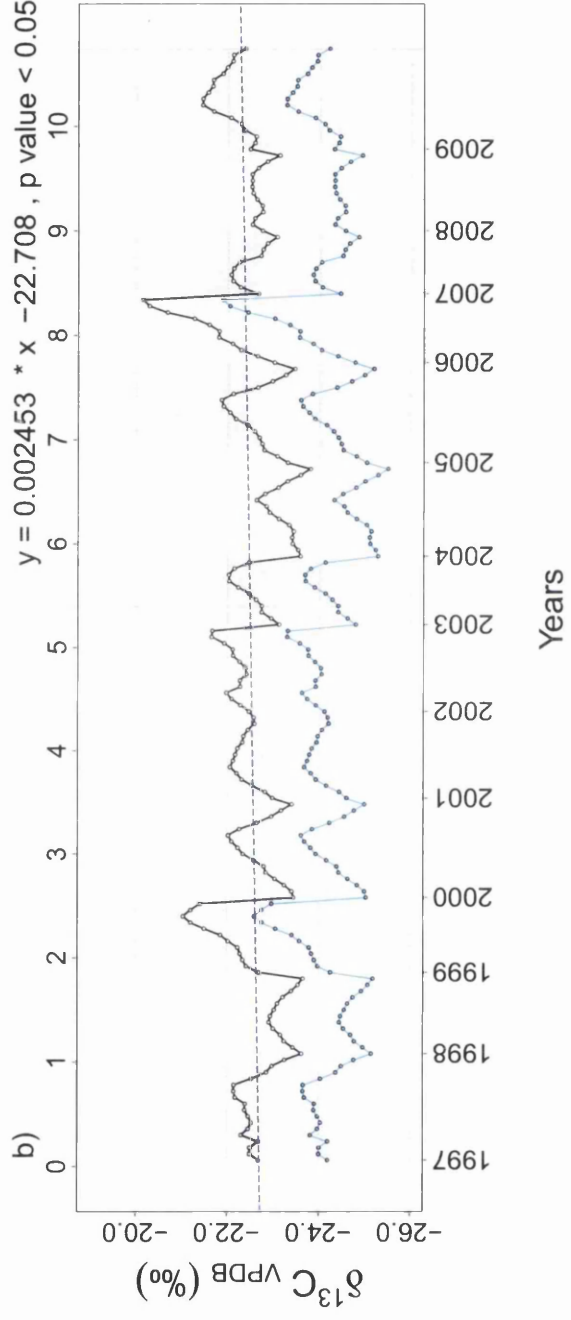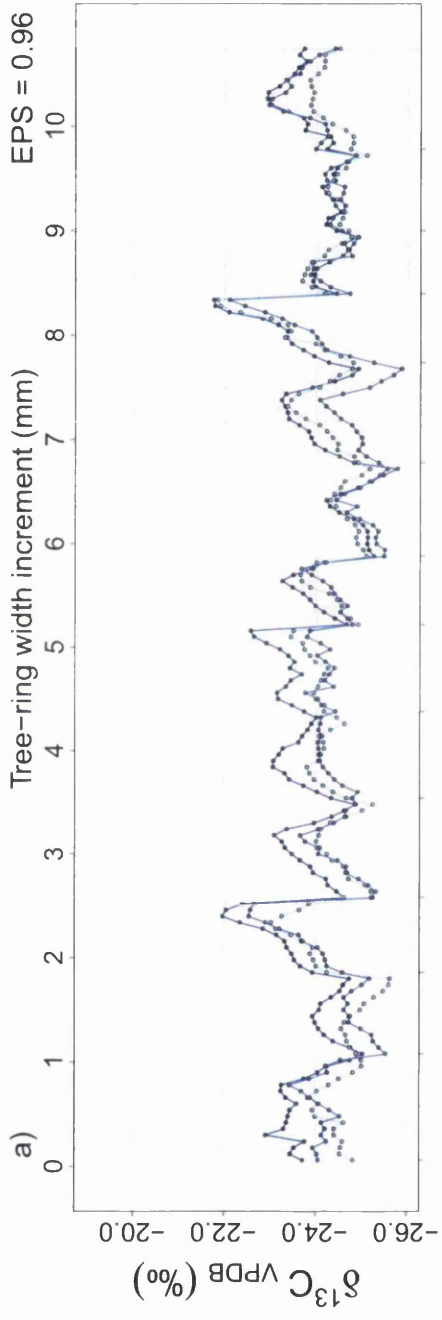
Figure 3.18: *(a) The three stable carbon isotope time series from the studied pines at Hyytiälä (see Figure 3.12). (b) Averaged stable carbon isotope series using the three above series (grey open circle) and the atmospheric corrected time series (black open circle). The trend of the atmospheric corrected series is displayed (blue long dashed line) with equation and p value on the topright corner of the sub-Figure.*
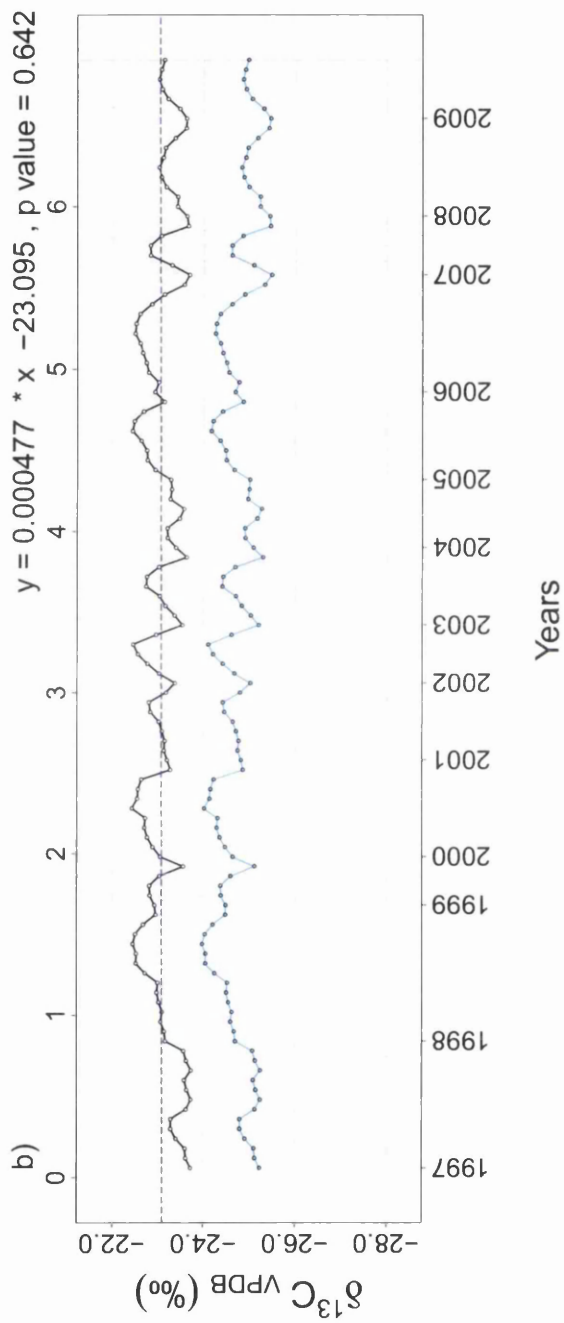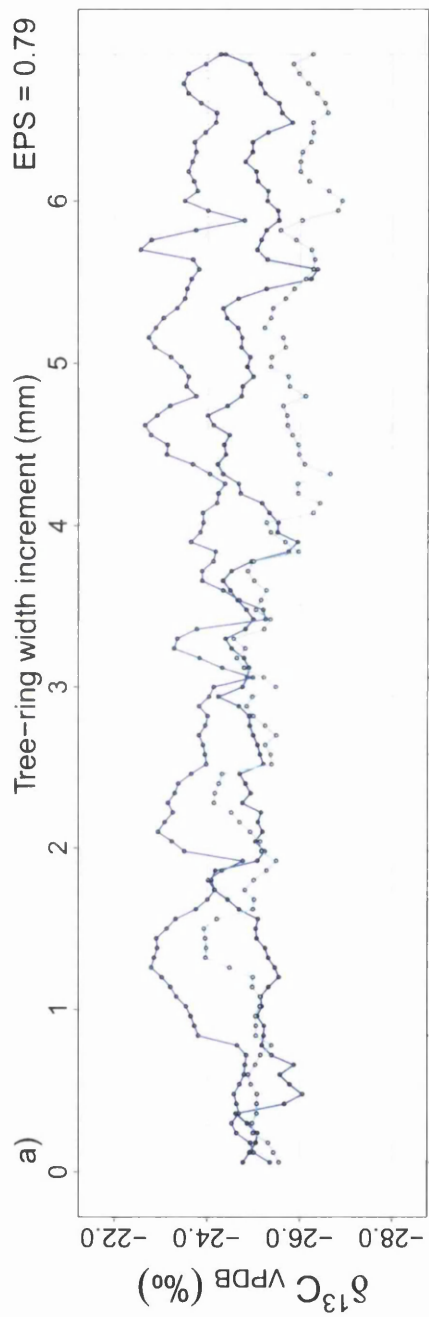
Figure 3.19: (a) The three stable carbon isotope time series from the studied pines at Norunda (see Figure 3.13). (b) Averaged stable carbon isotope series using the three above series (grey round dots) and the atmospheric corrected time series (black round dots). The trend of the atmospheric corrected series is displayed (blue dashed line) with equation and p value on the topright of the sub-Figure.
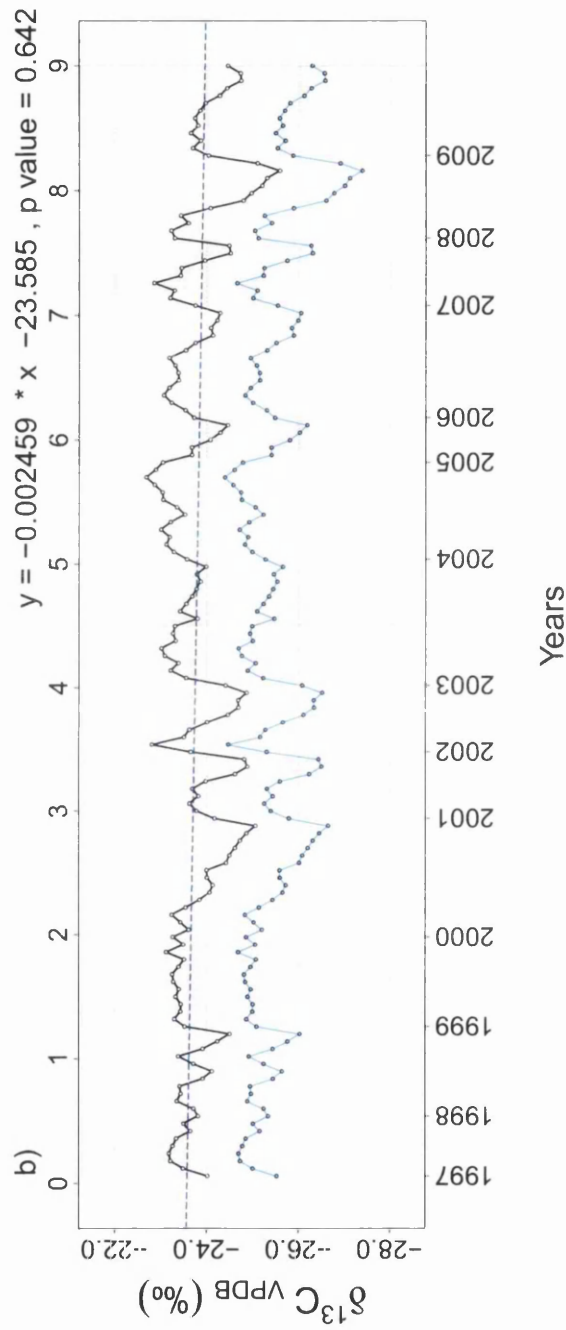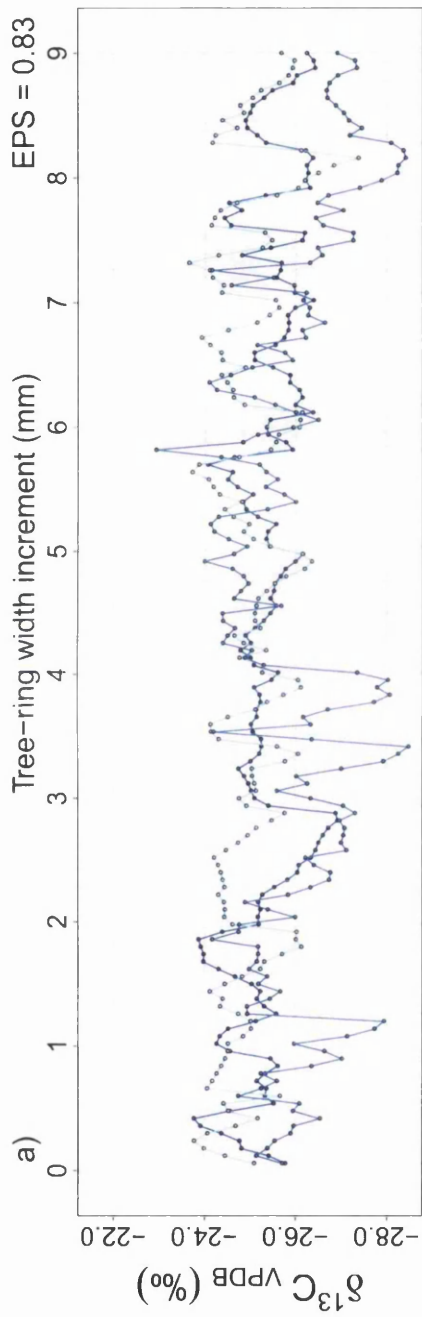
Figure 3.20: *(a) The three stable carbon isotope time series from the studied pines at Loobos (see Figure 3.14). (b) Averaged stable carbon isotope series using the three above series (grey round dots) and the atmospheric corrected time series (black round dots). The trend of the atmospheric corrected series is displayed (blue dashed line) with equation and p value on the topright of the sub-Figure.*

3.5.7 Seasonal correction

To evaluate the source air effect at Hyytiälä, open access data of air $\delta^{13}C$ samples from the NOAA Earth System Research Laboratory were used and downloaded at $http://www.esrl.noaa.gov/$. The Pallas-Sammaltunturi station was selected for its similarity in terms of forest stand to Hyytiälä and the abundant flask data recorded from 2002 to 2009. For Norunda and Loobos, the closest study site selected in this database was Hainrich (Germany). Air $\delta^{13}C$ measurements at canopy height are then examined to determine if a seasonal correction is necessary.

For Hyytiälä, air $\delta^{13}C$ data exist from 2002 to 2009 with numerous measurements during each month. It is then possible to build a monthly dataset with confidence intervals showing the seasonal variation through the year. For Hainich, two years have been intensively sampled (2002 and 2004) which permit some inter-annual comparison. However, the month of January has only been sampled during 2002 while April, May and June have only been sampled during 2004. Therefore, no confidence intervals can be calculated for these months. Figure 3.21 shows the seasonal variation in air $\delta^{13}C$ for Hyytiälä and for Hainich at the monthly resolution.

It is evident that both sites present a common evolution in air $\delta^{13}C$ values with a depletion in spring followed by an enrichment in summer and another depletion in winter. However, the enrichment phase starts much earlier at Hainich (from May to October) than at Hyytiälä where it starts in July until October. This information is compatible with a theoretical larger period of growth in mid latitude European locations compared to the northern Finland where the climate conditions are less permissive for growth. This would suggest that the photosynthesis process starts to deplete the atmosphere in ^{13}C earlier in middle Europe than in northern study sites. Another important point to notice is that despite a considerable annual variation in $\delta^{13}C$ values (0.83 ‰ for Hainich, 0.89 ‰ for Hyytiälä), when considering only the three summer months (June, July and August) where most of the tree growth is supposed to occur, the $\delta^{13}C$ seasonal amplitude is quite small (0.11 ‰ for Hainich and 0.26 ‰ for Hyytiälä). Establishing a correction for intra-annual time series of tree-ring $\delta^{13}C$ from air $\delta^{13}C$ would not modify significantly the intra-annual variation as the raw wholewood $\delta^{13}C$ seasonal amplitude is typically of 1.42 ± 0.59 ‰ at Hyytiälä, 1.07 ± 0.40 ‰ at Norunda, 2.05 ± 0.87 ‰ at Loobos. Therefore, the effect of seasonal $\delta^{13}C$ variation during the growing season will be considered as negligible in this study.

Figure 3.21: *Seasonal variation of air $\delta^{13}C$ values (a) at Pallas-Sammaltunturi (Finland) and (b) at Hainich (Germany). Values are expressed as monthly averages with ± standard deviation calculated over the period 2002 to 2009.*

3.5.8 Summary

A relatively low inter-tree $\delta^{13}C$ variability is present in the stable carbon isotope datasets which indicates the likelyhood that there will be a strong common signal at Hyytiälä. This expectation is confirmed by EPS values over the 0.85 treshold at the intra-annual resolution and shows that the trees are responding in a common behaviour to environmental forcing. The relatively high inter-site variation may indicate different climatic influences or a different response strength of the trees to climate events depending on their location. The effect of changing atmospheric $\delta^{13}C$ has been removed via the correction of McCarroll & Loader (2004) and resulted in the corrected $\delta^{13}C$ time series showing no significant trend at Hyytiälä and Norunda. Loobos $\delta^{13}C$ time series being the shortest of the three sites, the corrected time series still present a significant trend that could be due to a short range climatic effect. The amplitude of the depletion in $\delta^{13}C$ time series varies inter-annually at each site. Hyytiälä is the study site where the highest depletion mean level and highest variation amplitude is present in the $\delta^{13}C$ time series, followed by Norunda and Loobos which may indicate a clearer response to climate at Hyytiälä possibly due to greater variations in weather conditions during each year.

3.6 Dendrological information availability and properties at the three study sites

The microcore and dendrometer measurements recorded at the study sites can be used to help the determination of wood growth onset and cessation. Microcores record the radial cell number increase in the wood while the dendrometers record the radial expansion which can both be interpreted as indicators of wood formation. However, both techniques present limitations. Microcores have to be sampled in the period close to the effective onset of growth so only the first cell would have been formed and could be observable via microscopy. This condition is not always easy to obtain as sampling a large number of microcores in the probable period for onset is unrealistic. It is then a matter of intuition,to obtain a first microcore during the growing season that can provide a precise date of onset. It is more usual that the first microcore will show a few rows of formed cells and can be considered to represent a close estimation of the growth onset. When establishing the date of wood growth cessation, it is also necessary to keep in mind that radial cell counts will only state the cessation of cell production and do not integrate the final period of cell maturation when cells can still be influenced by weather conditions. There will be then an offset between the dates obtained by

microcores and the realistic dates of the total wood growth cessation. Dendrometer records also exhibit limits when they are used to precisely determine growth onset and cessation. Water content in the trunk varies during spring, known as the water shrinkage effect, which induces a negative variation of the radial increment at the crucial period of time when the onset of wood formation can occur. In parallel, the temperature is also increasing during this period of time which can expand the wood without the formation of new wood cells. The combined effect of these events creates a noise signal for radial expansion which can lead to inaccurate estimation of wood growth onset (Mäkinen *et al.*, 2003). Finally, the radial increment formed toward the end of the growing season is becoming smaller and smaller during the late summer and an absolute date for growth cessation is impossible to determine accurately. Therefore, the dates proposed in this section to estimate a realistic growing season are to take with the consideration that they can be relatively inaccurate but at least can be an indication of inter-annual and inter-site variation in the seasonal pattern of tree growth.

At the selected study sites, dendrological data are only available for a few years. At Hyytiälä, microcore measurements have been recorded from 2007 to 2009 (figure 3.22) with also three years of Figure measurements at the half hourly resolution during year 2007 (figure 3.23), 2008 (figure 3.23) and 2009 (figure 3.23) for three trees. It is noticeable for both type of records that tree growth can vary individually and independently from the year recorded causing an offset in the final number of cells or the tree radius expansion from one tree to another. When comparing microcores and dendrometers measurements at Hyytiälä during 2007, 2008 and 2009, microcores state a start of cell growth by the end of May, while dendrometer records would also state an onset of wood growth from mid May to end of May during these years. To determine the end of growth, microcores show an end of new cell expansion by the end of July to mid August. Figure measurements show a decrease in wood growth by the end of July with the start of a plateau period from the beginning of August.

At Norunda, daily dendrometer measurements were carried on eight trees for year 2010 (Figure 3.26) and 2011 (Figure 3.27). Despite a high variation in tree radial expansion between the eight records, there is a good agreement in a maximum growth event by the 20th of July (DOY 200) during year 2010 and around the 25th of June (DOY 176) for year 2011. For both years, the end of radial expansion occurs by the end of August (DOY 243) with only a small variation between the records. However, these measurements state that growth occurs only on short periods of time (one to two months only) which can question the validity of the

use of dendrometers to characterise the seasonal wood growth at Norunda.

Finally at Loobos, two years of dendrometer measurements are available at the hourly resolution for 2009 (Figure 3.28) and 2010 (Figure 3.29) for one tree. Both years are characterised by an important water shrinkage at the end of spring which can hide the start of growth. The convention applied in this case is to take the date when the cumulated growth start to increase again which would set the start of growth by the middle of May for 2009 and for 2010. The end of radial expansion is not well defined during the measurements of 2009 with an increase in the winter months. However, it is possible to distinguish a plateau period starting by the end of September for 2009 and the middle of September for 2010.

Without a long period of time when dendrometer have been running, it is difficult to comment on the inter-annual variability in the start and end of cell growth or radial expansion. However, an observation to make is that during these few recorded years, the onset and cessation of wood growth estimated via dendrometer or microcore techniques can be offset from a few days to a couple of weeks depending on the year observed. This variation is high enough to consider that estimated dates of onset and cessation of growth for each year are necessary to estimate when matching isotope time series with eddy covariance measurements on the same time scale.

To detect a latitudinal effect, the comparison of the dates of onset and cessation of wood growth via the dendrometer between the three study sites shows that Hyytiälä and Loobos have similar dates for radial growth onset estimates while the estimated cessation dates of radial expansion differ greatly with Hyytälä showing a plateau in radial expansion in August while growth last until September for Loobos. The comparison with Norunda can be doubtful as only a very short period of growth is detectable with the dendrometer records which would induce that this site has the shortest period for growth than Hyytiälä and Loobos. However, Hyytiälä would theoretically be more restricted in wood growth due to low temperature limitations at this latitude. There could still be a water supply effect to consider at Norunda to be the cause of such short growing period but it is likely that the dendrometer records only give an approximate information on growth duration. All dendrological information are resumed in Table 3.6.

Table 3.6: *Availability of the dendrological information, the period sampled, approximative onset and cessation at Hyytiälä, Norunda and Loobos.*

Site	Type	Period sampled	Nb of trees	Approx. onset	Approx. cessation
Hyytiälä	Microcores	2007-2009	4	Late May	Late July / Mid August
Hyytiälä	Dendrometers	2007-2009	3	Mid May / End May	Late July / Mid August
Norunda	Dendrometers	2010-2011	8	Late June / Late July	Late August
Loobos	Dendrometers	2009-2010	1	Mid May	Mid September / Late September
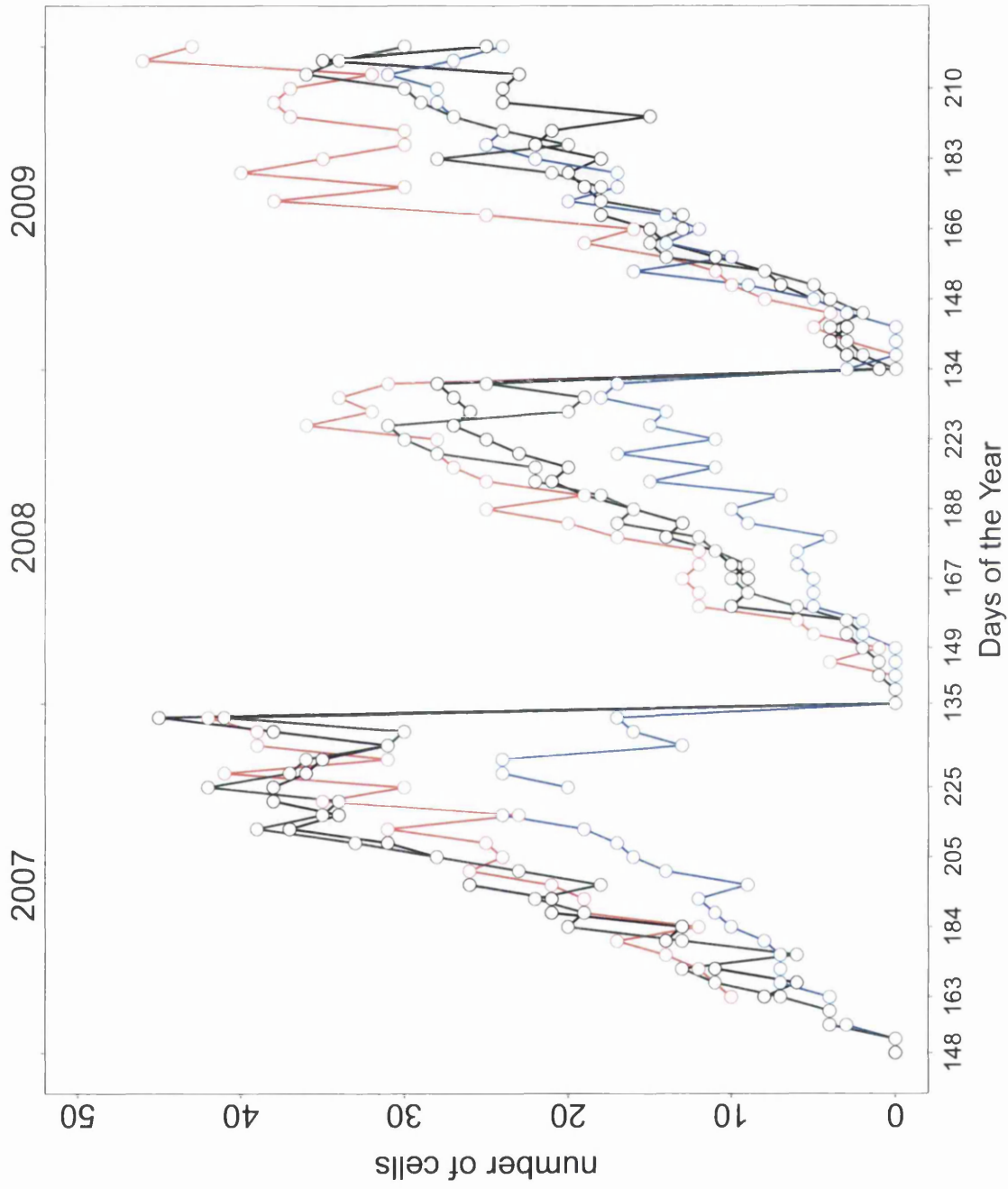
Figure 3.22: *Absolute number of cells plotted against days of the year during growing seasons 2007, 2008 and 2009 measured with microcoring (continuous red, blue, black, green lines) for four Scots pine in Hyytiälä (Finland). Data aquisition has been performed by the local team.*
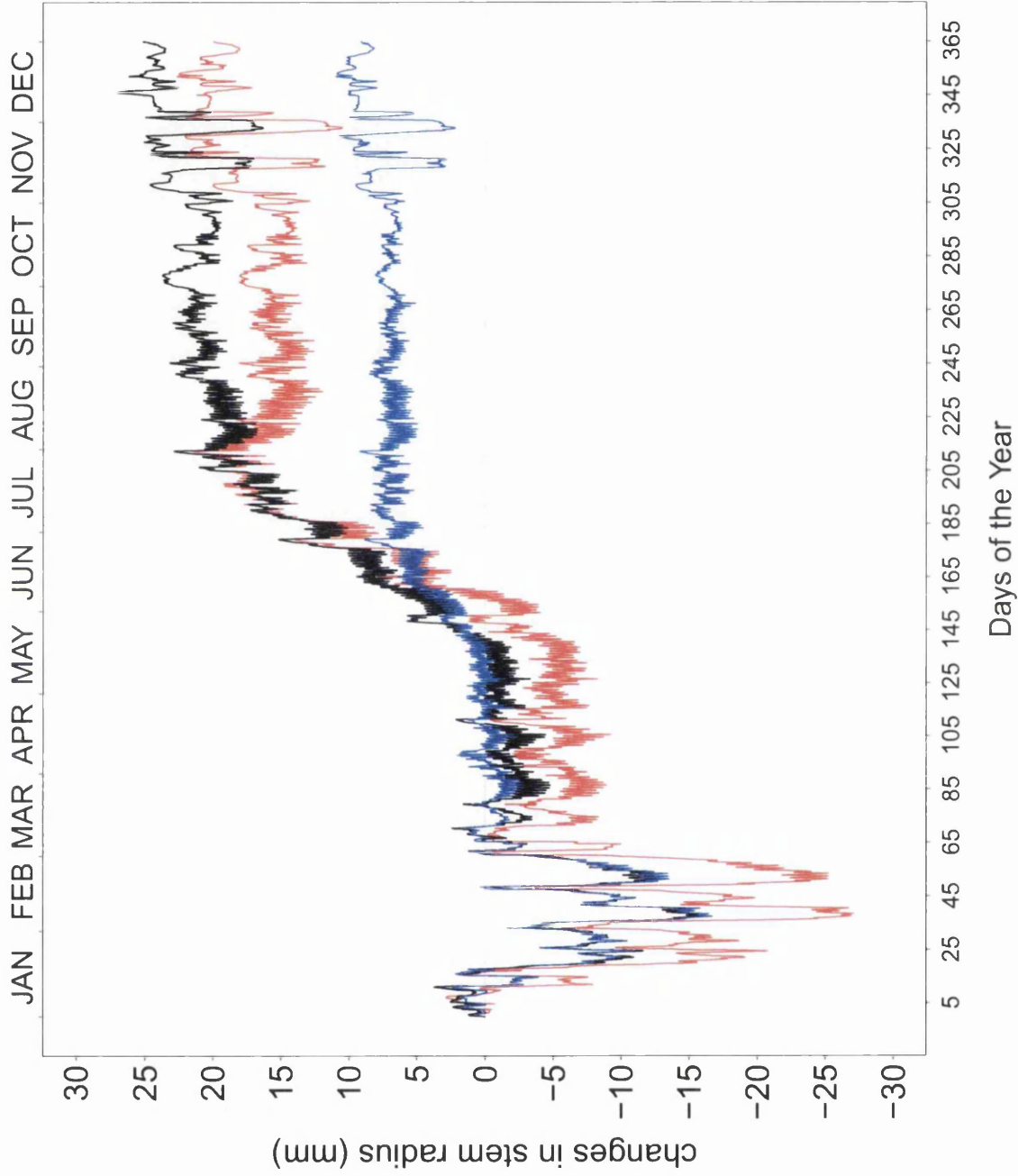
Figure 3.23: *Absolute changes in stem radius plotted against days of the year measured by dendrometers (continuous red, blue, black lines) during the year 2007 for three Scots pines in Hyytiälä (Finland). Data aquisition has been performed by the local team.*
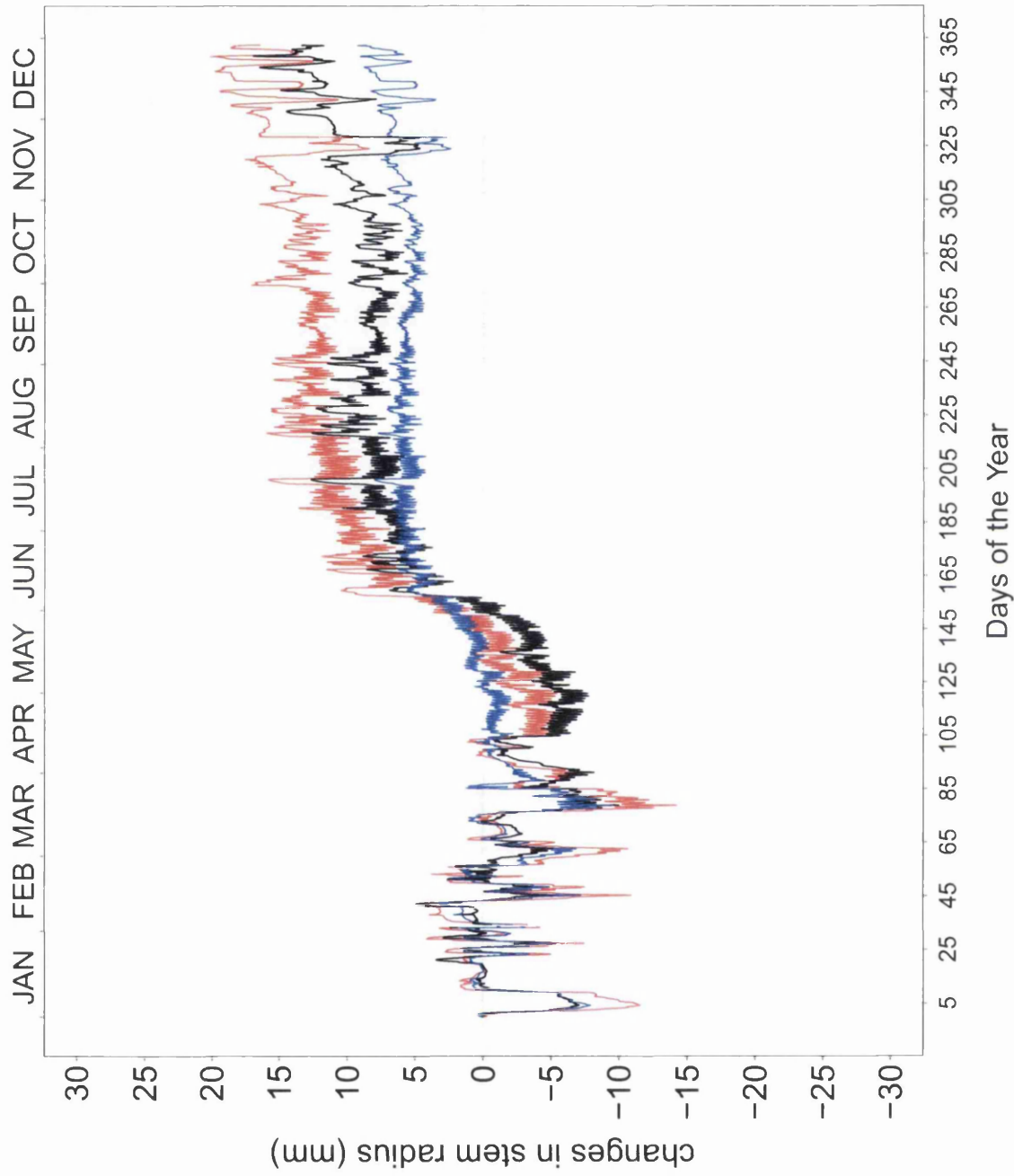
Figure 3.24: *Absolute changes in stem radius plotted against days of the year measured by dendrometers (continuous red, blue, black lines) during the year 2008 for three Scots pines in Hyytiälä (Finland). Data aquisition has been performed by the local team.*

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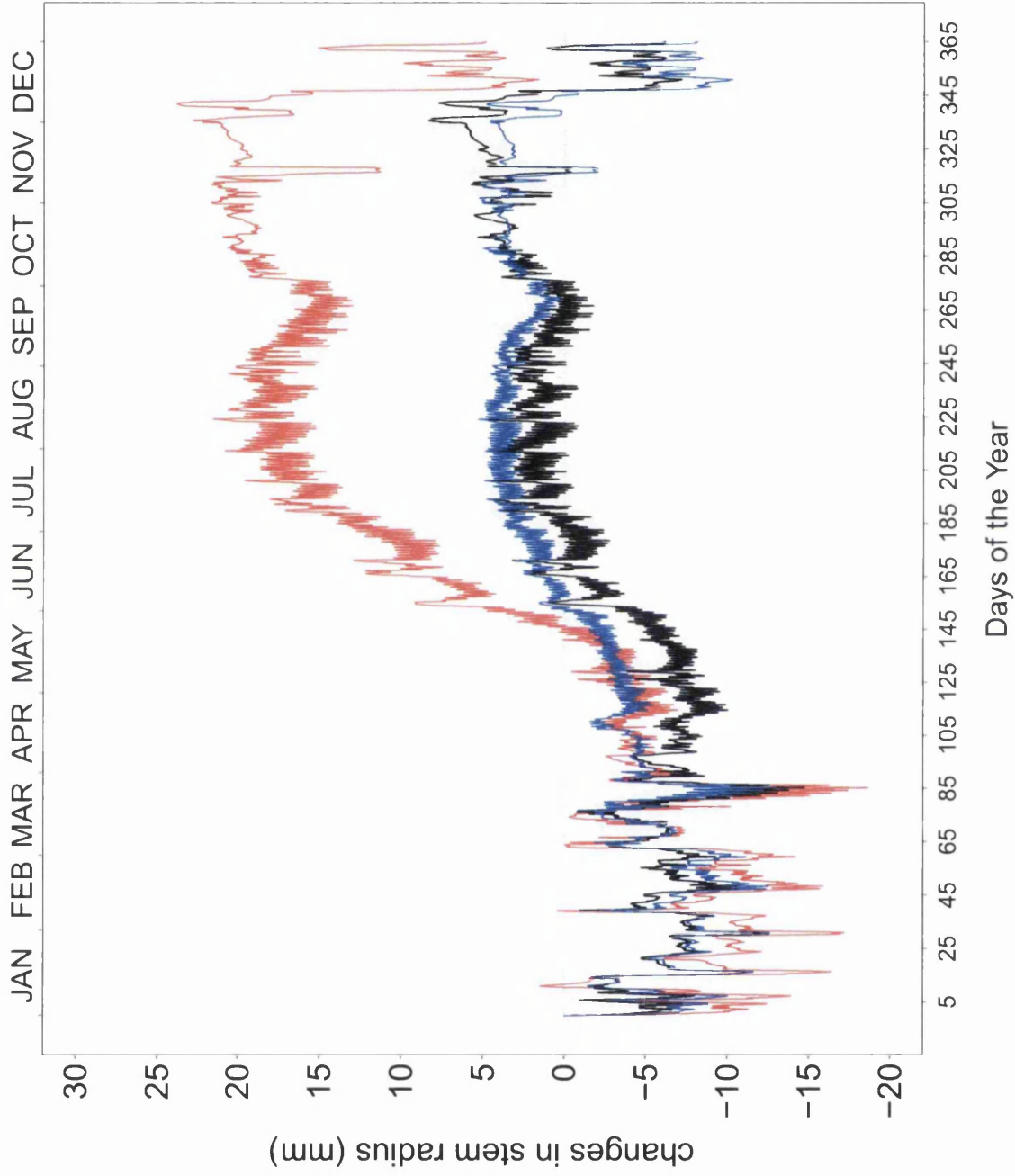
Figure 3.25: *Absolute changes in stem radius plotted against days of the year measured by dendrometers (continuous red, blue, black lines) during the year 2009 for three Scots pines in Hyytiälä (Finland). Data aquisition has been performed by the local team.*
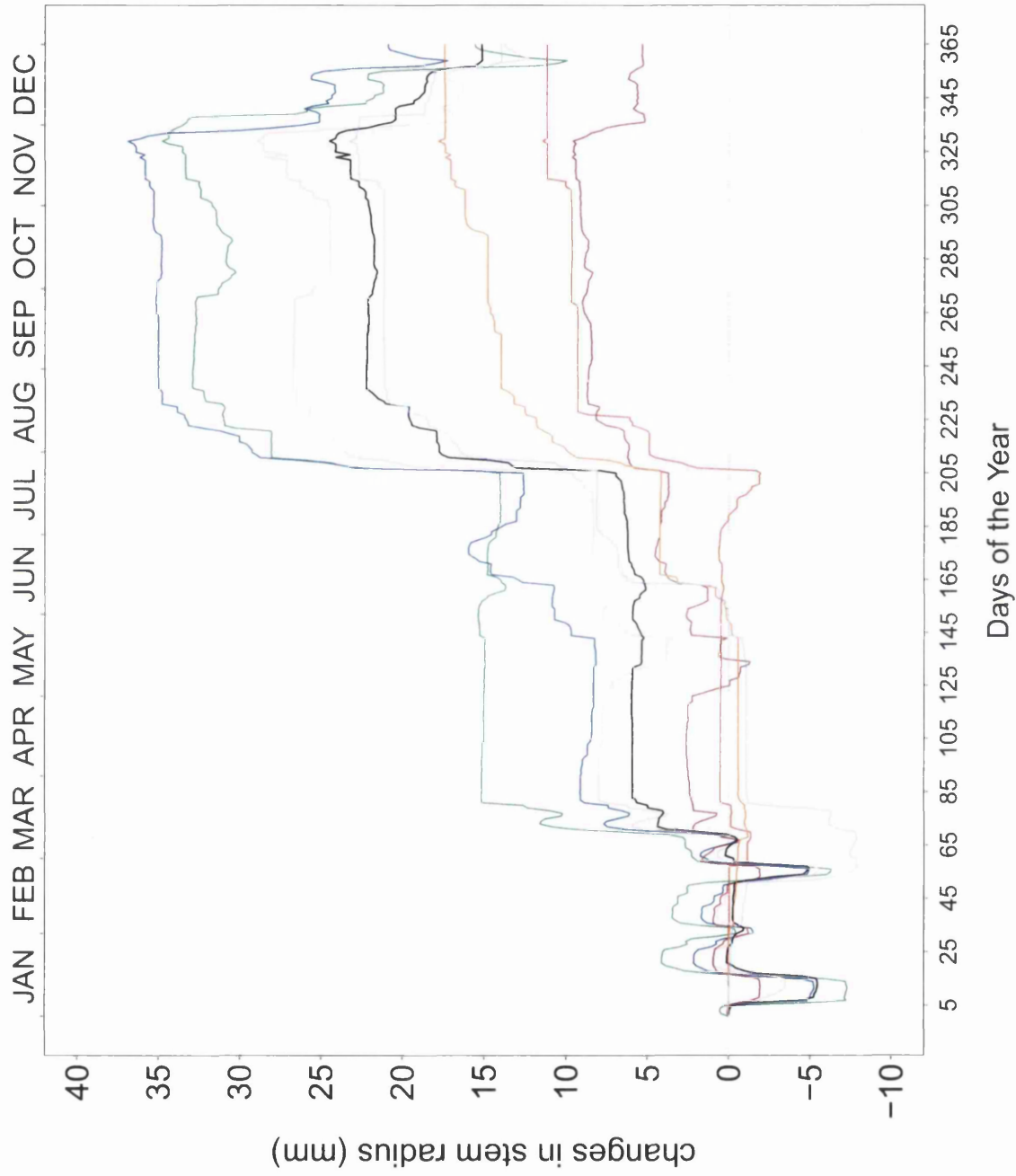
Figure 3.26: *Absolute changes in stem radius plotted against days of the year measured by dendrometers (continuous coloured lines) during the year 2010 for eight Scots pines in Norunda (Sweden). Data aquisition has been performed by the local team.*
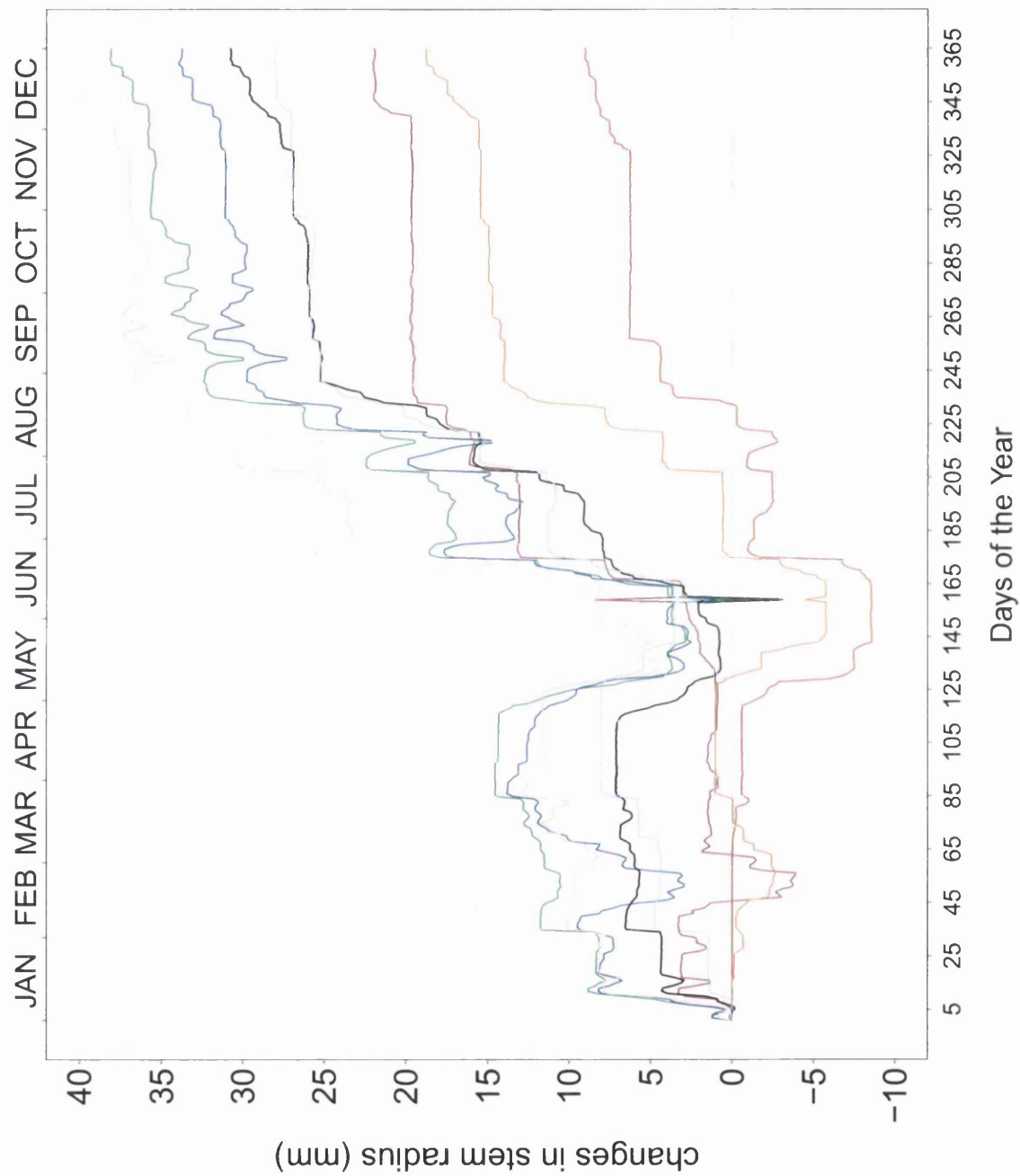
Figure 3.27: *Absolute changes in stem radius plotted against days of the year measured by dendrometers (continuous coloured lines) during the year 2011 for eight Scots pines in Norunda (Sweden). Data aquisition has been performed by the local team.*
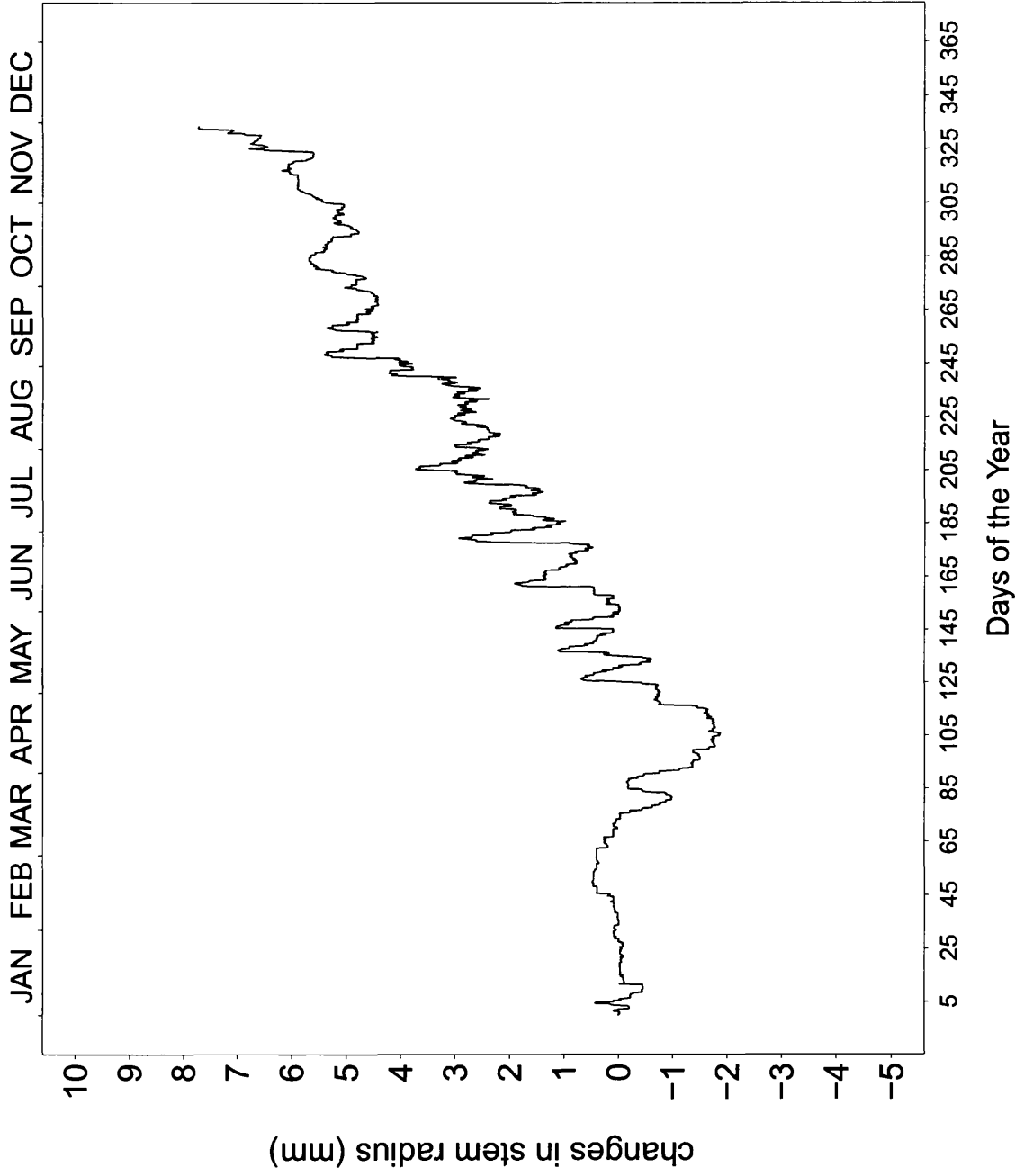
Figure 3.28: *Absolute changes in stem radius plotted against days of the year measured by dendrometers (continuous black line) during the year 2009 for one Scots pine in Loobos (the Netherlands). Data aquisition has been performed by the local team.*
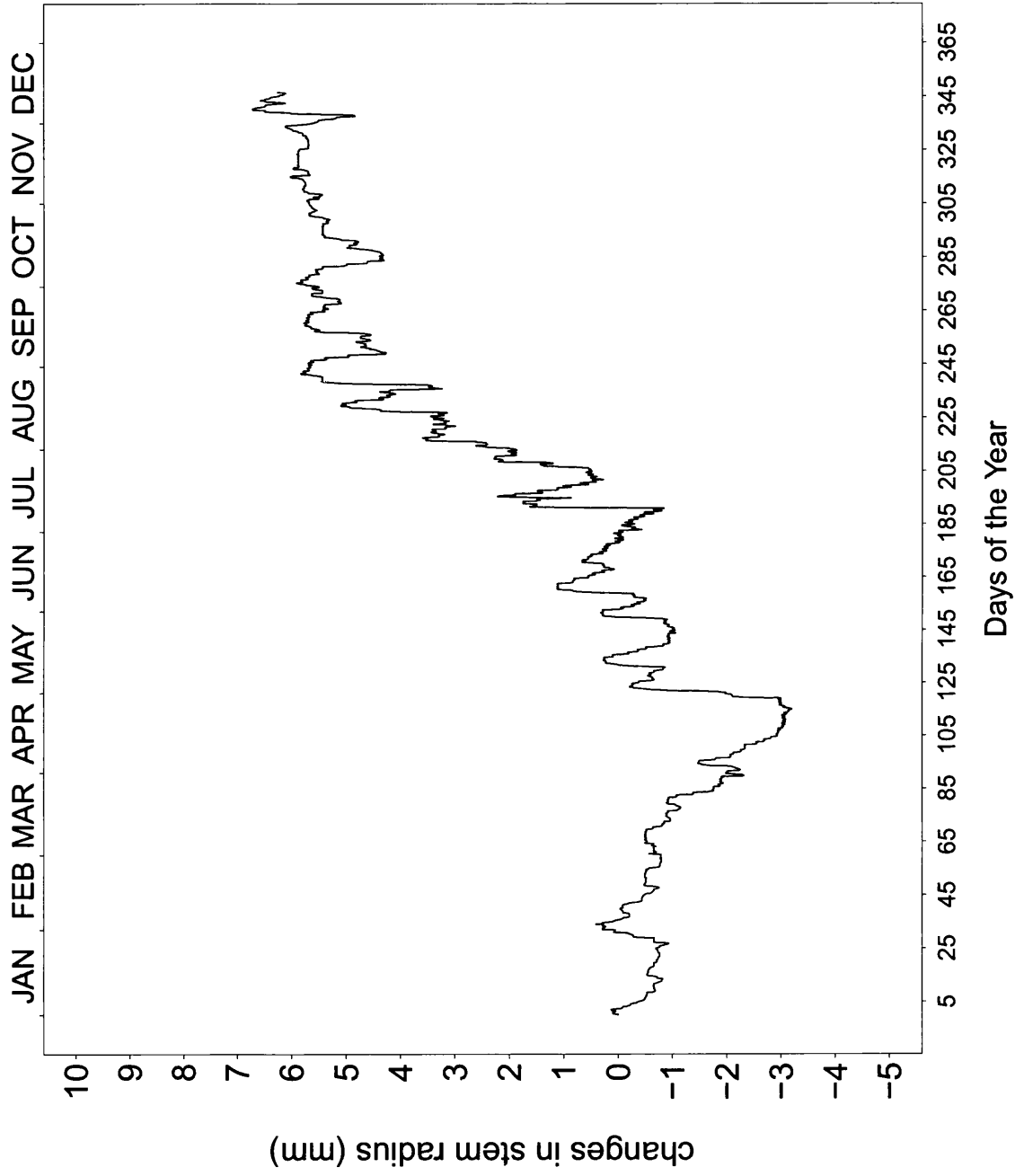
Figure 3.29: *Absolute changes in stem radius plotted against days of the year measured by dendrometers (continuous black line) during the year 2010 for one Scots pine in Loobos (Netherlands). Data aquisition has been performed by the local team.*

3.7 Weather datasets

3.7.1 Introduction

Flux-tower data were exclusively used to compare $\delta^{13}C$ time series and climatic factors. The advantage of such data is that it measures on-site weather variation at a very high resolution. For example, when comparing temperature and precipitation data from Norunda with the nearest weather station at Uppsala (data not presented). It was clear that the data recorded by the flux-tower differed significantly both in mean and variance. The forest ecosystem alter the local weather enough to provoke such differences.

Before proceeding to the comparison between the $\delta^{13}C$ time series and climatic factors, it is necessary to characterise the different local climatic datasets at each site. The flux-tower stations located directly at the study sites have been running since 1996 and recorded fluxes and meteorological data. As flux-tower data are kept in various formats, the procedure to build a homogenised dataset will be first presented in this section. The weather data will be then presented in tables and climate diagrams showing the properties of the main climatic drivers and its seasonal variation through the study period. Finally, each site will be characterised in comparison with the two others to investigate which environmental stresses are more pronounced at what sites.

This section will present:

- the procedure to build subsets of weather data usable for weather forcing investigations;

- the overview of the available weather dataset at each site;

- the variability of the weather dataset through the study period and between the study sites;

3.7.2 Procedure for data handling

Scripts in R have been created to assist in the post-processing and exploration of the flux-tower data (Figure 3.30). The focus was to create matching time series of climatic information to compare with the stable carbon isotope values. Because the different flux-tower research teams maintain their data in a variety of formats, most of the functions are site specific. Generally, the variables are given as character strings and the values as numbers. The first step in processing the data is to transform the external dataset from each site to a standard format from which the functions can extract the relevant information. For that purpose, it is necessary to read the original files provided by the research teams at the study sites and store the data into a R dataframe. Cleaning and manipulation processes take place after the import: variables of interest were renamed and not-used variables and observations were dropped to ease the use of the dataset for the intended analysis and standardise the datasets between the different sites into a similar data format. Data gaps through the datasets were recorded as -9999 for all variables. These values are filtered so they do not appear in the time series and do not enter in the calculation of mathematical indices. In a similar way, outliers were removed to avoid their contribution in calculations. The range of variation selected to discard outliers was set up depending on the climatic variable considered and is presented in Table 3.7 for each variable. The addition of a day of the year (DOY) variable in the dataset permits the visualisation of the data into various time resolutions (day, month, year) by mathematical operations (averages, quartiles) depending on the desired analysis. Selection of the radial growing season period to match carbon stable isotope measurements with weather variables needed to exclude flux-tower data prior and after the estimated growing season. Each isotope measurement is then matched with the weather variables on the time span calculated via the Gompertz procedure. Selected weather data for the comparison with stable carbon isotope time series are air temperature, photosynthetic active radiation (PAR) and precipitation.

Table 3.7: *Filtering threshold values for weather and flux variables. Any values below the lower or above the treshold values areremoved from the initial dataset.*

Variable	lower threshold	upper threshold	units
Temperature	-50	50	°C
PAR	0	2000	μmol m^{-2} s^{-1}
Precipitation	0	100	mm
NEE	30	-50	μmol m^{-2} s^{-1}
Evapotranspiration	0	6	μmol m^{-2} s^{-1}
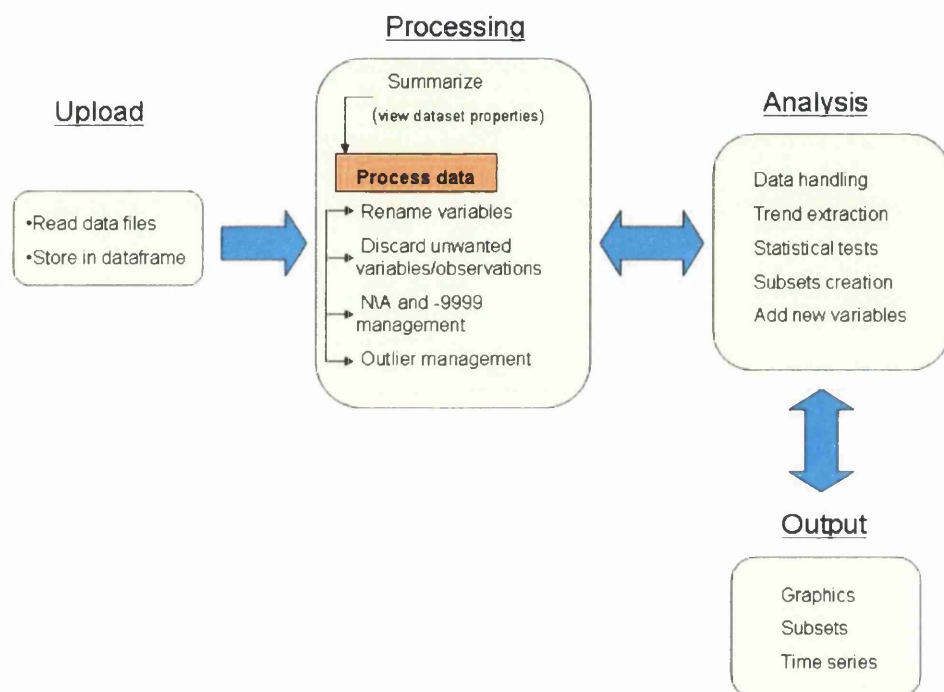
Figure 3.30: *Typical sequence of data analysis.*

3.7.3 Hyytiälä

3.7.3.1 Temperature datasets at the Hyytiälä site for the period 1997-2009

Temperature records are available at Hyytiälä for the full study period at the half hourly resolution. Temperature is expressed in degree Celcius (°C). The variation of this weather variable is high through the year. The average minimum temperature calculated over the study period is -23.67 ± 5.01 °C ranging from -32.12 to -14.80 °C. The average mean temperature for each year is 4.31 ± 0.57 °C ranging from 3.26 to 5.19 °C. The average maximum temperature for the study period is 26.91 ± 1.15 °C ranging from 25.48 to 28.77 °C. All temperature inter-annual values are presented in Table 3.8. The minimum temperatures have the greatest variation which suggests a larger variability in the winter temperatures than during the other seasons. Figure 3.31 presents a climatic diagram with monthly mean temperature values averaged over the period 1997-2009. The evolution of the temperature during an average year consist of an increase from winter with three months experiencing negative temperatures (January, February, March) with the minimum value in February (-6.52 °C) till a maximum value in July (16.2 °C) and then another decrease leading to a return to negative average values in November and December.

3.7.3.2 Radiation at the Hyytiälä site for the period 1997-2009

Photosynthetically active radiation (PAR) records at Hyytiälä cover the full study period at the half hourly resolution. As the seasonal cycle presents a high variation in the sunshine exposure, this weather variable is highly variable through the year. The average minimum PAR matches the night conditions and is always equal to 0 μmol m^{-2} s^{-1}. The average mean PAR for the study period is 298.61 ± 15.45 μmol m^{-2} s^{-1} ranging from 274.80 to 325.30 μmol m^{-2} s^{-1} between years. The average maximum PAR for the study period is 1752.69 ± 97.70 μmol m^{-2} s^{-1} ranging from 1621 to 1939 μmol m^{-2} s^{-1}. These standard deviation values show that mean and maximum PAR remains relatively stable through the years which suggest that the amount of light exposure does not vary much inter-annually. The PAR annual values for each year are presented in Table 3.8. Figure 3.31 presents the climatic diagram with the monthly mean PAR values averaged over the period 1997-2009. During winter, two months experience low PAR (January, February). The monthly PAR values increase with particularly high values during May, June and July with its maximum in June (620.86 μmol m^{-2} s^{-1}) and then decrease again with low values in October, November and December reaching its lowest value in December (11.39 μmol m^{-2} s^{-1}).

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3.7.3.3 Precipitation at the Hyytiälä site for the period 1997-2009

Precipitation records are available for the full study period at Hyytiälä. Precipitation is expressed in millimetres (mm). Variation in the amount of rain falling on the ecosystem varies from 0 to 100 mm. To understand precipitation effect, it is more common to consider the sum of precipitation than the average for a given resolution. At the inter-annual level, the average precipitation sum for the study period is 498.24 ± 106.10 mm ranging from 255.71 to 694.98 mm. This is a considerable variation between years, showing that the effect of droughts can impact the growth of trees during dry spring/summer periods. Inter-annual precipitation sums are presented in Table 3.8. Figure 3.31 displays the monthly mean precipitation values averaged over the period 1997-2009 as part of the climatic diagram. During the winter and spring transition, four months are characterised by low precipitation (January, February, March, April) with the lowest value being February (29.23 mm). Precipitation increases during summer reaching a maximum in July (93.13 mm) and then decreases steadily to reach lower values in winter at the exception of October. This information is critical considering the amount of water that will be available for trees during the growing season. If low rain events occurs in spring, it is likely that the trees will rapidly deplete the water in the soil and then rely on summer rain events to continue growth.

Table 3.8: *Temperature (°C), PAR (μmol m^{-2} s^{-1}) and precipitation (mm) measurements at Hyytiälä for the period 1997-2009.*

Year	Temperature (°C)			PAR (μmol m^{-2} s^{-1})			Precipitation (mm)
	Minimum	Mean	Max	Minimum	Mean	Max	Sum
1997	-20.81	4.321	27.42	0	287.2	1939	400.47
1998	-23.96	3.265	25.88	0	283.7	1755	694.98
1999	-32.12	4.304	28.69	0	315.5	1797	542.97
2000	-17.62	5.193	27.54	0	295.6	1674	488.61
2001	-28.38	3.899	26.66	0	303.0	1662	477.63
2002	-28.79	4.010	25.78	0	325.3	1916	495.76
2003	-27.17	3.715	28.28	0	288.8	1696	455.65
2004	-21.08	4.134	26.22	0	283.9	1790	255.71
2005	-20.88	4.599	26.72	0	309.4	1826	544.59
2006	-26.54	4.859	28.77	0	319.7	1678	598.10
2007	-26.09	4.839	25.55	0	292.9	1739	456.47
2008	-14.80	5.008	25.48	0	274.8	1621	593.79
2009	-19.53	3.899	26.90	0	302.1	1692	472.49
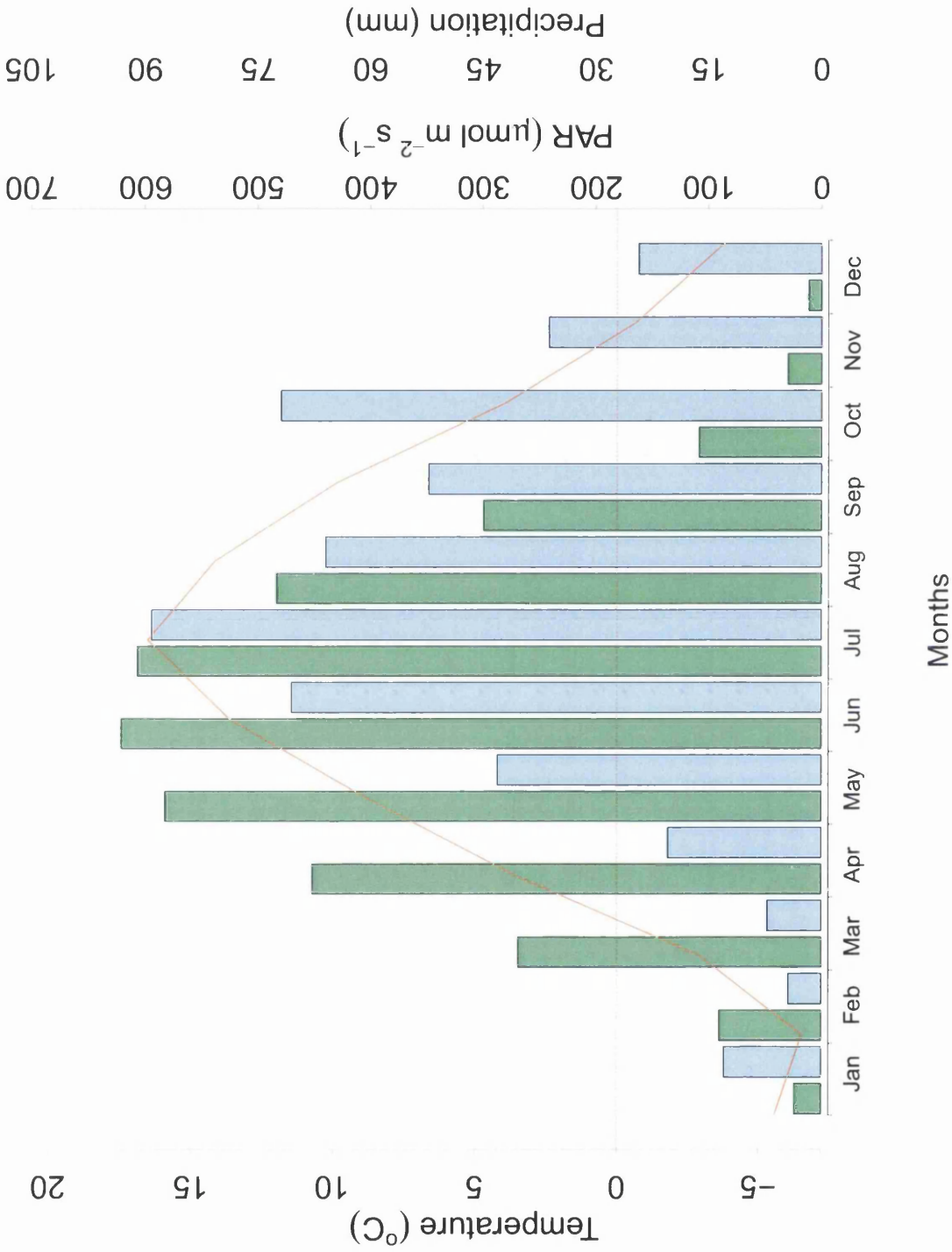
Figure 3.31: *Climate diagram of monthly averages of temperature (°C), PAR (μmol m⁻² s⁻¹) and precipitation (mm) at Hyytiälä for the period 1997-2009. Temperature values (orange continuous line) varies in a maximum range between -6.52 °C (February) and 16.52 °C (July) through the year, the matching scale is displayed on the left of the diagram. PAR and precipitation are displayed as bars (green and blue respectively). Each segment represents the averaged value of one month of the year over the period 1997-2009. Scales of PAR and precipitation are displayed on the right side of the diagram with PAR the closer and precipitation on the far side. Monthly averaged PAR range is 11.39 μmol m⁻² (December) to 620.86 μmol m⁻² s⁻¹ (June). Monthly averaged precipitation range is 29.23 mm (February) to 93.13 mm (July).*

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3.7.4 Norunda

3.7.4.1 Temperature datasets at the Norunda site for the period 1997-2009

Norunda temperature records are available for the study period. Variation in the recorded values is less extreme than at Hyytiälä with a tighter range from -25 °C to 35 °C. When considering the annual averages of temperature, the minimum value calculated over the study period is -17.43 ± 2.928 °C ranging from -22.35 to -12.47 °C. The average mean temperature for the study period is 6.40 ± 0.43 °C ranging from 5.51 to 7.23 °C. The average maximum temperature for the study period is 28.28 ± 2.30 °C ranging from 23.75 to 30.74 °C. All inter-annual temperature values are presented in Table 3.9. A different pattern than at Hyytiälä is observable with a greater inter-annual variation in temperature. Figure 3.32 presents the monthly mean temperature values averaged over the period 1997-2009 in a climatic diagram. During winter, two months experience mean negative temperatures (January, February) while the minimum average value is occurring in February (-2.30 °C). The temperature increases until its maximum in July (16.26 °C) and then decreases again to reach negative values in December. At Norunda, the period when the photosynthesis cannot occur due to temperature limitation seem to be shorter than at Hyytiälä while the maximum temperature is also occurring in July.

3.7.4.2 Radiation datasets at the Norunda site for the period 1997-2009

The PAR records at Norunda are also available for the study period. Compared to Hyytiälä, the range of variation of PAR is tighter. The average PAR for the study period is equal to 190.05 ± 18.04 μmol m^{-2} s^{-1} ranging from 190.06 to 220.50 μmol m^{-2} s^{-1}. The maximum PAR for the study period is 1631.08 ± 105.94 μmol m^{-2} s^{-1} ranging from 1377 to 1773 μmol m^{-2} s^{-1}. Despite having lower values at Norunda, the standard deviation from mean and maximum values are equivalent at Hyytiälä and Norunda. Therefore, the inter-annual variation is similar at both sites but the sunshine intensity is greater during a typical year at Hyytiälä. All inter-annual PAR values are presented in Table 3.9. The low mean value for year 1998 is due to missing data and is not representative of a realistic mean level, this year is therefore excluded from other calculations. Figure 3.32 presents the monthly mean PAR values averaged over the period 1997-2009 in a climatic diagram. During winter and spring transition, three months experience low PAR values (January, February and March). The PAR increases with particularly high values during May, June and July until its maximum in July (385.77 μmol m^{-2}

s^{-1}) and then decreases again with low values in October, November and December reaching its lowest value in December (10.56 μmol m^{-2} s^{-1}). This variation shows a similar pattern than at Hyytiälä however the PAR reaches lower values during the summer time.

3.7.4.3 Precipitation datasets at Norunda site for the period 1997-2009

Precipitation records at Norunda are only available for 5 years during the study period (1997, 1998, 2000, 2001, 2002). When considering these years, the average annual precipitation sum is 404.27 ± 70.47 mm ranging from 300.97 to 476.79 mm. The sum of precipitation for these five years are presented in Table 3.9. Figure 3.32 presents the monthly mean precipitation values in a climatic diagram considering only the five years available. Compared to Hyytiälä, the monthly precipitation sum seems to be more evenly distributed during the year with still a detectable pattern with an evolution from a drier winter towards a wetter summer. Two months are experiencing lower precipitation (April, December) with the lowest value being in December (8.18 mm). The maximum in precipitation occurs in July (75.12 mm) and then decreases steadily to reach lower values in winter (with the exception of October reaching values close to the July maximum). The input of precipitation in March to supply trees during the potential start of photosynthesis seems to be a considerable factor that could explain less depleted δ^{13}C values at Norunda.

Table 3.9: *Temperature (°C), photosynthetic active radiation (μmol m^{-2} s^{-1}) and precipitation (mm) properties at Norunda for the period 1997-2009.*

Year	Temperature (°C)			PAR (μmol m^{-2} s^{-1})			Precipitation (mm)
	Minimum	Mean	Max	Minimum	Mean	Max	Sum
1997	-16.01	6.57	29.66	0	220.50	1773	429.63
1998	-12.47	6.62	23.75	0	81.28	1743	476.79
1999	-20.65	6.40	29.51	0	216.00	1749	N.A
2000	-16.34	6.00	23.89	0	154.40	1666	447.46
2001	-22.35	5.51	29.37	0	183.50	1671	300.97
2002	-19.26	6.41	27.18	0	206.90	1643	366.49
2003	-21.13	6.20	28.70	0	194.80	1680	N.A
2004	-17.43	6.17	28.67	0	185.60	1678	N.A
2005	-17.43	6.52	30.66	0	189.20	1556	N.A
2006	-16.44	7.23	30.42	0	173.40	1377	N.A
2007	-17.08	6.58	27.84	0	185.90	1541	N.A
2008	-12.70	6.92	30.74	0	185.90	1579	N.A
2009	-17.34	6.09	27.26	0	184.60	1660	N.A
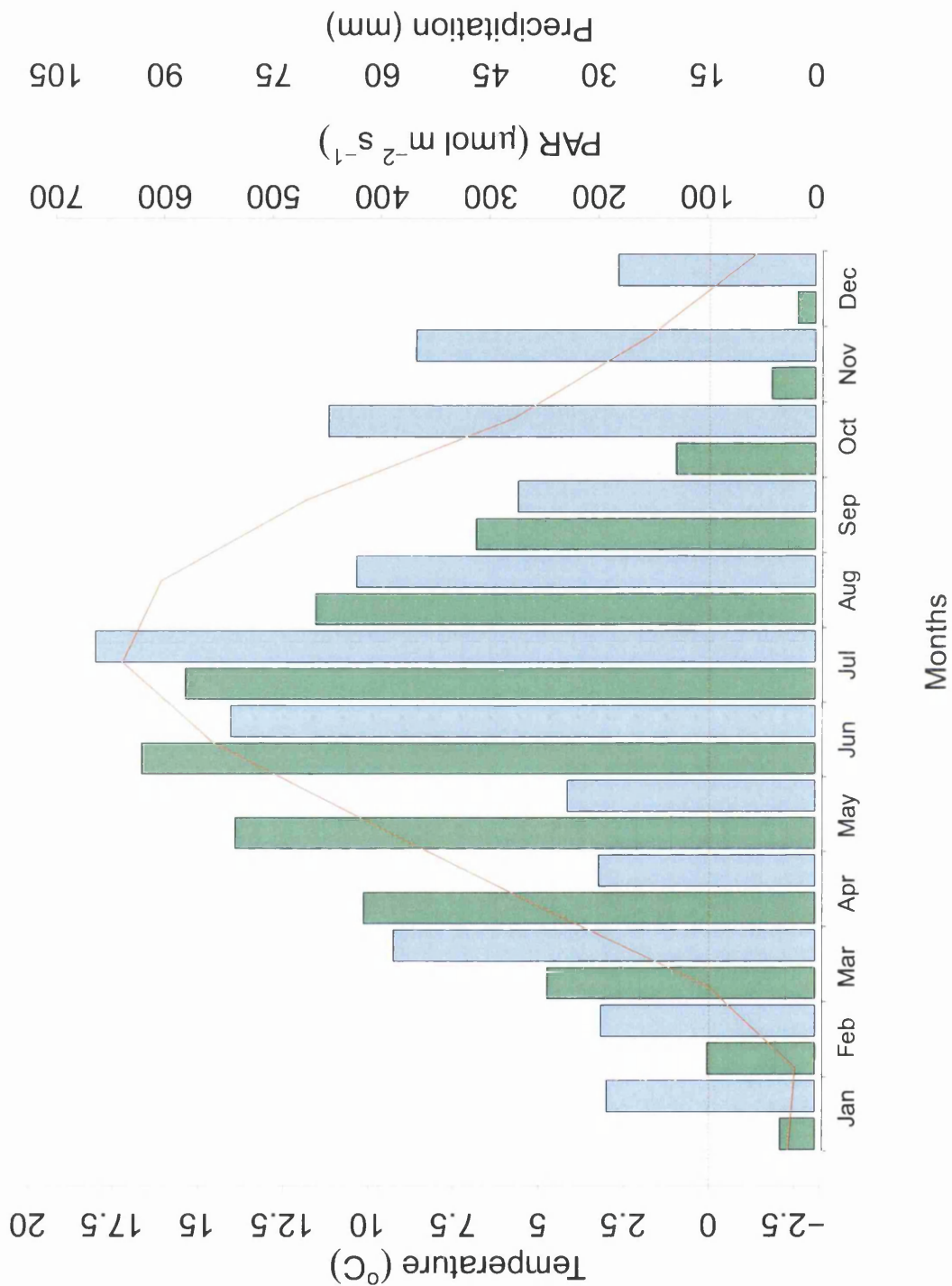
Figure 3.32: *Climate diagram of monthly averages of temperature (°C), PAR (µmol m^{-2} s^{-1}) and precipitation (mm) at Norunda for the period 1997-2009. Temperature values (orange continuous line) varies in a maximum range between -2.30 °C (February) and 16.26 °C (July) through the year, the matching scale is displayed on the left of the diagram. PAR and precipitation are displayed as bars (green and blue respectively). Each segment represent the averaged value of one month of the year over the period 1997-2009. Scales of PAR and precipitation are displayed on the right side of the diagram with PAR the closer and precipitation on the far side. Monthly averaged PAR range is 10.56 µmol m^{-2} s^{-1} (December) to 385.77 µmol m^{-2} s^{-1} (July). Monthly averaged precipitation range is 8.18 mm (December) to 75.12 mm (July).*

3.7.5 Loobos

3.7.5.1 Temperature datasets at the Loobos site for the period 1997-2009

Temperature records are available at Loobos for the full study period. Out of the three study sites, the variation range of temperature at Loobos is the tightest due to more elevated minimum temperatures during winter. At the inter-annual resolution, the minimum temperature calculated over the study period is -11.06 ± 3.00 °C ranging from -17.35 to -7.19 °C. The mean temperature for the study period is 10.18 ± 0.35 °C ranging from 9.59 to 10.65 °C. The average maximum temperature for the study period is 32.07 ± 1.67 °C ranging from 29.66 to 35.19 °C. Therefore, Loobos experiences the warmest temperatures out of the three study sites. All inter-annual temperature values are presented in Table 3.10. It is noticeable that the inter-annual temperature variation remains low. Figure 3.33 presents the monthly mean temperature in a climatic diagram. This study site does not present months with negative temperature averages like the two other study sites. The minimum average value is found in January (3.12 °C). The temperature increases until its maximum in August (17.58 °C) and then decreases again to lower values in winter. The maximum temperature is shifted from July to August compared to the two other sites with a higher value reached.

3.7.5.2 Radiation datasets at the Loobos site for the period 1997-2009

Photosynthetically active radiation (PAR) records are limited at Loobos to nine continuous years during the study period (2001 to 2009). The maximum intensity of PAR seems to be the highest out of the three site (2100 μmol m^{-2} s^{-1}). The annual PAR average is 238.91 ± 14.96 μmol m^{-2} s^{-1} ranging from 212.50 to 253.40 μmol m^{-2} s^{-1}. The annual PAR maximum for the study period is 1965.38 ± 78.33 μmol m^{-2} s^{-1} ranging from 1801 to 2051 μmol m^{-2} s^{-1}. Therefore, inter-annual PAR averages are greater than at Norunda but lower than at Hyytiälä while the inter-annual PAR maximum is greater than both at Norunda and at Hyytiälä. This inter-annual pattern shows that the light is not as intense than at Hyytiälä but the maximum values reached at Loobos are greater during the summer time. The standard deviation is small and shows that the inter-annual variation is small. All PAR inter-annual values are presented in Table 3.10. Figure 3.33 presents the monthly PAR averages for the available eight years in a climatic diagram. During winter, two months experience mean low PAR (January, February) with its lowest value in January (31.86 μmol m^{-2} s^{-1}). The PAR increases with particularly high values during May, June and July with its maximum in June (439.99 μmol m^{-2} s^{-1}), it then decreases again with low values in October, November and December.

The occurrence of the maximum PAR in June is the earliest of the three study sites. Therefore, the availability of light declines much earlier than at the northern sites.

3.7.5.3 Precipitation datasets at the Loobos site for the period 1997-2009

Five years of precipitation records are available at Loobos (1997, 1998, 2000, 2001, 2002). At the inter-annual resolution, the average precipitation sum for these five years of available data is 895.15 ± 200.93 mm ranging from 613.60 to 1256.11 mm. Therefore, Loobos receives the greatest precipitation amounts out of the three study sites with an average value nearly double the amount recorded at Hyytiälä and Norunda. All annual values are presented in Table 3.10. Figure 3.33 presents the monthly precipitation averages over the period 1997-2009. During the whole year, precipitation stays high with just three months having lower precipitation (April, May, June), the lowest value being in April (54.10 mm). The month with the maximum precipitation is July (89.65 mm).

Table 3.10: *Temperature ($^\circ$C), photosynthetically active radiation ($\mu mol\ m^{-2}\ s^{-1}$) and precipitation (mm) properties at Loobos for the period 1997-2009.*

Year	Temperature ($^\circ$C)			PAR ($\mu mol\ m^{-2}\ s^{-1}$)			Precipitation (mm)
	Minimum	Mean	Max	Minimum	Mean	Max	Sum
1997	-17.35	9.797	31.09	NA	NA	NA	768.05
1998	-8.72	9.592	30.78	NA	NA	NA	1256.11
1999	-10.42	10.530	29.66	NA	NA	NA	909.42
2000	-8.78	10.430	32.75	NA	NA	NA	1051.12
2001	-14.31	9.685	31.46	0	115.9	1834	1160.90
2002	-9.41	10.430	31.77	0	212.5	1906	973.20
2003	-12.14	10.280	35.19	0	243.9	1801	663.60
2004	-7.19	10.010	31.73	0	219.4	2051	984.20
2005	-14.66	10.250	32.11	0	253.4	2018	794.60
2006	-8.40	10.640	34.54	0	247.9	1979	825.40
2007	-8.95	10.650	30.58	0	240.2	1973	1004.40
2008	-10.49	10.060	30.94	0	242.5	1997	632.40
2009	-12.89	9.990	34.26	0	251.5	1998	613.60
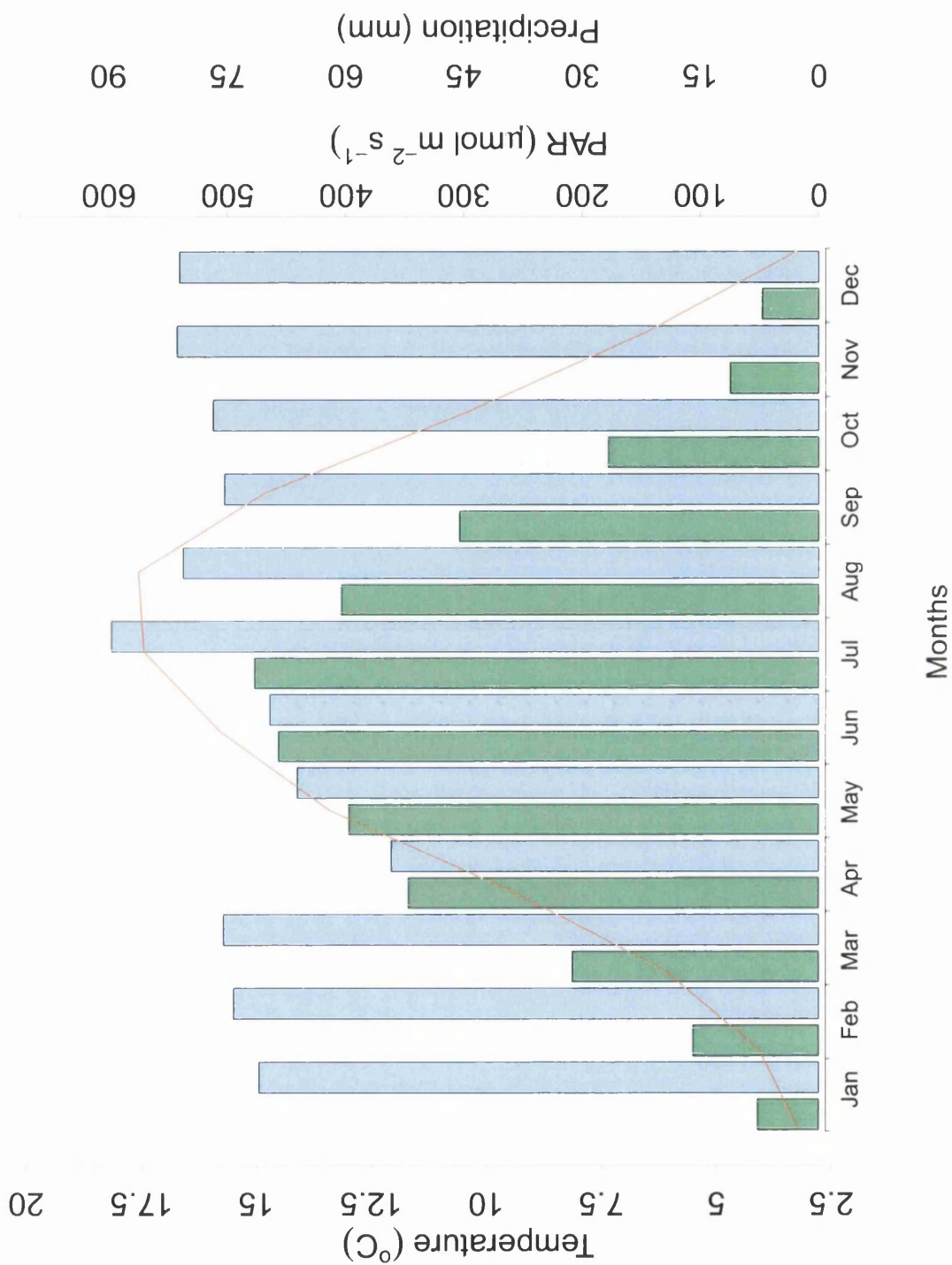
Figure 3.33: *Climate diagram of monthly averages of temperature (°C), PAR (µmol m⁻² s⁻¹) and precipitation (mm) at Loobos for the period 1997-2009. Temperature values (orange continuous line) varies in a maximum range between 3.12 °C (January) and 17.58 °C (August) through the year, the matching scale is displayed on the left of the diagram. PAR and precipitation are displayed as bars (green and blue respectively). Each segment represent the averaged value of one month of the year over the period 1997-2009. Scales of PAR and precipitation are displayed on the right side of the diagram with PAR the closer and precipitation on the far side. Monthly averaged PAR range is 31.86 µmol m⁻² s⁻¹ (January) to 439.98 µmol m⁻² s⁻¹ (June). Monthly averaged precipitation range is 54.10 mm (February) to 89.65 mm (July).*

3.7.6 Summary

The availability of weather data at Hyytiälä, Norunda and Loobos permits the characterisation of the variability of the weather between years and sites. For the study period, the weather variables are relatively stable through the years. However, the minimum temperature recorded at Hyytiälä shows high inter-annual variation that may be an indication of more or less intense winters and would be a factor to consider for ice melting occurrences and the release of temperature constraints on growth. It is also interesting to note that Norunda shows the lowest precipitation amounts while having a lesser constraint coming from temperature with a longer period when temperatures exceed 0 °C. It is therefore possible that the water constraint may become the primary driver of isotope variability at this study site. Finally, Loobos shows the highest values of both temperature and precipitation which would suggest that this study site is relatively protected against water stress and cold temperature constraints. Average weather data are summarised for each study site in Table 3.11.

Table 3.11: *Summary of mean Temperature (°C), mean photosynthetically active radiation ($\mu mol\ m^{-2}\ s^{-1}$) and mean precipitation (mm) properties at the three study sites averaged over for the period 1997-2009.*

	Temperature (°C)		
Year	Minimum	Mean	Max
Hyytiälä	-23.67 ± 5.01	4.31 ± 0.57	26.91 ± 1.15
Norunda	-17.43 ± 2.93	6.40 ± 0.43	28.28 ± 2.30
Loobos	-11.05 ± 3.00	10.18 ± 0.35	32.07 ± 1.67

	PAR (μmol m^{-2} s^{-1})		
Year	Minimum	Mean	Max
Hyytiälä	0	298.61 ± 15.45	1752.69 ± 97.70
Norunda	0	181.69 ± 34.77	1639.69 ± 106.07
Loobos	0	225.24 ± 43.33	1950.78 ± 85.36

	Precipitation (mm)
Year	Sum
Hyytiälä	498.25 ± 106.10
Norunda	404.27 ± 70.47
Loobos	895.15 ± 200.93

3.8 Conclusion

The greatest attention was taken to produce reliable and replicable high resolution carbon isotope series using a new methodology involving the presented laser systems. At the inter-annual resolution, the raw $\delta^{13}C$ time series show no significant correlation with tree-ring width measurements during the study period. EPS values at the inter-annual and the intra-annual resolution show a significant common signal at Hyytiälä but not at Norunda and Loobos according to the 0.85 threshold test on the EPS statistic. After the time series corrections of post-industrial atmospheric changes in $\delta^{13}C$, no significant trends are present in the corrected datasets with the exception of Loobos which presents the shortest length of isotope measurements. The seasonal variation of atmospheric $\delta^{13}C$ values has been investigated and judged negligible over the three main months of growth (June to August) and no seasonal correction has been applied to the $\delta^{13}C$ time series. The availability of dendrological information being limited and relatively imprecise at the study sites for the period considered, a method is required to be developed to model the growth period and the rate of growth to compensate for these limitations. The dates obtained via the dendrological methods will serve for parametrisation of the model during the years when the data are available. Finally, the weather dataset has been characterised for the three study sites with the identification of the possible weather forcings. Hyytiälä experiences high variability in temperatures while at Norunda, the precipitation amounts are the lowest of the three study sites. Finally at Loobos, the weather records show abundant rain events coupled with temperature above 0 °C during the longest period of the year suggesting a lack of stress coming from either temperature or water limitation. The following chapter will focus on the determination of the growing season period and wood growth modelling.

Chapter IV : Investigation of wood growth properties and their modelling via the Gompertz equation.

4.1 Introduction

To allow comparison between stable carbon isotope time series and climate datasets at the intra-annual resolution, the timing of the wood formation onset and cessation is required to match a common time scale between the different datasets within the growing season. Instead of using raw dendrological measurements that can be relatively unprecise, normalisation and smoothing techniques will be applied to ease the characterisation of the seasonal wood growth during the years when dendrological data are available (Section 4.2). However, due to the limited availability of dendrological information during of a few years, a range of methods has been tested against the dendrological measurements to provide the most accurate estimates for onset and cessation dates and to determine the radial growth during the years when dendrological data are unavailable at Hyytiälä, Norunda and Loobos (Section 4.3). These estimates will then be used to constrain a Gompertz model aiming at obtaining the growth rate and duration of wood cell formation during the period 1997 to 2009 (Section 4.4). Finally, this chapter will present a simple method to test the inclusion of cell life time in the modeling of the relationship between $\delta^{13}C$ and climate (Section 4.5)

The objectives of this chapter are to:

- normalise the dendrological data available at each site;

- investigate the dates of growth onset and cessation during years with dendrological information to build a method capable of predicting these dates during years when dendrological data are unavailable;

- characterise intra- and inter-site variability of the wood growth onset and cessation;

- model the growth rate during each year by applying the Gompertz equation;

- include the life time of radial cells during the growing season into the growth model.

4.2 Normalisation of dendrological information at each study site for the period 2007-2010

4.2.1 Dendrometer measurements

Due to inter-tree variability, the seasonal radial growth of individual trees presents differences in the rate of growth and the maximum growth attained during each year. Therefore, normalising the dataset in percentage of growth and averaging all trees into a unique growth curve will provide a clearer display of the common growth signal at each study site. As dendrometer measurements are affected by external factors such as temperature and sap flow in the trunk, the use of a smoothing tool will permit reducing the effect of unwanted non-climatic variation. It is then possible to smooth the signal by the use of smoothing splines to represent the seasonal growth of each year at each study site. This particular smoothing tool has been suggested by Cook & Peters (1981) for tree-ring and dendrological purposes which profit from an absence of assumptions about the shape of the curve that will be fitted to the data and its flexibility in the smoothing intensity which provides a better fit to environmental data than polynomial fitting. When not specified, the smoothing procedure in this study is performed with the span parameter tuning the smoothing intensity equal to 0.8 to keep the best representativity of the variation in the time series while providing an adequate smoothing power.

The convention to estimate onset dates by observing dendrometer measurements in this study is to select the inflexion point from null growth to positive growth during the period previous to the rapid radial increment in summer. For cessation dates, the day of the year (DOY) representing the best the transition from the rapid growth period to the winter plateau is selected. Figures 4.34, 4.35 and 4.36 display the normalised dendrological dataset for Hyytiälä for the years 2007, 2008 and 2009. The estimated dates of onset and cessation are shown as green dashed vertical lines. For Hyytiälä, the onset dates are found to occur on DOY 125, 120 and 115 while cessation dates are selected on DOY 210, 235 and 220 respectively, for the years 2007, 2008 and 2009. At Norunda, onset dates occur on DOY 137 and 148 and cessation dates on DOY 258 and 280, respectively, for years 2010 and 2011 (Figures 4.37 and 4.38). Finally at Loobos, DOY 105 and 107 are selected to represent the onset of wood formation while cessation dates are found to be on DOY 265 for both 2009 and 2010 (Figures 4.39 and 4.40). Despite the dendrometer records of 2009 showing no stable plateau period at the end of the year, the date selected seems reasonable as it matches a decrease in the rate of growth after the summer period.

The subsequent dates are summarised in Table 4.12. Due to the limited time period when these measurements are available, no statistical test was performed to quantify the relationship between growth dates and study sites. However, the simple observation and comparison of these dates shows that for the years available, a gradient exists between the study sites with Loobos presenting the earliest dates of onset followed by Norunda and lastly by Hyytiälä. The cessation dates are closely located at Loobos and Norunda but not at Hyytiälä, where cessation can occur approximately a month earlier than at the two other sites. In Section 4.3, these dates will serve to test which approach can best model the growing season when dendrological information is not available.

Table 4.12: *Onset, cessation and length of radial growth period in days of the year at Hyytiälä, Norunda and Loobos estimated by using the available dendrometer measurements.*

Hyytiälä			
Year	Onset (DOY)	Cessation (DOY)	Length (DOY)
2007	125	210	85
2008	120	235	115
2009	115	220	105

Norunda			
Year	Onset (DOY)	Cessation (DOY)	Length (DOY)
2010	137	258	121
2011	148	280	132

Loobos			
Year	Onset (DOY)	Cessation (DOY)	Length (DOY)
2009	105	265	160
2010	107	265	158
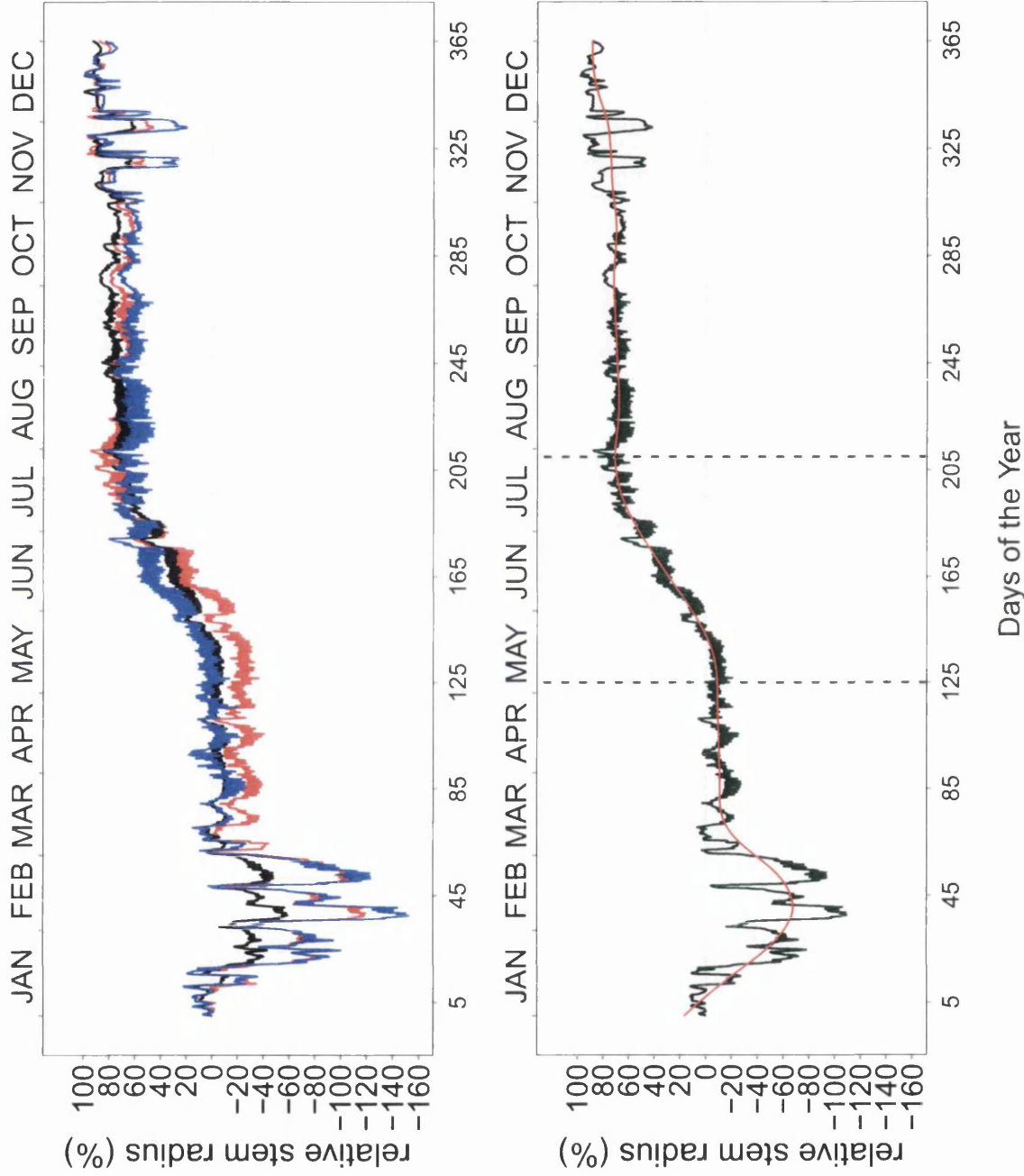
Figure 4.34: *Normalisation procedure for dendrometer measurements for year 2007 at Hyytiälä. a) the three time series of dendrometer measurements expressed as a percentage of change in stem radius from tree 1 (black line), tree 2 (red line) and tree 3 (blue line). b) the averaged time series (green line) with the application of smooth splines (light green line). Onset and cessation dates are indicated by vertical green dashed line.*
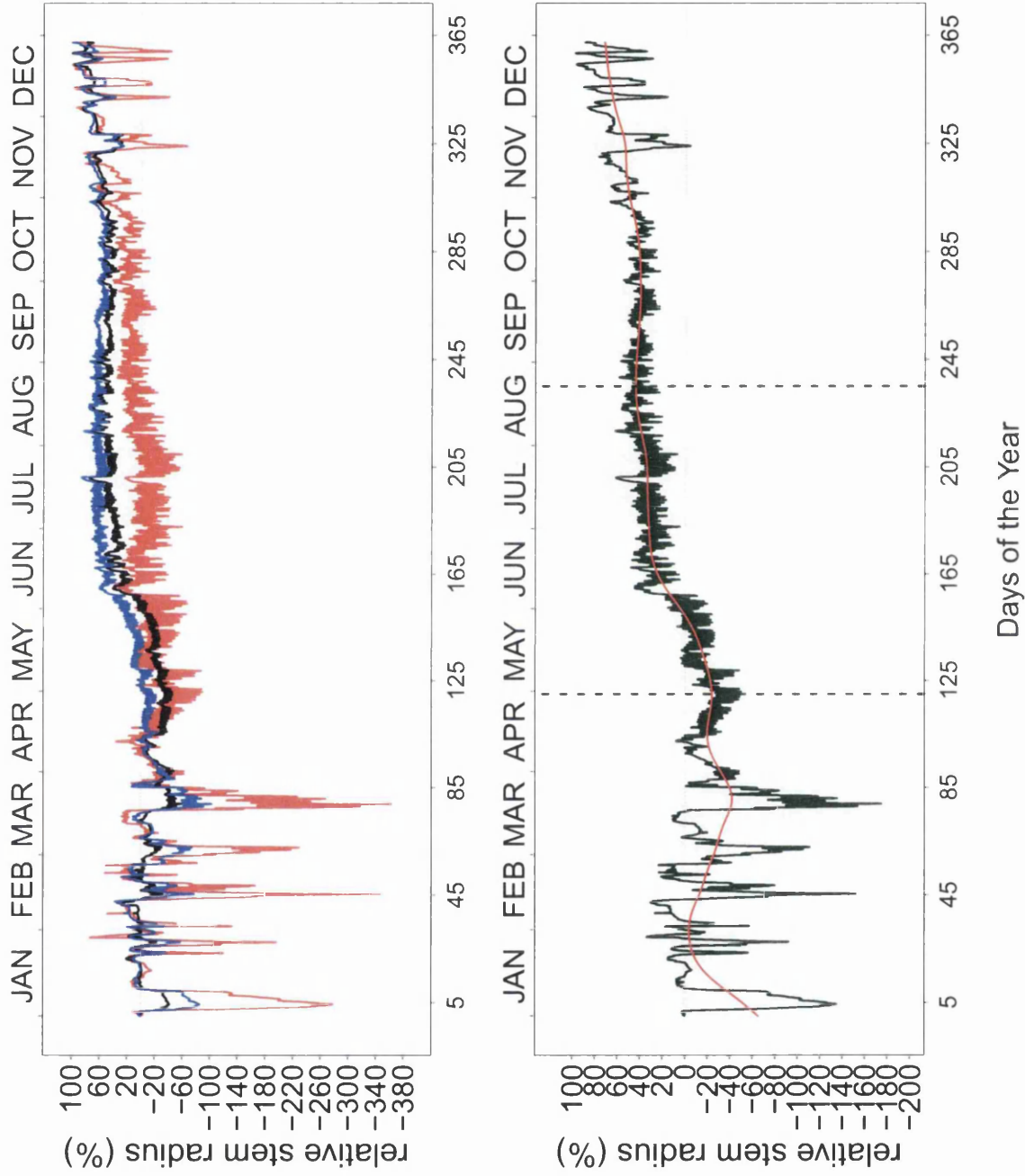
Figure 4.35: *Normalisation procedure for dendrometer measurements for year 2008 at Hyytiälä. a) the three time series of dendrometer measurements expressed as a percentage of change in stem radius from tree 1 (black line), tree 2 (red line) and tree 3 (blue line). b) the averaged time series (green line) with the application of smooth splines (light green line). Onset and cessation dates are indicated by vertical green dashed line.*
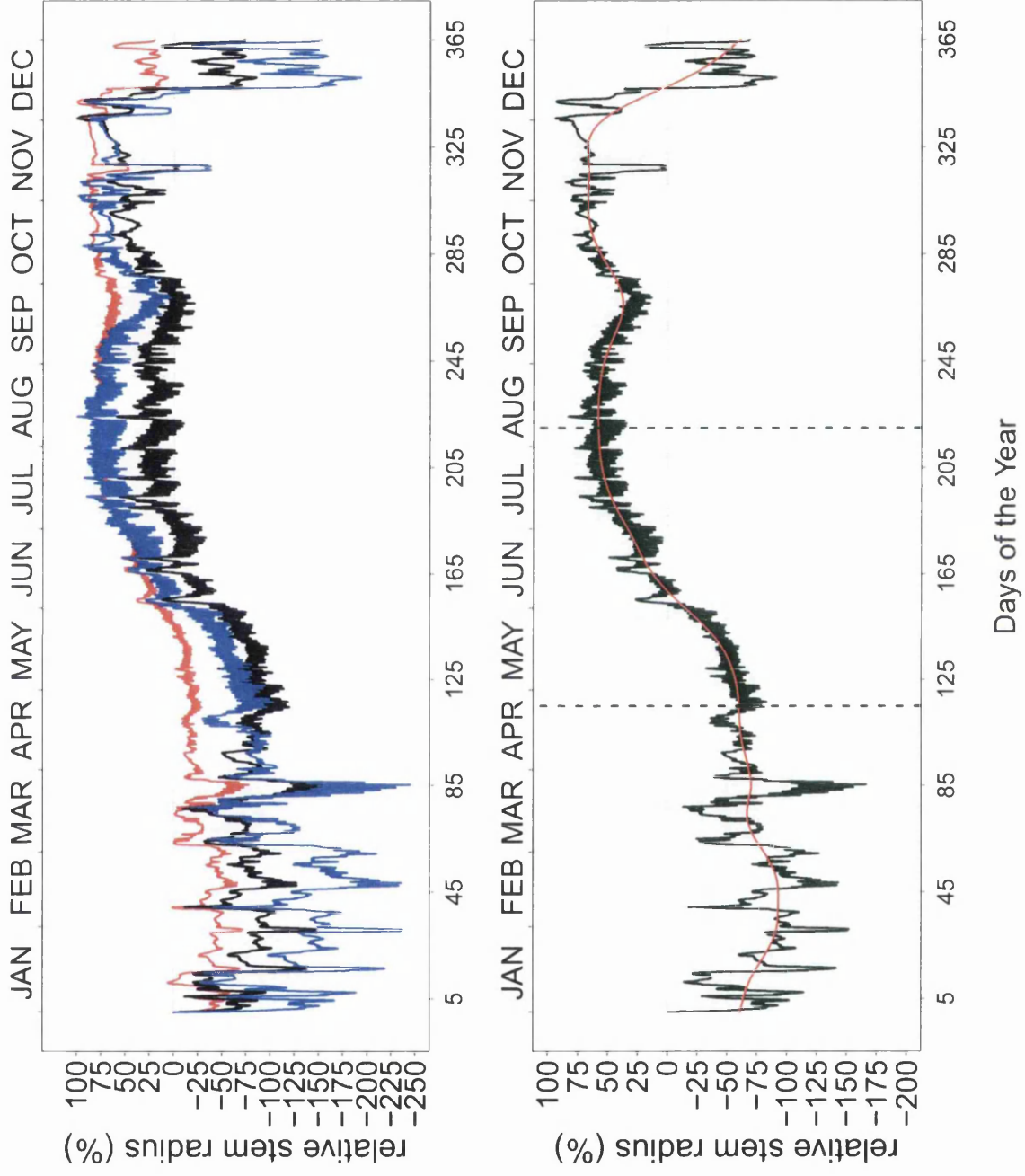
Figure 4.36: *Normalisation procedure for dendrometer measurements for year 2009 at Hyytiälä. a) the three time series of dendrometer measurements expressed as a percentage of change in stem radius from tree 1 (black line), tree 2 (red line) and tree 3 (blue line). b) the averaged time series (green line) with the application of smooth splines (light green line). Onset and cessation dates are indicated by vertical green dashed line.*
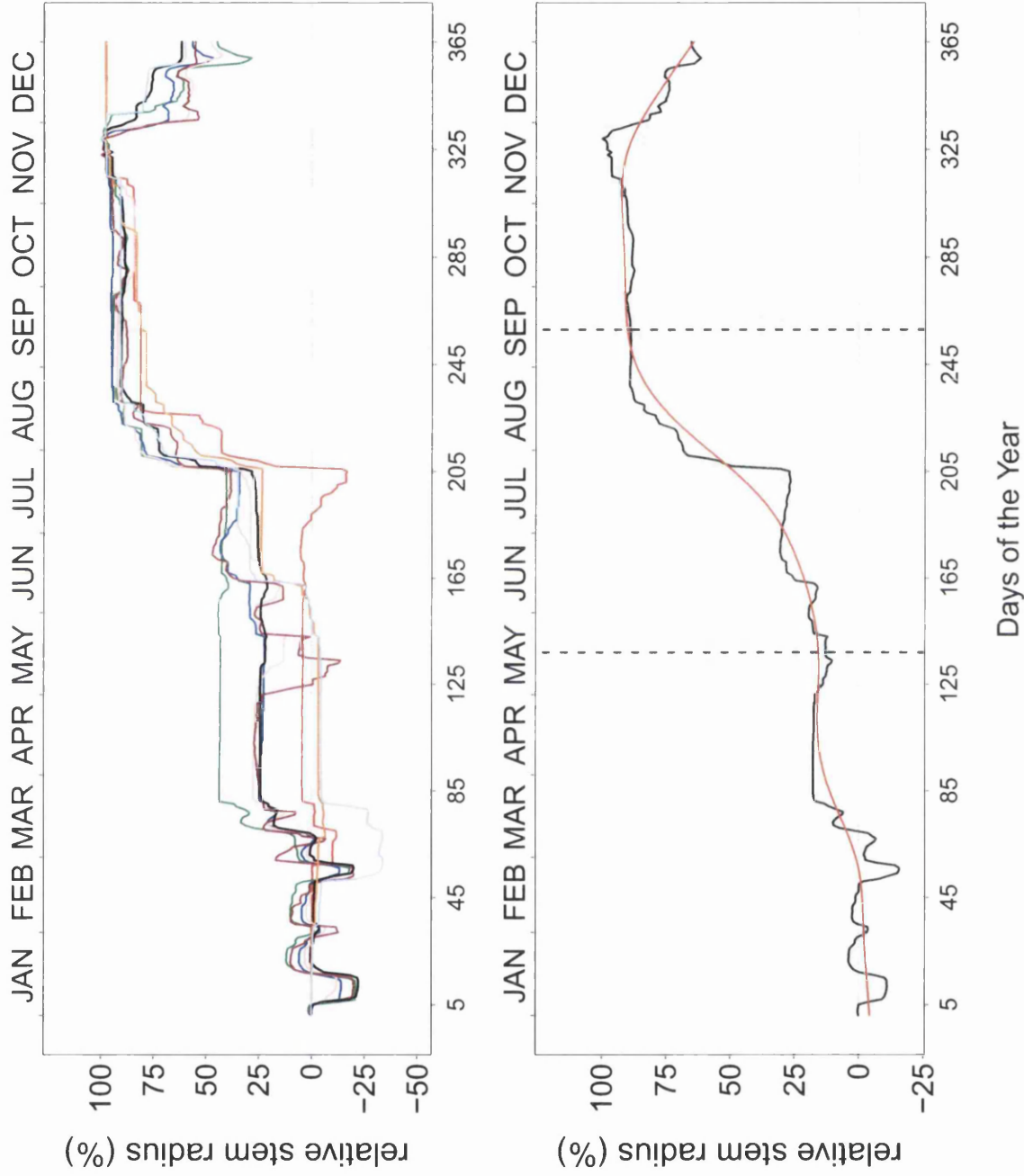
Figure 4.37: *Normalisation procedure for dendrometer measurements for year 2010 at Norunda. a) the eight time series of dendrometer measurements expressed as a percentage of change in stem radius (coloured lines). b) the averaged time series (green line) with the application of smooth splines (light green line). Onset and cessation dates are indicated by vertical green dashed line.*
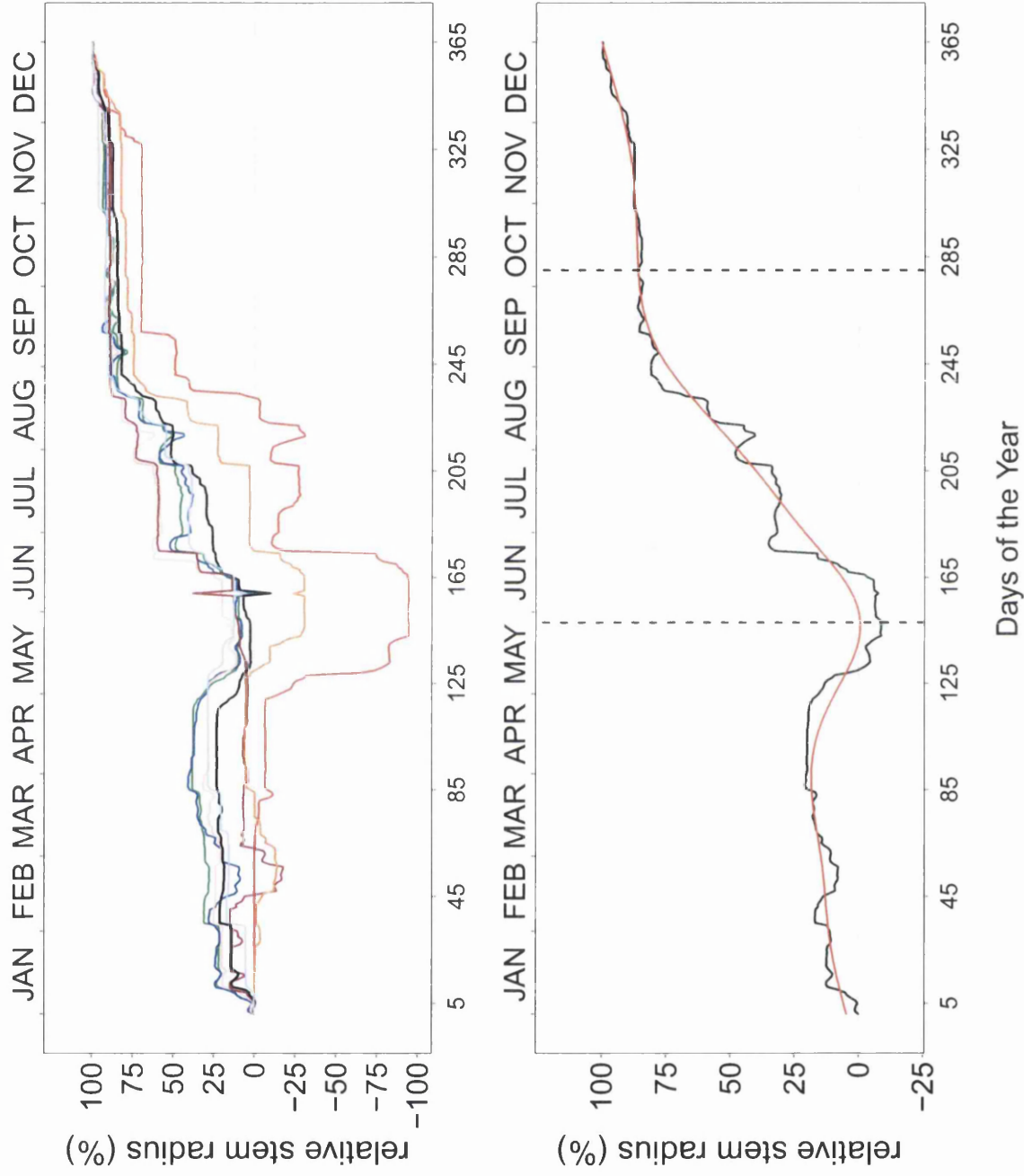
Figure 4.38: *Normalisation procedure for dendrometer measurements for year 2011 at Norunda. a) the eight time series of dendrometer measurements expressed as a percentage of change in stem radius (coloured lines). b) the averaged time series (green line) with the application of smooth splines (light green line). Onset and cessation dates are indicated by vertical green dashed line.*
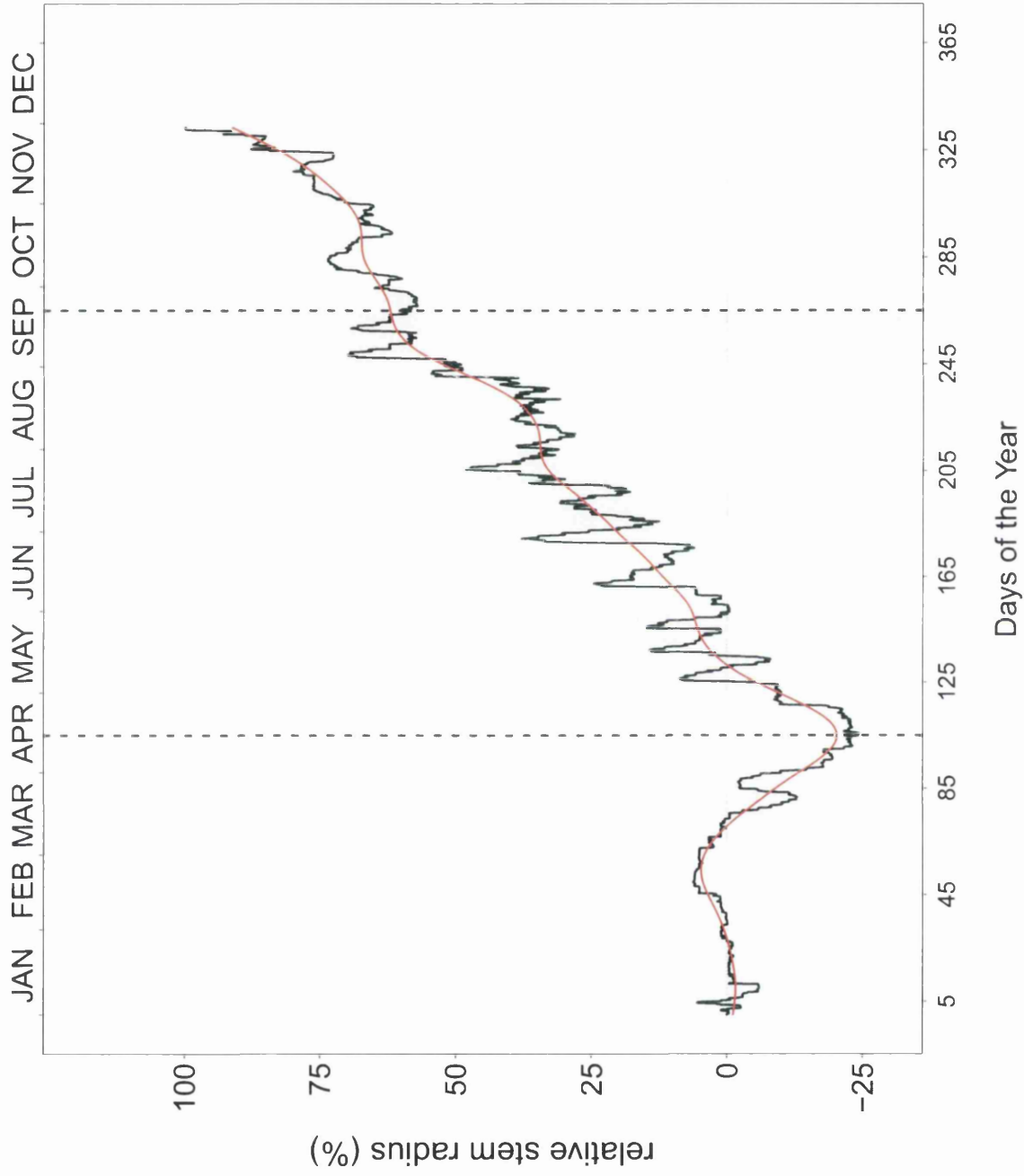
Figure 4.39: *Normalisation procedure for dendrometer measurements for year 2009 at Loobos displaying the averaged time series of dendrometer measurements (green line) with the application of smooth splines (light green line). Onset and cessation dates are indicated by vertical green dashed line.*
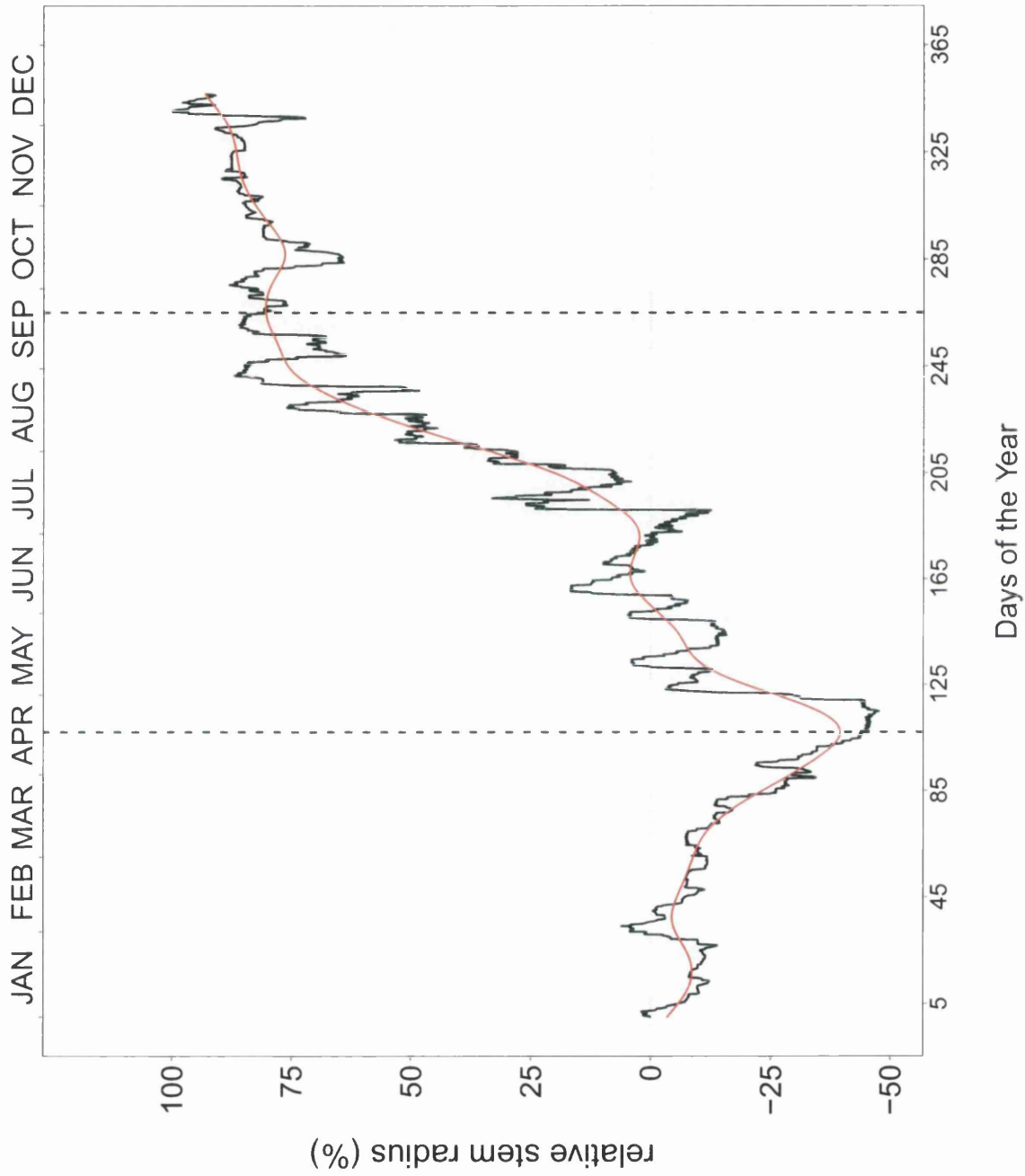
Figure 4.40: *Normalisation procedure for dendrometer measurements for year 2010 at Loobos displaying the averaged time series of dendrometer measurements (green line) with the application of smooth splines (light green line). Onset and cessation dates are indicated by vertical green dashed line.*

4.2.2 Microcore measurements

Due to the availability of both dendrometer and microcore measurements at Hyytiälä, the comparison of the two types of measurements to obtain wood growth onset and cessation dates can be carried out to assess if both records lead to similar results in terms of wood growth characterisation. Similar to the dendrometer technique, the microcores are subject to inter-tree and inter-annual variability. The inter-tree variability can be suppressed by normalising the measurements in percentage of growth instead of number of cells and proceed to averaging many tree microcore records to obtain a unique growth curve representative of the study site for each year. No smoothing spline procedure is needed for microcore measurements to visualise growth onset and cessation as no external factor should be interfering with the number of cell and therefore there is no necessity to attenuate unwanted noise. Figure 4.41 displays these operations for the three years (2007 to 2009) at Hyytiälä. To determine the dates for onset and cessation of cell increment, the first date to be located just before the first count of new cells is selected to be the onset date for wood growth while the date when a maximum of cells are counted before the start of a decline is selected to be the cessation date. With this method, the following dates have been determined to be the extent of wood growth for years 2007 to 2009 at Hyytiälä by using microcores (Table 4.13). When comparing the dates obtained from dendrometers and the ones obtained via microcore measurements, it can be observed that the dates vary considerably from one method to the other. A difference from 19 to 26 days is found for onset events while the cessation dates differ from 5 to 18 days. Due to this difference, the selection of the dendrological technique may provide different results when evaluating the climate forcing at Hyytiälä. Therefore, dates from both techniques will be used in the next sections to assess which method is the more appropriate to produce wood growth dates during the years when dendrological data are unavailable.
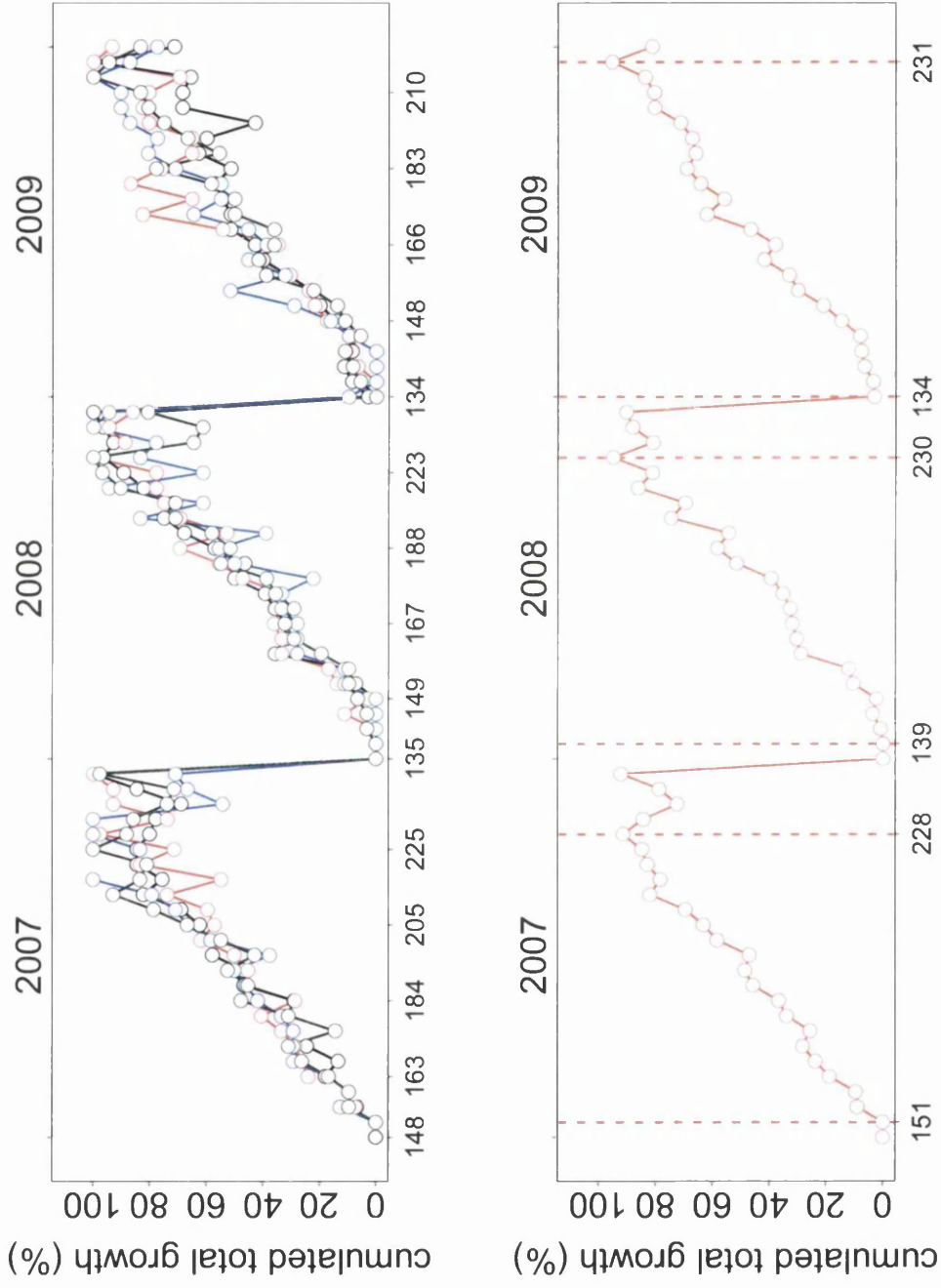
Figure 4.41: *Normalisation procedure of the microcore measurements during year 2007, 2008 and 2009 at Hyytiälä. a) the four time series of microcore measurements expressed as percentage of total growth from tree 1 (black line), tree 2 (red line), tree 3 (blue line) and tree 4 (green line). b) the averaged time series (orange line) with onset and cessation dates indicated (vertical orange dashed line).*

Table 4.13: *Onset, cessation and difference with the dendrometer measurements at Hyytiälä observed by microcore measurements for the period 2007-2009.*

Year	Onset (DOY)	Difference (Days)
2007	151	26
2008	142	22
2009	134	19
Date	Cessation (DOY)	Difference (Days)
2007	228	18
2008	230	5
2009	231	11

4.3 Determination of wood growth when dendrological data are unavailable

4.3.1 Introduction

A range of approaches can be carried out to estimate when wood growth occurs at the study sites thanks to the availability of CO_2 flux data and measurements of environmental variables during the years supplied with dendrological information. The first approach uses the NEE, representative of the photosynthetic activity, to characterise the period of wood growth. A Similar approach can be carried out with evapotranspiration and have been previously described by Cocozza *et al.* (2012). Finally, recurrent environmental conditions during onset and cessation can be investigated and could serve as triggering conditions for a model predicting wood growth when the dendrological data are unavailable. This final approach includes the use of smoothing splines and cumulative variables to investigate which thresholds are the most successful in predicting wood growth.

4.3.2 Estimation of radial growth by using daily average net ecosystem exchange.

The first investigation to determine radial growth dates consists in the examination of the relationship between the net carbon exchange (NEE) of the forest ecosystem and the dendrological data. The fluctuation of the NEE represents the measurement of the carbon flux exchange between the plants and the atmosphere during a period of time. Therefore, using the NEE to determine the period when the vegetation is performing its photosynthetic activity and respiration could be related to the period when radial growth occurs. Another parallel investigation is

to consider the relationship between the temperature variation and the NEE. As photosynthetic and respiration processes are temperature dependent, a close link between temperature and NEE is expected and can provide an additional tool to estimate growth periods at the study sites. The typical variation for NEE during a year of observation is characterised by a bell shape pattern. Each year starts by a winter dormancy period with positive values of NEE driven by respiration until the photosynthesis starts which will be detectable in the NEE time series by the occurence of more negative values. These negative values will reach a peak in summer and will then progressively return to positive values of NEE with the cessation of the photosynthetic activity for the following winter. The three years when dendrological information is available at Hyytiälä have been used to test if a model of growth based on NEE is valid. The study sites of Norunda and Loobos were not analysed for this method due to the absence of NEE records for the period considered.

Figures 4.42a, 4.43a and 4.44a display the temperature records for year 2007, 2008 and 2009 respectively. To better understand the influence of temperature on the photosynthetic activity, temperature values have been processed into daily maximum and minimum values. Therefore, cold limitation to growth will appear in the minimum temperature records while warm limitation involving water shortage may be detectable by observing the maximum temperature values. To ease the observation of the NEE variable, daily averaged values are represented in Figures 4.42b, 4.43b and 4.44b for year 2007, 2008 and 2009 respectively. Daily averaged values provide an indication of growth performance as they will better show the transition period from positive to negative NEE values during spring due to short periods when carbon assimilation occurs at the daily scale at the start of photosynthesis. Following the convention from atmospheric sciences, NEE is represented as negative values and states the depletion of CO_2 from the atmosphere at the profit of the vegetation. Finally, Figures 4.42c, 4.43c and 4.44c show the cumulated daily averages from NEE for 2007, 2008 and 2009 respectively. To ease the comparison with dendrometer records, the cumulated NEE is represented as a positive increment. Threshold values for the cumulated curve have been selected to characterise the main period when photosynthesis occurs. The date for onset of the photosynthesis is attributed when 2 % of the annual maximum cumulated NEE is reached. The selection of 2 % instead of 1 % or 5 % is made as it matches the transitional period between winter dormancy and the following rapid increase in cumulated NEE values. The threshold of 99% is selected to match the period when the cumulated NEE curve is close to meet the characteristic plateau period when the photosynthetic activity has ceased.

All dates produced by this method are presented in Table 4.14 for the period 1997 to 2009. During the three years when dendrological data are available, it is noticeable that the dates produced by this method are quite different than the ones coming from dendrological information. Estimated onset dates via NEE are systematically set earlier, DOY 82 for 2007, DOY 93 for 2008 and DOY 104 for 2009 than the dates from dendrological records. Estimated cessation dates also occur later, DOY 291 for 2007, DOY 294 for 2008 and DOY 286 for 2009. These dates are significantly different from those from the dendrological records and do not show a pattern where NEE records could be used to set up radial growth dates at Hyytiälä. Therefore, a more precise method would be preferable to obtain estimated dates during the years when dendrological data is unavailable at the study sites.

Table 4.14: *Onset, cessation and length of radial growth at Hyytiälä estimated by the method of the daily average net ecosystem exchange for the period 1997-2009.*

Year	Onset (DOY)	Cessation (DOY)	Length (Days)
1997	116	285	169
1998	104	284	180
1999	95	292	197
2000	103	291	188
2001	100	293	193
2002	91	281	190
2003	104	289	185
2004	99	298	199
2005	97	291	194
2006	106	291	185
2007	82	291	209
2008	93	294	201
2009	104	286	182
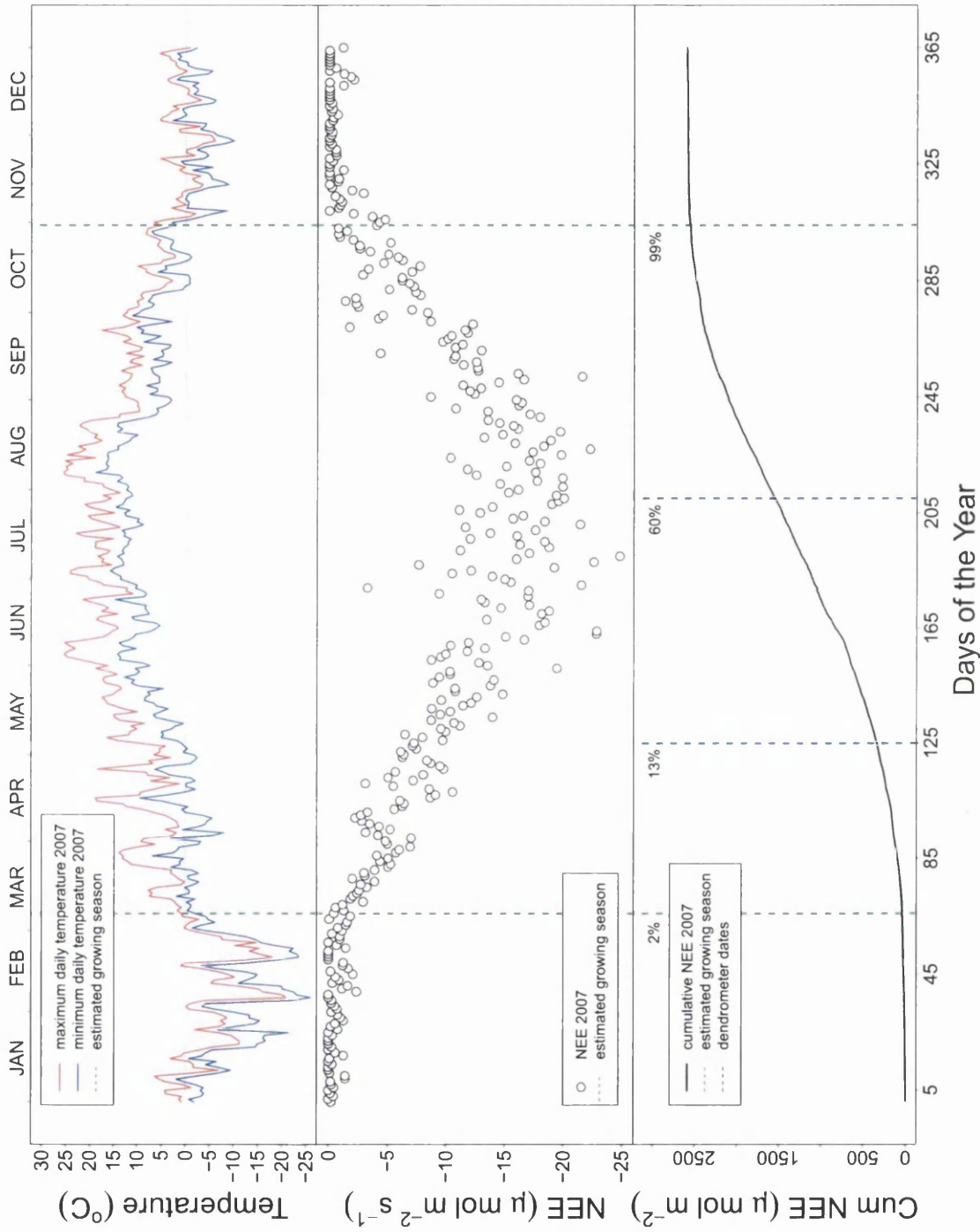
Figure 4.42: *Procedure to build a model of wood growth based on NEE measurements during year 2007 at Hyytiälä. Vertical green dashed lines represent the days of the year matching 2% and 99% of cumulated NEE. Vertical blue dashed lines represent the onset and cessation dates determined via dendrometer measurements. a) minimum (blue solid line) and maximum (red solid line) daily temperature (°C). b) daily average NEE (μmol m^{-2} s^{-1}) (black open circles). c) cumulated NEE (μmol m^{-2}) (black solid line).*
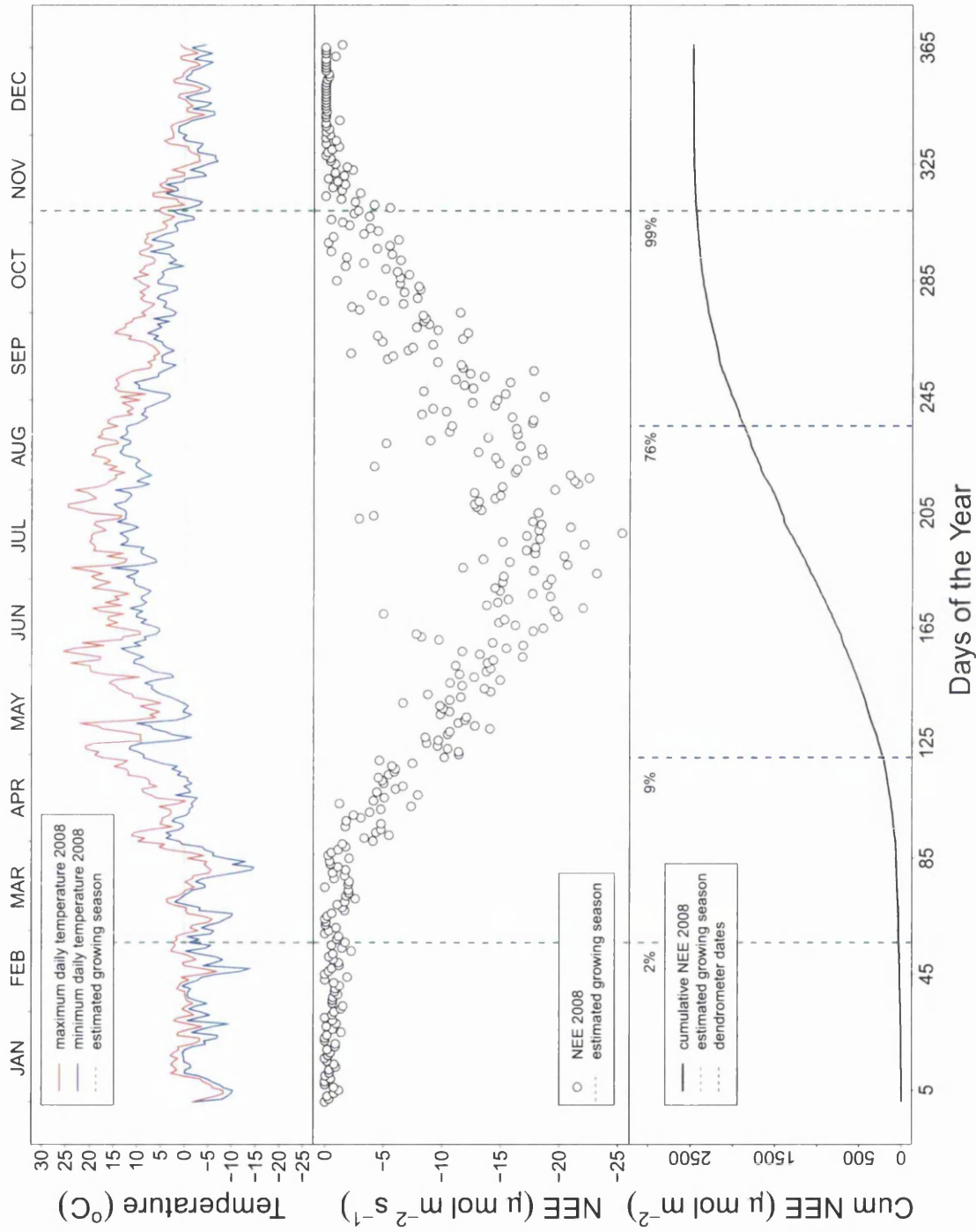
Figure 4.43: *Procedure to build a model of wood growth based on NEE measurements during year 2008 at Hyytiälä. Vertical green dashed lines represent the days of the year matching 2% and 99% of cumulated NEE. Vertical blue dashed lines represent the onset and cessation dates determined via dendrometer measurements. a) minimum (blue solid line) and maximum (red solid line) daily temperature (°C). b) daily average NEE (μmol m⁻² s⁻¹) (black open circles). c) cumulated NEE (μmol m⁻²) (black solid line).*
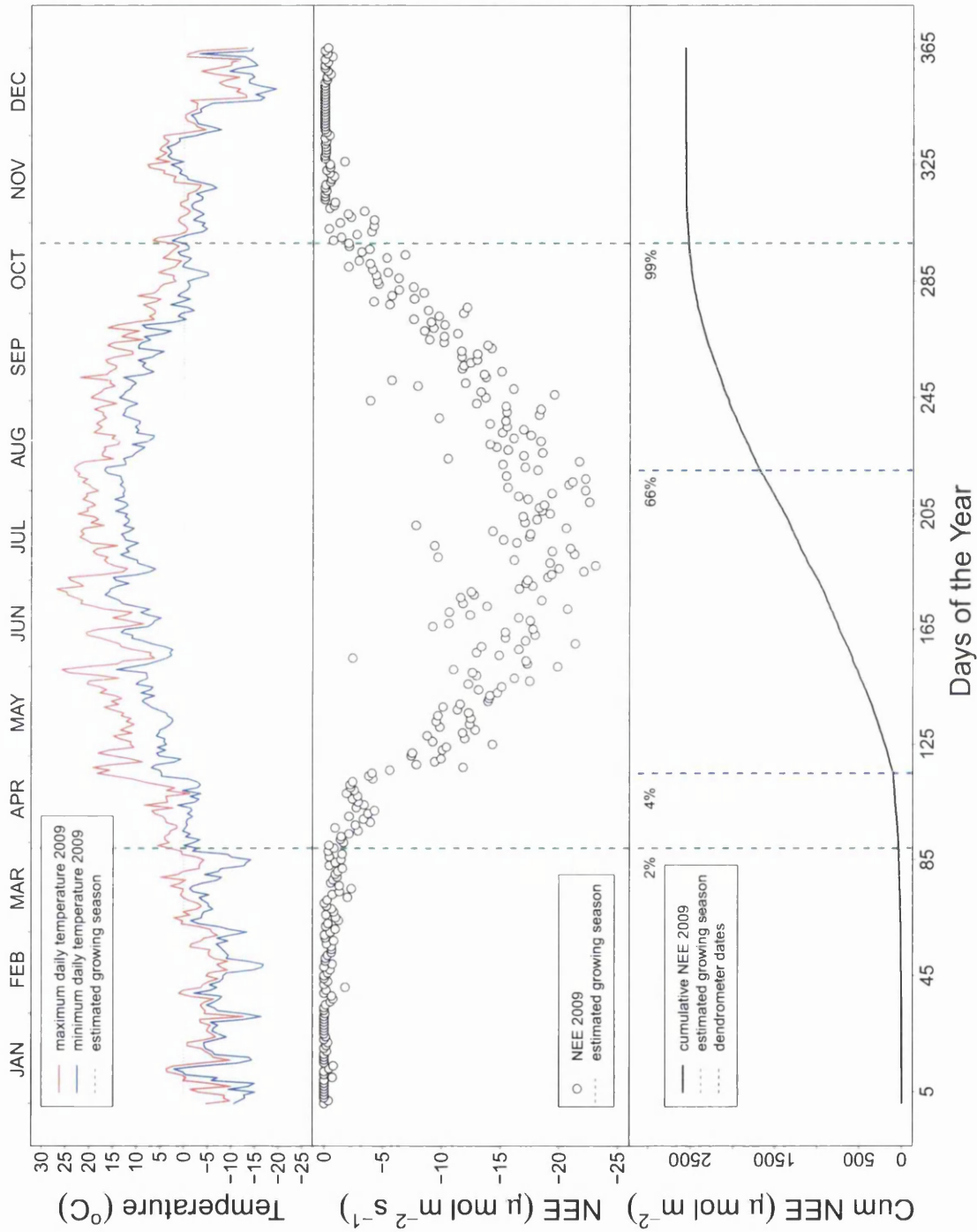
Figure 4.44: *Procedure to build a model of wood growth based on NEE measurements during year 2009 at Hyytiälä. Vertical green dashed lines represent the days of the year matching 2% and 99% of cumulated NEE. Vertical blue dashed lines represent the onset and cessation dates determined via dendrometer measurements. a) minimum (blue solid line) and maximum (red solid line) daily temperature (°C). b) daily average NEE (μmol m^{-2} s^{-1}) (black open circles). c) cumulated NEE (μmol m^{-2}) (black solid line).*

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4.3.3 Estimation of radial growth by using evapotranspiration

Cocozza *et al.* (2012) proposes the use of evapotranspiration to estimate the period when tree radial growth is occurring instead of using NEE. Similar to the previous method, Figures 4.45a, 4.46a and 4.47a display the temperature records via maximum and minimum daily values, Figures 4.45b, 4.46b and 4.47b shows the daily average evapotranspiration flux while Figures 4.45c, 4.46c and 4.47c shows the cumulative evapotranspiration flux for each year of growth. Unfortunately at Norunda and Loobos, evapotranspiration data were unavailable at the time of the study. Therefore, this method is tested on the three years when dendrological data are available at Hyytiälä (2007 to 2009). The intra-annual behaviour of evapotranspiration is quite similar to NEE with a bell shape pattern from winter dormancy to a summer peak and a progressive return to a winter plateau period. Therefore, a similar approach can be tested and was first conducted by Cocozza *et al.* (2012) which stated a close link between temperature, dendrometer records and cumulative evapotranspiration at two study sites in Italy on olive trees during year 2005 and 2006. The advantage of such a procedure consists in using multiple environmental information in parallel to dendrological measurements to establish dates of wood growth with a greater confidence.

At Hyytiälä, a close link is observable between the daily minimum temperature and the edges of the bell shape pattern from the intra-annual evapotranspiration as shown in Figures 4.45, 4.46 and 4.47 respectively, for the years 2007, 2008 and 2009. When setting a threshold at 10% of cumulated evapotranspiration to represent the onset of radial growth, it also matches the transition from negative to positive daily minimum temperature. This behaviour is also happening at the other edge of the bell shape, with a 95% threshold value. This relationship may then be used as a convention for determining radial growth dates during the study period from 1997 to 2009. When comparing the dates from dendrological information, it is noticeable that estimated onset dates are more realistic than when using NEE. However, the difference between the two sets of dates is still considerable with the evapotranspiration method estimating onset dates on DOY 107, DOY 97 and DOY 110 for year 2007, 2008 and 2009. In terms of cumulated evapotranspiration, this represents a variation from less than 1% (year 2009) to 5% (year 2007 and 2008), but as the slope increases slowly at the start of the growing period, it represents a difference of 23 days in 2008. In the case of the cessation dates, the difference with dendrological datasets is even greater. The cessation dates estimated on DOY 291, DOY 315 and DOY 281 by using the evapotranspiration

method are more than two months later than when estimated by the dendrological data. There is also a major difference in the cumulated evapotranspiration at cessation dates estimated by the dendrological information with values from 63 % to 78 % compared to the selected 95% threshold. Therefore, even if this method seems to provide acceptable onset dates for the characterisation of the growing season, there is still significant differences with the dates found by dendrological means especially for cessation dates. Estimated dates for onset and cessation are found using this method are in Table 4.15 for Hyytiälä.

Table 4.15: *Onset, cessation and length of radial growth at Hyytiälä estimated by the evapotranspiration method for the period 1997-2009.*

Year	Onset (DOY)	Cessation (DOY)	Length (Days)
1997	102	248	146
1998	116	263	147
1999	109	250	141
2000	122	263	141
2001	120	249	129
2002	120	251	131
2003	124	250	126
2004	116	254	138
2005	117	259	142
2006	119	267	148
2007	107	262	155
2008	97	275	178
2009	110	260	150
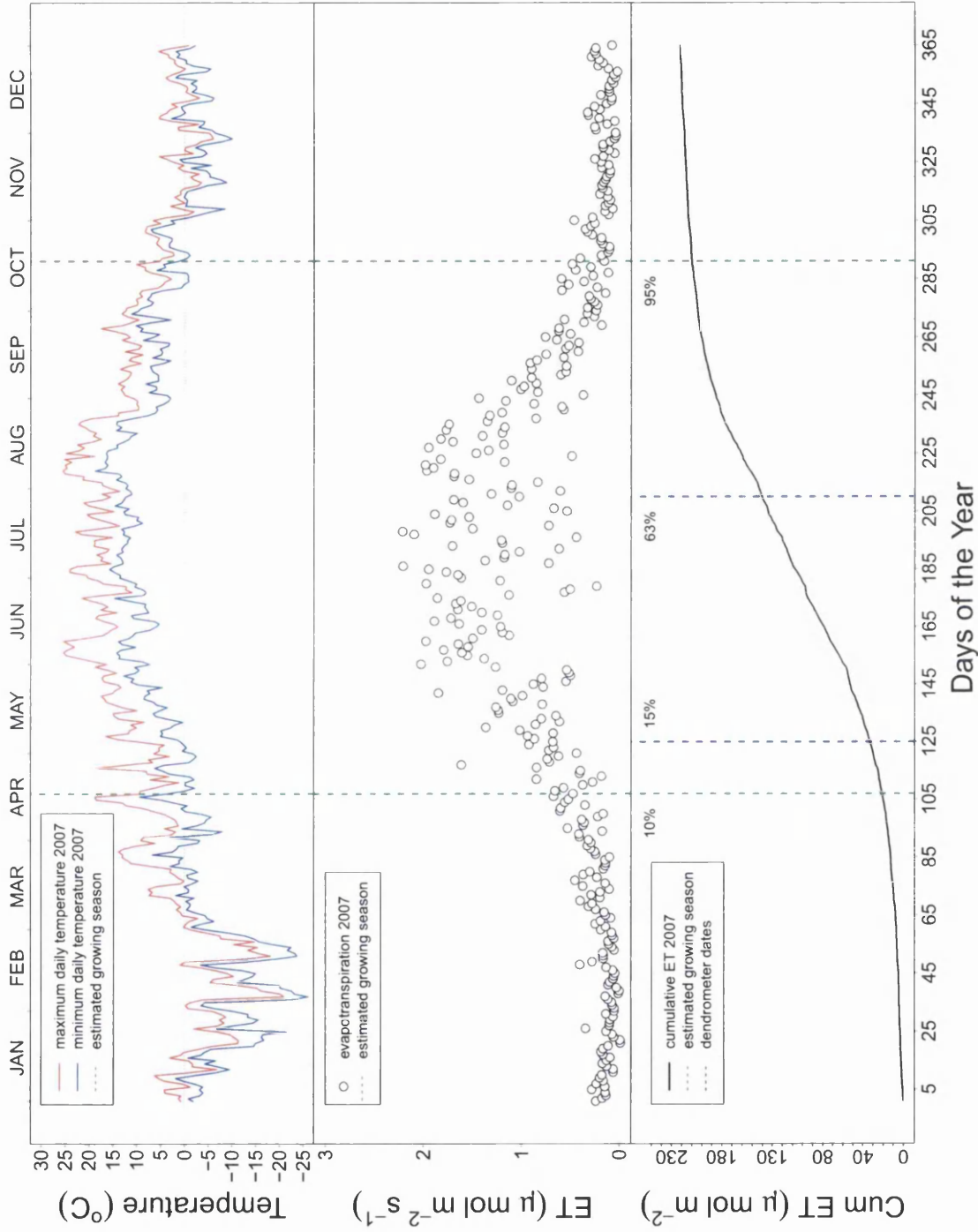
Figure 4.45: *Procedure to build a model of wood growth based on evapotranspiration (ET) measurements during year 2007 at Hyytiälä. Vertical green dashed lines represent the days of the year matching 10% and 95% of cumulated ET. Vertical blue dashed lines represent the onset and cessation dates determined via dendrometer measurements. a) minimum (blue solid line) and maximum (red solid line) daily temperature (°C). b) daily average evapotranspiration (µmol m⁻² s⁻¹) (black open circles). c) cumulated evapotranspiration (µmol m⁻²) (black solid line.)*

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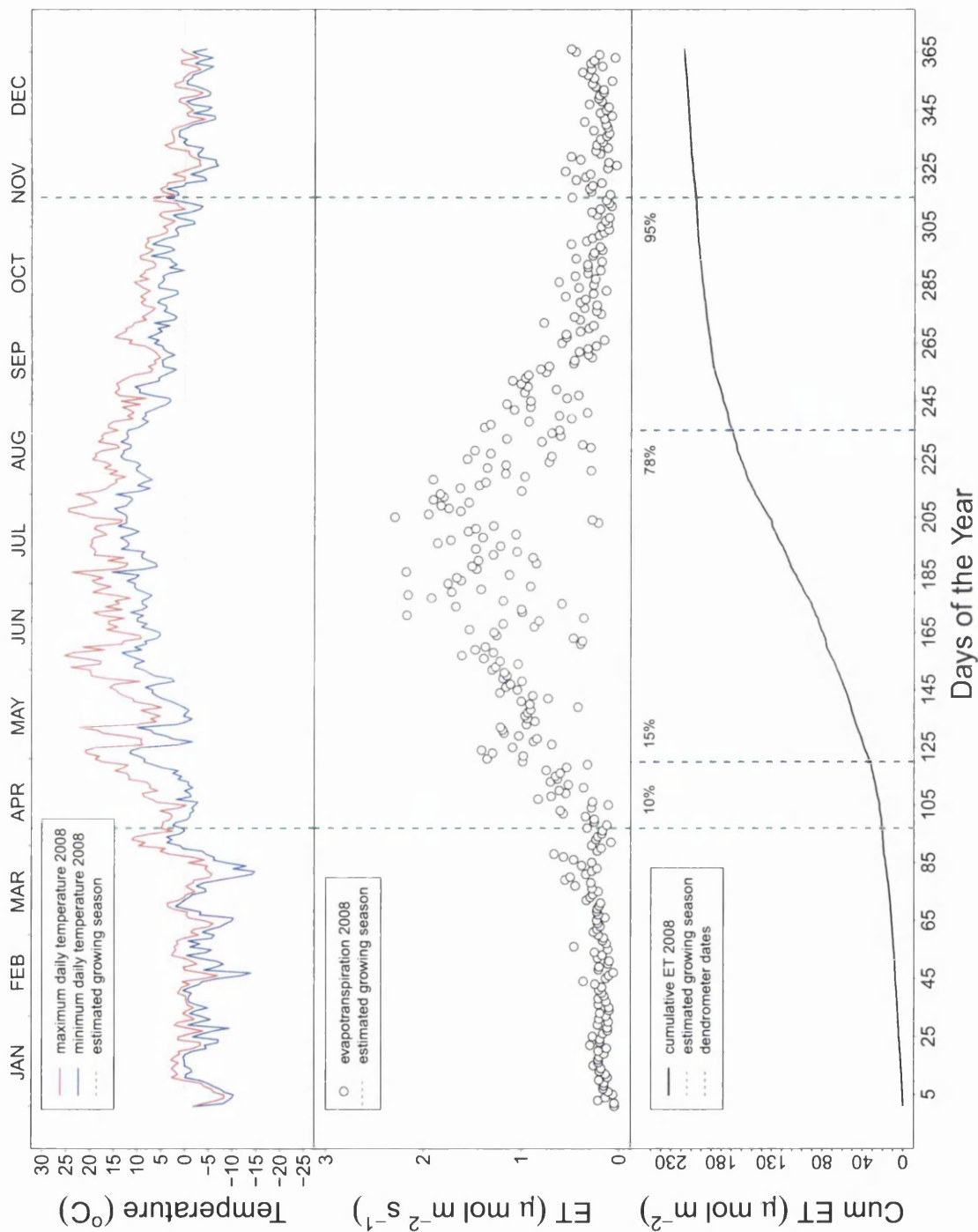
Figure 4.46: *Procedure to build a model of wood growth based on evapotranspiration (ET) measurements during year 2008 at Hyytiälä. Vertical green dashed lines represent the days of the year matching 10% and 95% of cumulated ET. Vertical blue dashed lines represent the onset and cessation dates determined via dendrometer measurements. a) minimum (blue solid line) and maximum (red solid line) daily temperature (°C). b) daily average evapotranspiration (μmol m⁻² s⁻¹) (black open circles). c) cumulated evapotranspiration (μmol m⁻²) (black solid line.)*

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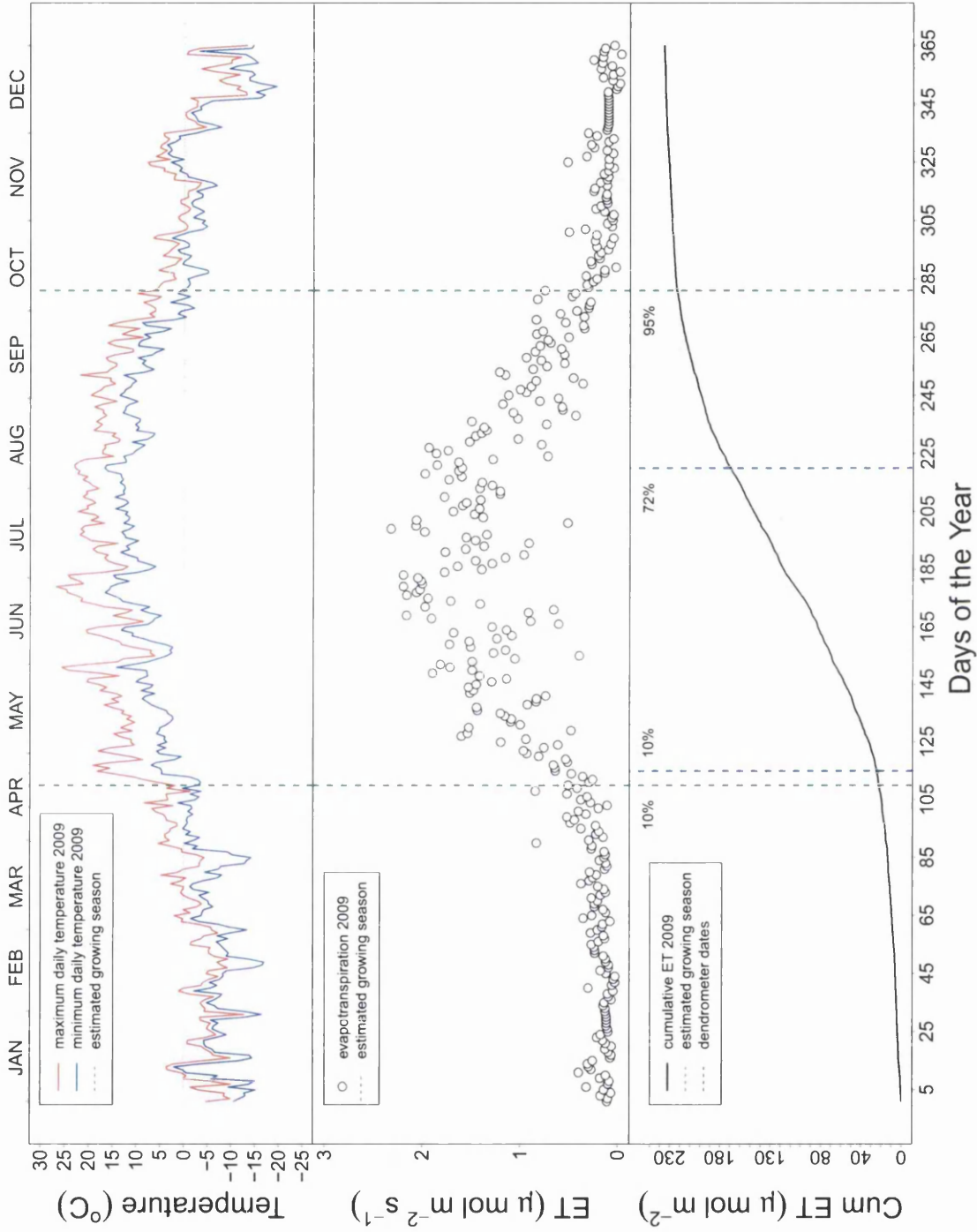
Figure 4.47: *Procedure to build a model of wood growth based on evapotranspiration (ET) measurements during year 2009 at Hyytiälä. Vertical green dashed lines represent the days of the year matching 10% and 95% of cumulated ET. Vertical blue dashed lines represent the onset and cessation dates determined via dendrometer measurements. a) minimum (blue solid line) and maximum (red solid line) daily temperature (°C). b) daily average evapotranspiration (μmol m⁻² s⁻¹) (black open circles). c) cumulated evapotranspiration (μmol m⁻²) (black solid line.)*

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4.3.4 Estimation of radial growth by making use of co-occuring environmental conditions

4.3.4.1 Co-occuring weather conditions when radial growth is determined by dendrometer measurements

An alternative method to estimate the period of wood growth consists in selecting environmental variables that covary with the tree physiological activity during the annual cycle. Literature shows evidence of a temperature effect on wood growth at the treeline for both high altitude and northern latitude with critical thresholds ranging from 0 °C to 10 °C for air temperature and 3 °C to 5 °C for soil temperature depending on tree species (Körner, 2003a). Photoperiod as a control over phenology such as bud burst and leaves unfolding (Chuine, 2010; Körner & Basler, 2010) and on wood growth (Wodzicki, 1964) has also been investigated. This method proposes to determine if common environmental conditions can be found during different years of growth for events such as the onset and cessation of wood production. Therefore, if these conditions are found, they can be used as thresholds to wood growth formation. To permit a clearer observation of the intra-annual variation for PAR and temperature, these variables have been smoothed using smoothing splines as described in Section 4.2 (span = 0.8). By suppressing the noise from daily variation, each day of the year is characterised by a unique value of smoothed temperature or PAR.

The values found on the dates for onset and cessation of wood growth estimated via the dendrometer information are presented in Table 4.16. When analysing the environmental characteristics at the dates selected for radial growth onset, it is noticeable that all three sites present similar values of PAR with values from 370 to 389 μmol m^{-2} s^{-1} (mean: 376.00 $\pm$ 6.69 μmol m^{-2} s^{-1}) while temperature values are more variable with a range of values from 6.25 to 12.40 °C (mean: 9.08 $\pm$ 2.59 °C). When analysing inter-site variability, a temperature gradient is observable with Hyytiälä presenting the lowest temperature recorded during the onset of growth while Norunda and Loobos show higher values. Cessation values of smoothed PAR and temperature are more variable. PAR values spread from 145 to 356 μmol m^{-2} s^{-1} (mean: 251.67 $\pm$ 80.83 μmol m^{-2} s^{-1}) and the temperature range is also considerable with values from 10.96 to 16.50 °C (mean: 13.65 $\pm$ 2.19 °C). Due to the high variation of temperature values during both the wood growth onset and cessation between the different years, this environmental variable seems to be unwise to use in the perspective of setting a threshold value determining wood growth properties. However, using PAR seems to be reliable for wood onset formation.

While it is not possible to statistically test the stability of such a relationship between PAR and the onset of radial growth due to the small sample of years when the dendrological data is available, this method has the potential to provide radial growth onset dates with a better accuracy than the approaches based on flux data. However, establishing cessation dates using smoothed PAR seems unreliable and would suggest that another method is necessary to obtain realistic wood growth cessation dates.

When PAR data quality is not high enough to support these findings as the smoothing splines technique does not allow any gaps in the PAR data, a procedure of gap filling is performed by using the calculation of the potential downwelling shortwave radiation at the surface according to Stull (1988) assuming no cloud cover (Figure 4.48). This procedure determines what radiation level should be occurring during a typical year of growth according to the latitude and longitude of the study site. However, it is expected that the use of gap filling during the critical period of radial growth onset and cessation will lead to less accurate date estimation.

The threshold value selected to trigger wood growth onset is the average value of 376 μmol m^{-2} s^{-1} found at the three study sites. The set of estimated dates for wood growth is presented in Table 4.17 with the indication of when gap filling can be a source of uncertainty. Figures 4.49, 4.50 and 4.51 show the procedure for the date determination during year 2007, 2008 and 2009 at Hyytiälä.

Table 4.16: *Photosynthetically active radiation (μmol m^{-2} s^{-1}) and temperature (°C) at Hyytiälä, Norunda and Loobos at the dates estimated by the available dendrometer measurements.*

		Onset				
Year	Hyytiälä	Norunda	Loobos	Hyytiälä	Norunda	Loobos
	PAR (μmol m^{-2} s^{-1})			Temperature (°C)		
2007	375			6.50		
2008	376			8.50		
2009	375		372	6.25		12.40
2010		370	389		11.80	9.02
2011		NA			NA	
		Cessation				
2007	339			16.50		
2008	214			12.00		
2009	356		239	15.97		13.57
2010		145	217		10.96	12.87
2011		NA			NA	

Table 4.17: *Onset of radial growth in days of the year at Hyytiälä, Norunda and Loobos estimated by the method of smooth splines applied on photosynthetically active radiation for the period 1997-2009 by using dendrometer measurements. Gap filling procedure when performed during the critical period for onset dates are followed by (gp).*

Year	Hyytiälä	Norunda	Loobos
	Onset (DOY)		
1997	113 (gp)	134	126 (gp)
1998	133	135 (gp)	126 (gp)
1999	123	125	126 (gp)
2000	122	132 (gp)	126 (gp)
2001	127 (gp)	120	127 (gp)
2002	124	125	114 (gp)
2003	127 (gp)	136	106 (gp)
2004	110	127	134
2005	129	136	123
2006	114	152	116
2007	125	146	95
2008	120	132	108
2009	115	130	104
2010	NA	139	103
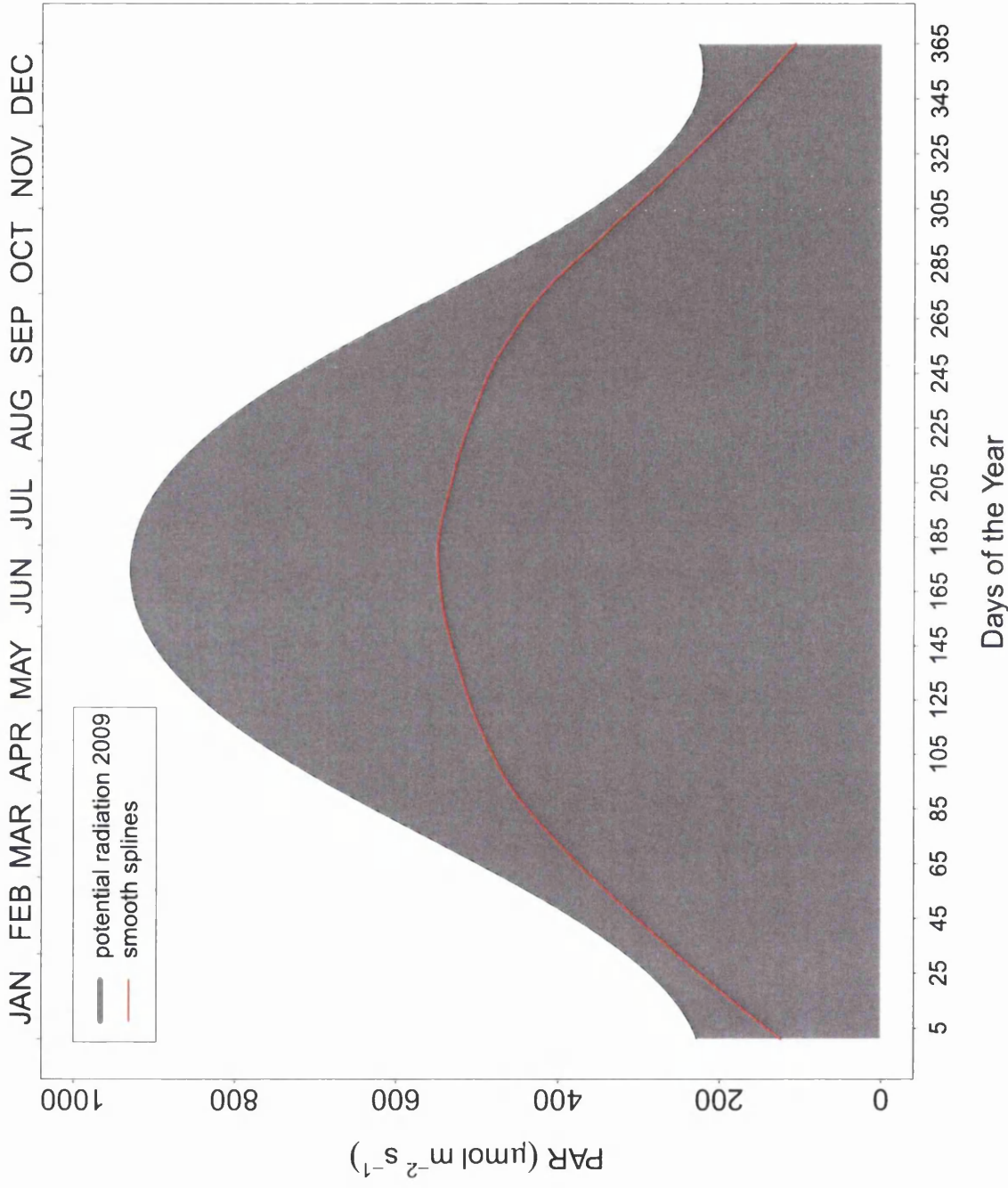
Figure 4.48: *Procedure to gapfill PAR by using the calculation of the potential downwelling shortwave radiation at the surface according to Stull (1988) assuming no cloud cover. The potential radiation calculated at at Hyytiälä for 2009 is displayed as a grey area with the smooth splines applied to the potential radiation (red solid line).*
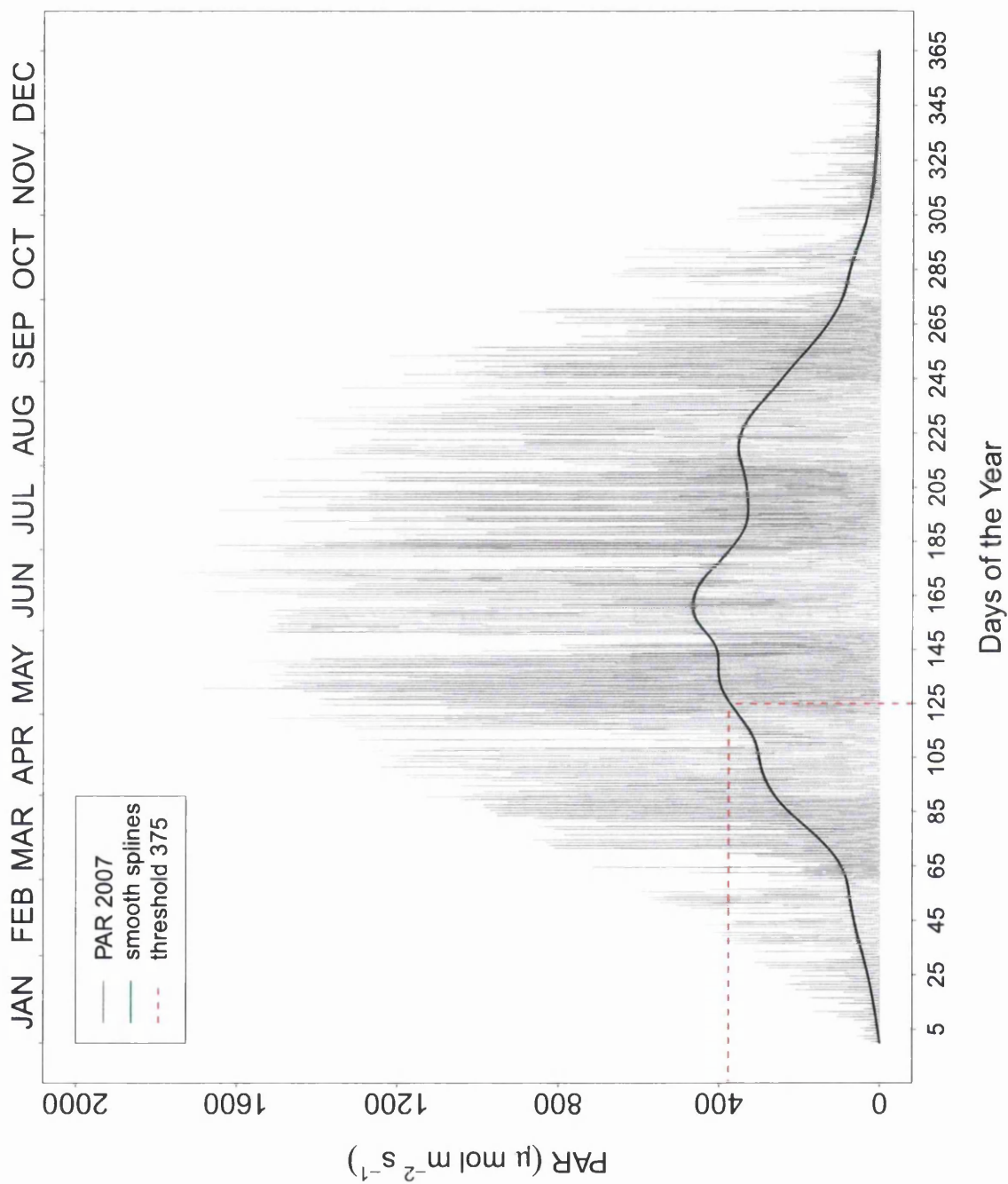
Figure 4.49: *Growing season onset date determination via the PAR threshold value method for year 2007 at Hyytiälä. The PAR variation at the half-hourly resolution is shown as a grey solid line while the PAR threshold at 375 $\mu mol\ m^{-2}\ s^{-1}$ and the smooth splines are displayed by a red dashed line and a green solid line respectively.*
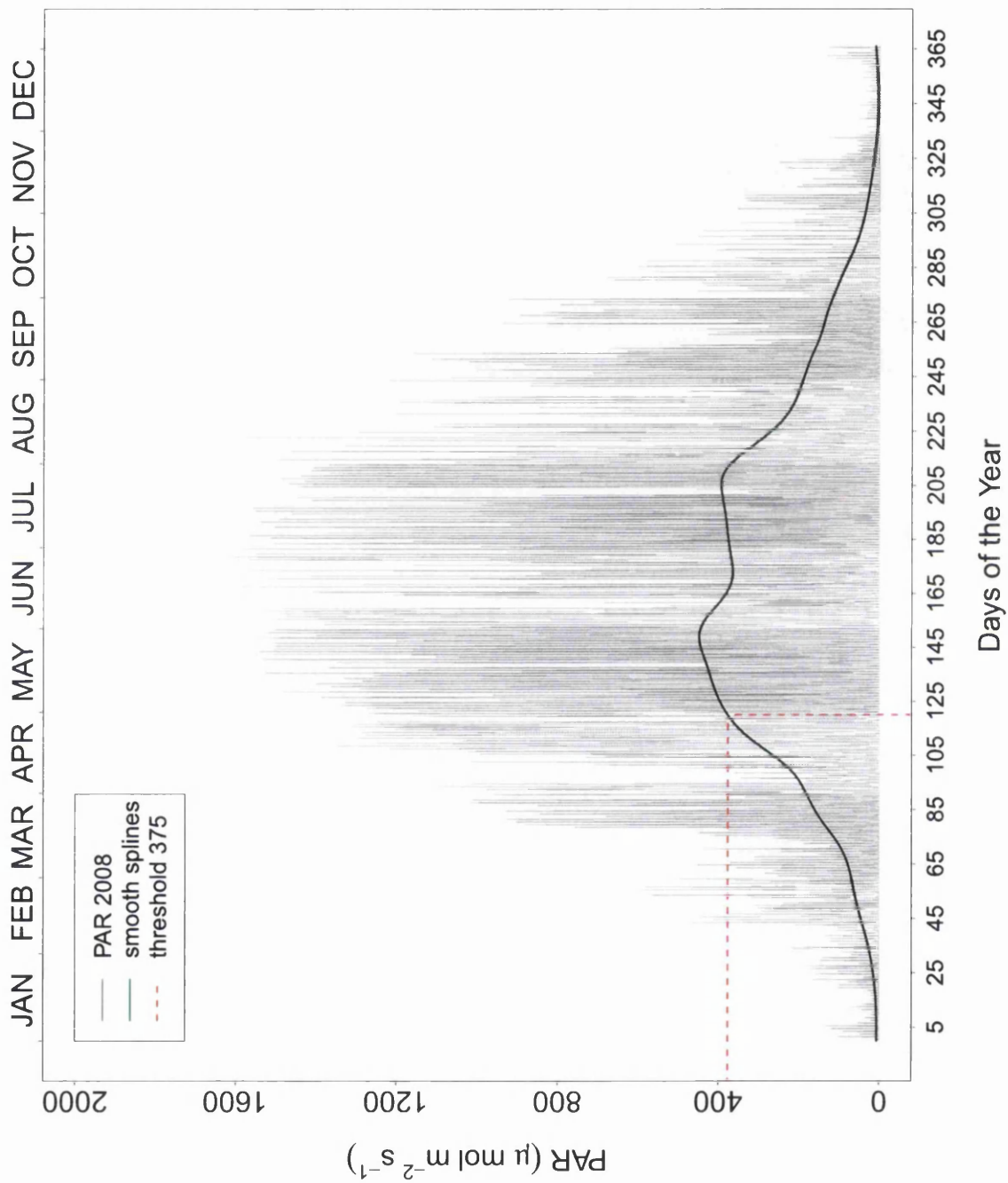
Figure 4.50: *Growing season onset date determination via the PAR threshold value method for year 2008 at Hyytiälä. The PAR variation at the half-hourly resolution is shown as a grey solid line while the smooth splines are displayed by a red dashed line and a green solid line respectively.*
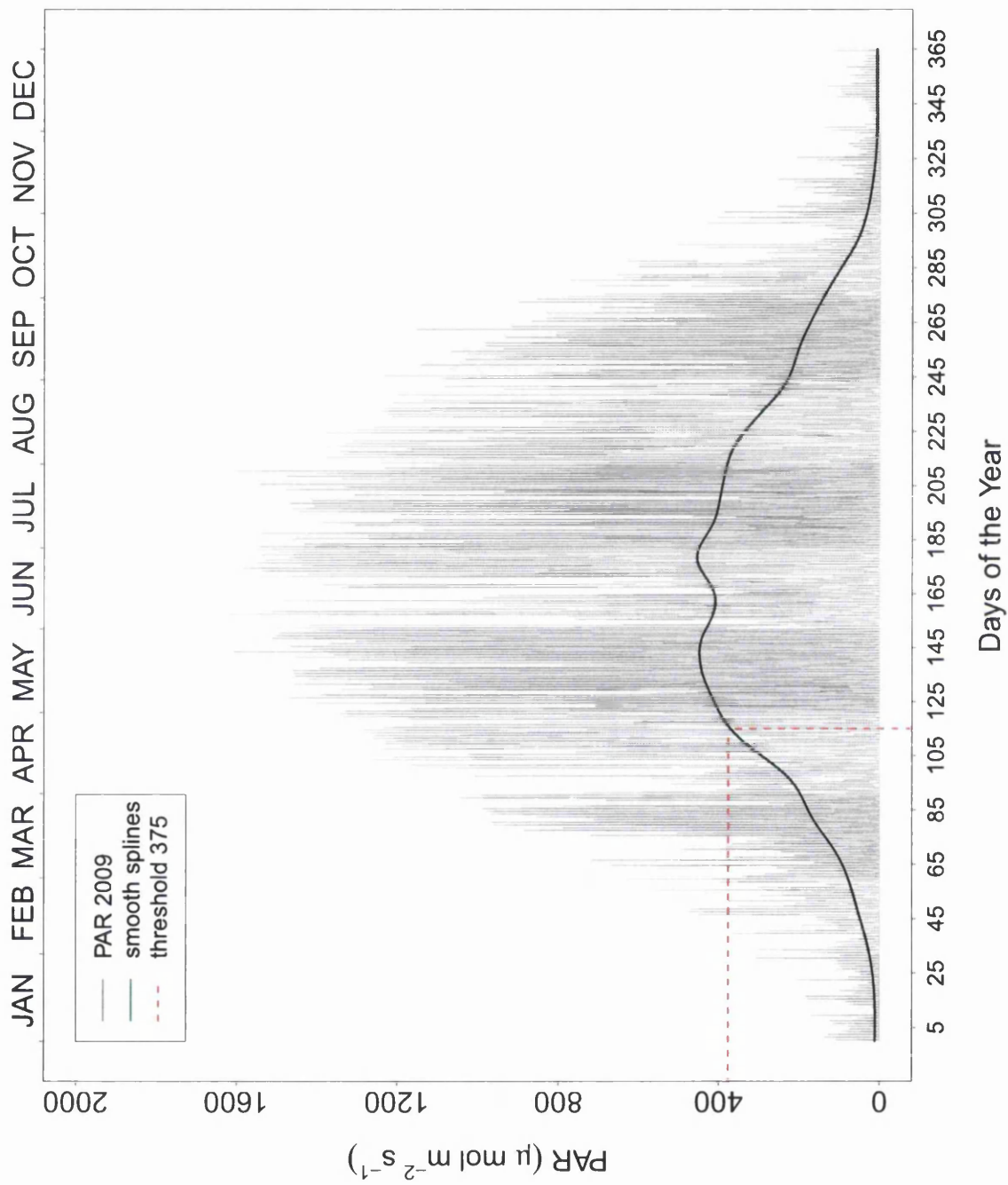
Figure 4.51: *Growing season onset date determination via the PAR threshold value method for year 2009 at Hyytiälä. The PAR variation at the half hourly resolution is shown as a grey solid line while the PAR threshold at 375 $\mu mol\ m^{-2}\ s^{-1}$ and the smooth splines are displayed by a red dashed line and a green solid line respectively.*

4.3.4.2 Co-occuring weather conditions when radial growth is determined by microcore measurements

Following the same procedure as described above, threshold values for temperature and PAR during the dates for onset and cessation of wood growth estimated from the microcores information are presented in table 4.18 for Hyytiälä for the years 2007 to 2009. Similar to the dates found with the dendrometers, critical PAR values found during the onset events are within a small range while temperature seems more variable with a high variation between 2007 (14.18 °C) and 2008 and 2009 (9.72 °C and 9.94 °C). For cessation dates, no clear critical values could be found on a inter-annual basis for both PAR and temperature. If thresholds are to be chosen to characterise wood formation, the average of the three years for PAR values is 435 μmol m^{-2} s^{-1} and seems to represent well the onset dates. However, when creating the dates for the period 1997 to 2009 using this threshold, some years (1998, 2000, 2003 and 2004) do not always reach this value of smoothed PAR which then cannot be attributed onset values. Therefore, to complete the set of dates, a threshold on air temperature at 10 °C is used despite being probably less accurate than the PAR method due to higher inter-annual variation. For cessation dates, temperature values from 12 to 16 °C have not been previously stated in the literature to be limiting to growth. Therefore, the same 10 °C threshold is used to determine wood growth cessation and to build a complete set of dates for microcores. The set of onset dates produced is shown in Table 4.19.

Table 4.18: *Photosynthetic active radiation (μmol m^{-2} s^{-1}) and temperature (°C) at Hyytiälä at the dates estimated by the available microcore data.*

Onset		
Year	PAR (μmol m^{-2} s^{-1})	Temperature (°C)
2007	431	14.18
2008	437	9.72
2009	437	9.94
Cessation		
2007	337	16.23
2008	236	12.97
2009	302	14.57

Table 4.19: *Onset, cessation and length of radial growth in days of the year at Hyytiälä estimated by the method of smooth splines applied on PAR and temperature for the period 1997-2009 at the dates of wood growth determined using microcores. Onset dates determined with temperature instead of PAR are indicated by (T). All dates for cessation of wood growth are determined by temperature.*

Year	Onset (DOY)	Cessation (DOY)	Length (Days)
1997	145	256	128
1998	154 (T)	238	141
1999	148	265	136
2000	138 (T)	247	122
2001	156	263	142
2002	134	255	120
2003	138 (T)	233	127
2004	156 (T)	261	141
2005	160	266	144
2006	156	271	145
2007	151	246	141
2008	141	244	128
2009	132	259	115

4.3.5 Estimation of radial growth on the basis of cumulated environmental variables

4.3.5.1 Cumulated weather variables when radial growth is determined by dendrometer measurements

The cessation of wood growth is still a challenging topic for dendrology and phenology studies (Menzel *et al.*, 2006). However, the assumption usually made is that trees have the necessity to finish the maturation of latewood cells before the return of cold temperatures prevents the photosynthesis cycle. Therefore, it is realistic to think that trees time the release of growth inhibitors via environmental controls with the objective to maximise the growth period without risking winter frost to stop the maturation process before its end. Photoperiodic conditions were found to influence the content of growth inhibitors as well as auxins (Nitsch & Nitsch, 1957; Phillips & Wareing, 1958; Kawase & Nitsch, 1958).

Wodzicki (1964) presented evidence that a decrease in the photoperiod induced the production of growth inhibitors and transition to latewood cells inducing maturation via cell thickening. However, as shown in Table 4.16, the values of PAR at cessation dates do not seem to present a good agreement over a theoretical value that would be triggering wood growth cessation. Another investigation is to assess if the cumulation of environmental variables such as degree days after the onset

of growth can lead to a threshold amount when the growth cessation will occur.

The method used for this study is to cumulate only air temperature above 5 °C which represents a limitation for enzymes to perform photosynthesis. However, all PAR values were cumulated without restrictions. Table 4.20 presents the cumulated temperature and PAR values at the observed cessation date using dendrometer records for 2007 to 2010. Figures 4.52 and 4.53 display the cumulated temperature and PAR at Hyytiälä during the period 2007 to 2009. As for the previous method using smoothed variables, it is noticeable that the cumulated temperature presents a greater variability in cumulated values than PAR at dates selected for growth onset and cessation. However, when analysing the values from cumulated PAR, it is observable that years 2008 and 2009 at Hyytiälä present very similar values for both growth onset and cessation while showing a great difference in the total amount of PAR received during each year. It is then a possibility that these values of cumulated PAR may serve as an indication for growth onset and cessation. However, year 2007 does not fit well this pattern and would show a difference of 17 days for onset (estimated DOY 108 instead of DOY 125) and 13 days for cessation (estimated DOY 223 instead of DOY 210) if thresholds are set at growth onset: 620,000 μmol m^{-2} s^{-1} and cessation: 2,700,000 μmol m^{-2} s^{-1}.

Having just one year of dendrometer measurements to analyse at Norunda (2010) does not permit inter-annual comparison of cumulated variables at this study site. However, the cumulated PAR is very similar to year 2008 at Hyytiälä and it may be interesting to compare the two study sites due to their relative geographic proximity. When applying the same thresholds, the difference for onset would be of 18 days (estimated DOY 119 instead of DOY 137) and for cessation of 20 days (estimated DOY 238 instead of DOY 258).

Finally at Loobos, two consecutive years are comparable (2009 and 2010) and present close values for both onset and cessation dates while following a very similar pattern for the cumulated PAR. Although these values are in a close range of the ones found at Hyytiälä for growth onset, they are significantly greater for growth cessation. Therefore, it is expected that Loobos being the most southern site out of the three selected study sites, the annual light input is greater than at Norunda and Hyytiälä and possibly induces a shift in the threshold value for growth cessation. It is also expected that the probability of frost damage does not occur until later in the winter due to higher temperature and that later growth cessations are an acceptable risk. If thresholds for growth are selected as equal to 750,000 μmol m^{-2} s^{-1} for onset and 3,900,000 μmol m^{-2} s^{-1} for cessation, the

onset date difference would be one day for both 2009 and 2010 (DOY 106 instead of DOY 105 or DOY 107) while the cessation date difference would be four days for 2009 (DOY 261 instead of DOY 265) and two days for 2010 (DOY 267 instead of DOY 265). When applying these thresholds to the period 1997-2010, a new set of dates can be produced to provide growth onset and cessation at the three study sites and is shown in Table 4.21. As for the previous method, gap filling is sometimes necessary and is indicated when critical for determining growth dates.

Table 4.20: *Values of cumulative temperature and PAR at Hyytiälä, Norunda and Loobos at the dates of onset and cessation observed by dendrometer measurements for the period 2007-2010.*

Year	Hyytiälä		Norunda		Loobos	
	Onset	Cessation	Onset	Cessation	Onset	Cessation
	Cumulative Temperature (°C)					
2007	7567	63000				
2008	4746	73344				
2009	1546	66907			18415	132302
2010			12109	101196	15335	126547
Year	Hyytiälä		Norunda		Loobos	
	Onset	Cessation	Onset	Cessation	Onset	Cessation
	Cumulative Radiation (μmol m^{-2} s^{-1})					
2007	849139	2466372				
2008	619619	2678576				
2009	621923	2700360			731725	3956545
2010			915471	2885676	773589	3867336
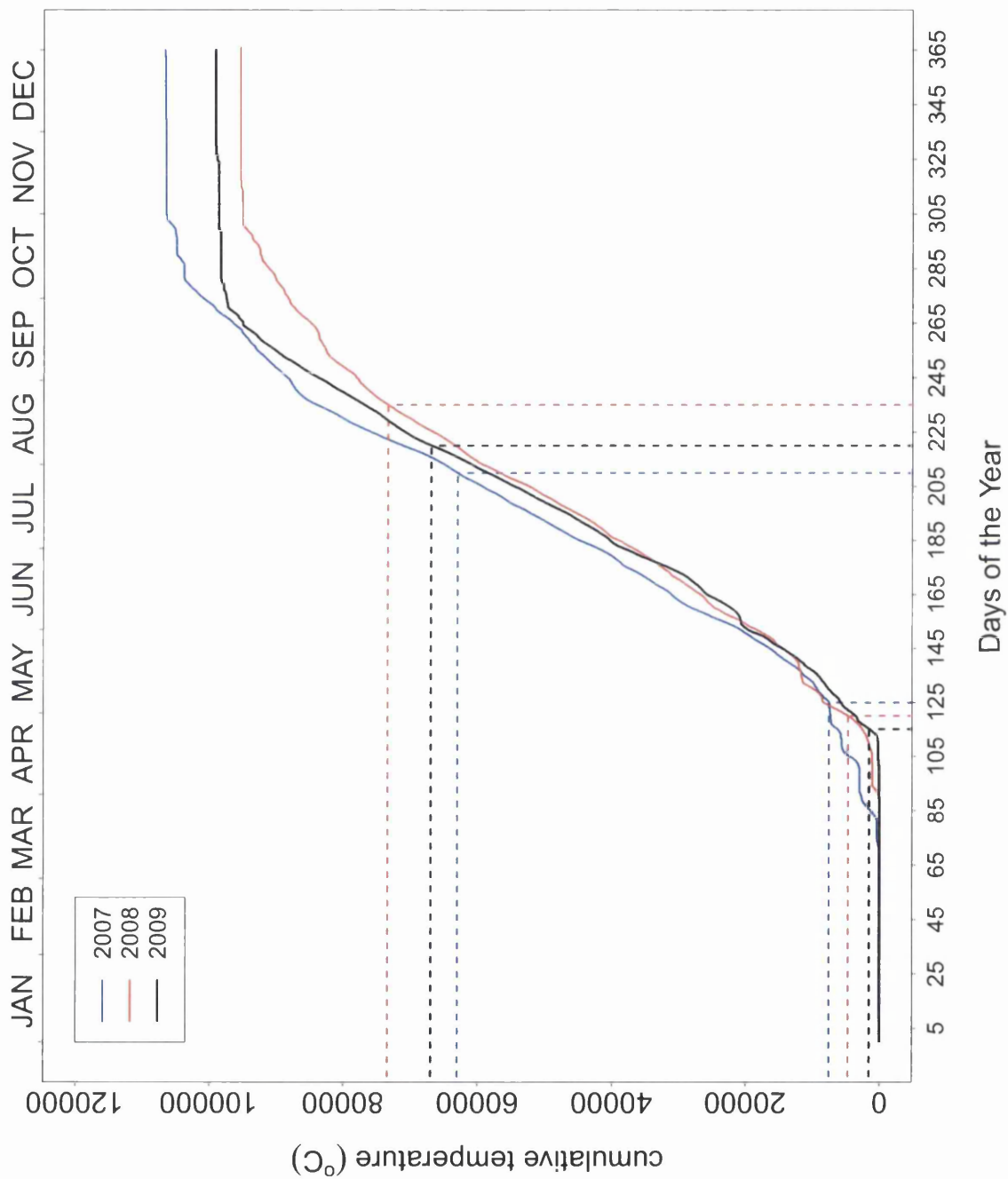
Figure 4.52: *Cumulative temperature (°C) at Hyytiälä for 2007 (blue solid line), 2008 (red solid line) and 2009 (black solid line). The vertical and horizontal dashed lines represent the values of cumulated temperature met during the days for onset and cessation estimated by dendrometers measurements for each year with the same colour pattern.*
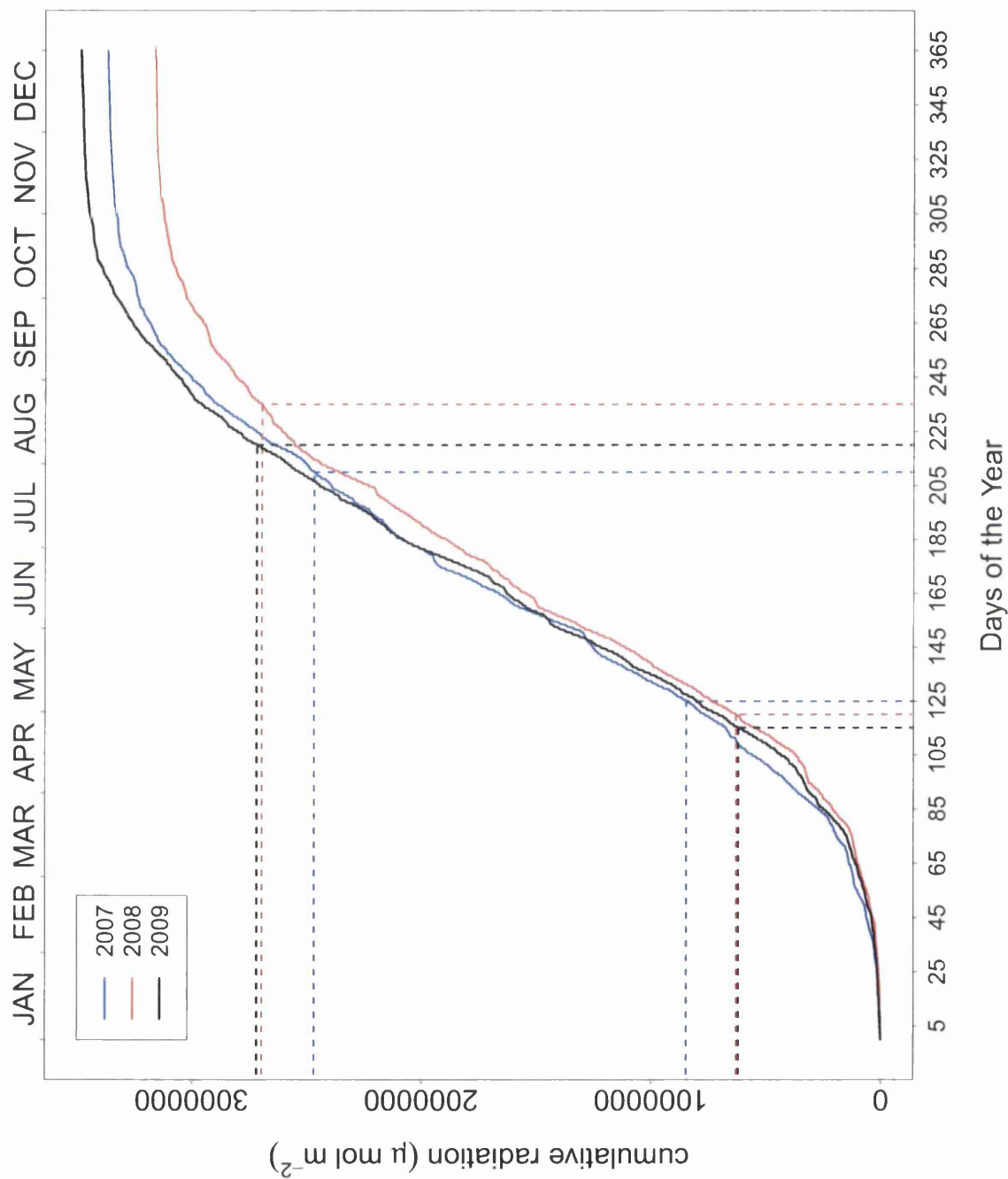
Figure 4.53: *Cumulative PAR ($\mu mol\ m^{-2}$) at Hyytiäiä for 2007 (blue solid line), 2008 (red solid line) and 2009 (black solid line). The vertical and horizontal dashed lines represent the values of cumulated PAR met during the days for onset and cessation estimated by dendrometers measurements for each year with the same colour pattern.*

Table 4.21: *Onset and cessation of radial growth in days of the year at Hyytiälä, Norunda and Loobos estimated by the method of cumulative variables applied photosynthetically active radiation for the period 2007-2010 by using dendrometer measurements. Gap filling procedure was applied during years when PAR values were missing and is specified by (gp) when applied during the critical periods for growth onset and cessation.*

Year	Hyytiälä Onset (DOY)	Hyytiälä Cessation (DOY)	Norunda Onset (DOY)	Norunda Cessation (DOY)	Loobos Onset (DOY)	Loobos Cessation (DOY)
1997	109 (gp)	213 (gp)	105	202	103 (gp)	297 (gp)
1998	105	227	110 (gp)	224 (gp)	103 (gp)	297 (gp)
1999	115	212	116	209	103 (gp)	297 (gp)
2000	110	226	100 (gp)	219 (gp)	103 (gp)	297 (gp)
2001	118 (gp)	234 (gp)	109	215	103 (gp)	304 (gp)
2002	108	214	110	215	99 (gp)	338 (gp)
2003	109 (gp)	225 (gp)	110	221	99 (gp)	273 (gp)
2004	108	227	112	230	111	311
2005	107	211	107	223	103	264
2006	113	208	122	250	107	265
2007	108	223	113	233	103	283
2008	119	235	117	227	106	277
2009	114	219	115	235	106	261
2010			119	238	106	267

4.3.5.2 Cumulated weather variables when radial growth is determined by microcore measurements

When observing the cumulated temperature and PAR using the wood growth dates obtained via microcore measurements, no clear pattern seems to be matching the onset and cessation dates of the period 2007 to 2009 (Figure 4.54 for temperature and Figure 4.55 for PAR). Cumulated values are displayed in Table 4.22. Therefore, no threshold values using these cumulated variables can be determined with confidence.

Table 4.22: *Cumulated Photosynthetic active radiation ($\mu mol\ m^{-2}$) and temperature (° C) at Hyytiälä at the dates estimated by the available microcore data.*

Onset dates		
Year	cumulated PAR (μmol m^{-2})	cumulated Temperature (°C)
2007	1306224	20233.74
2008	1053186	12954.82
2009	976750	8881.41
Cessation dates		
2007	2768762	78537.29
2008	2654028	70047.27
2009	2886978	74361.51
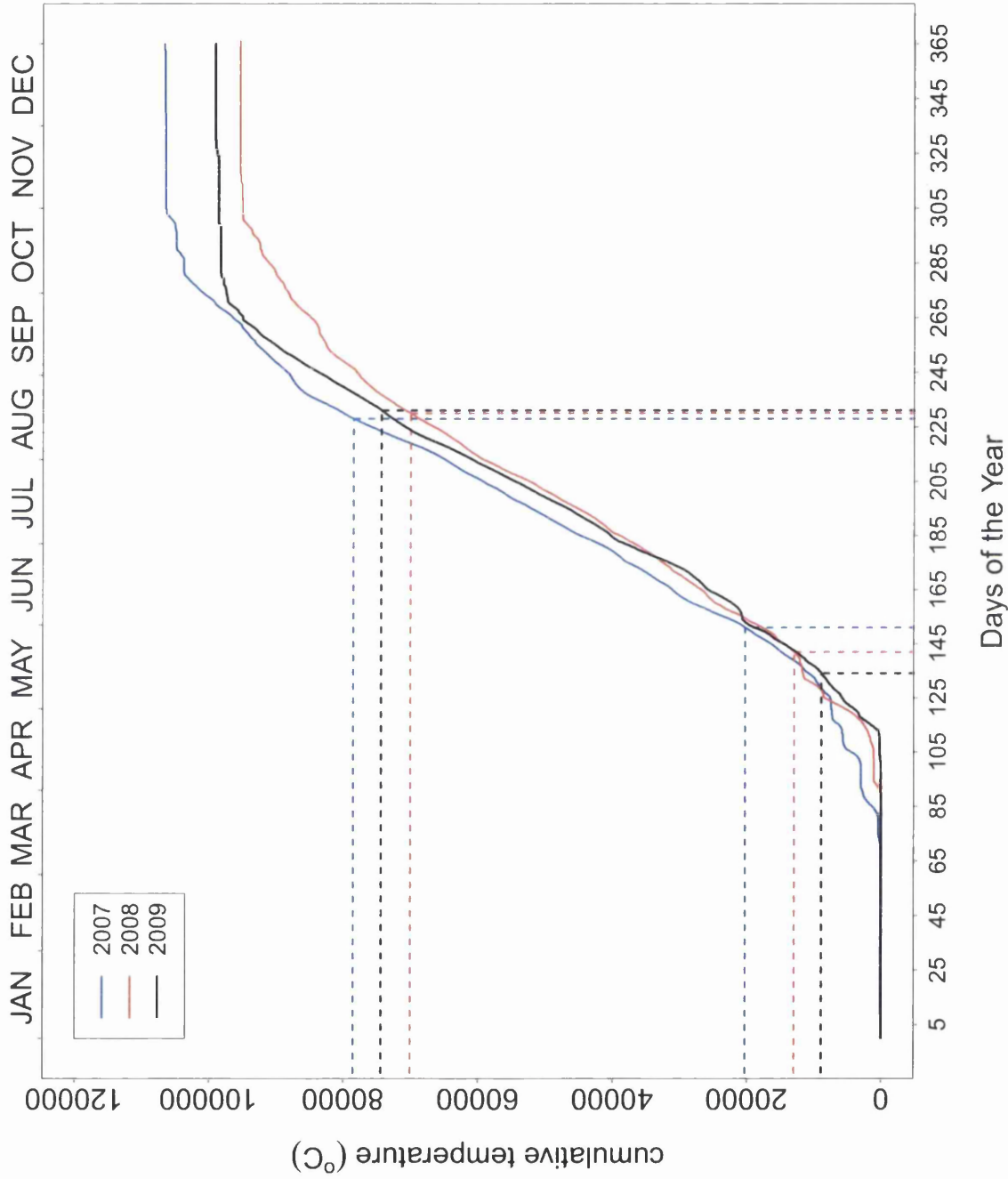
Figure 4.54: *Cumulative temperature (°C) at Hyytiälä for 2007 (blue solid line), 2008 (red solid line) and 2009 (black solid line). The vertical and horizontal dashed lines represent the values of cumulated temperature met during the days for onset and cessation estimated by microcore measurements for each year with the same colour pattern.*
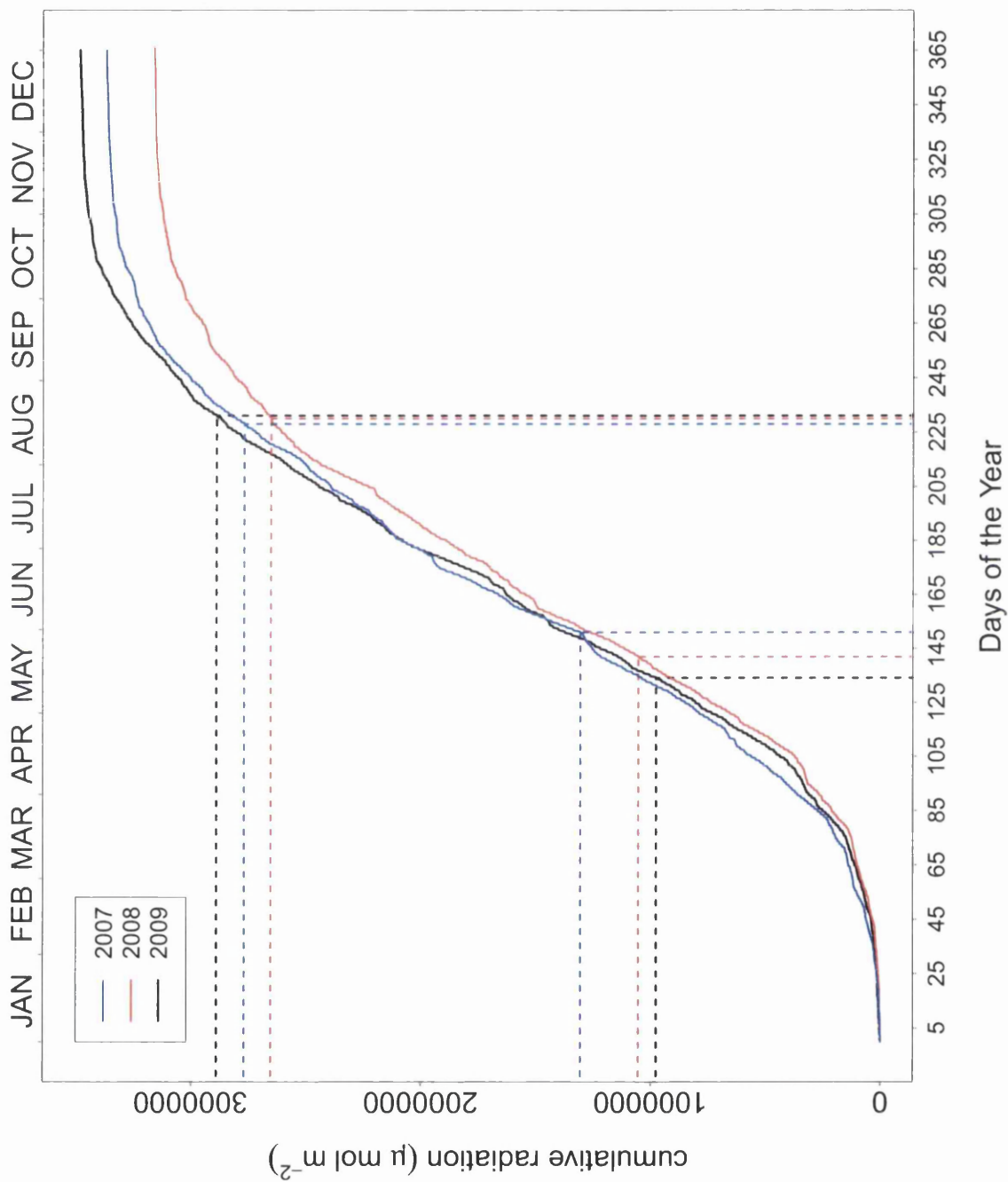
Figure 4.55: *Cumulative PAR (μmol m^{-2} s^{-1}) at Hyytiälä for 2007 (blue solid line), 2008 (red solid line) and 2009 (black solid line). The vertical and horizontal dashed lines represent the values of cumulated PAR met during the days for onset and cessation estimated by microcore measurements for each year with the same colour pattern.*

4.3.6 Comparison of the performance of the methods to estimate radial growth onset and cessation

The use of different types of dendrological records to assess wood growth formation at Hyytiälä does not provide a similar selection of dates for onset and cessation. When running a Wilcoxon rank-sum test on the two sets of dates, they are significantly different from each other for both onset and cessation (p value < 0.01). The growing season is longer when using dendrometer records with earlier onset dates and later cessations.

To compare the different methods predicting radial growth, Table 4.23 lists the estimated dates of onset and cessation for each method and study site. The use of NEE and evapotranspiration fluxes to predict wood growth has been tested at Hyytiälä and does not show a good potential. It is then likely that wood growth cannot be directly linked to carbon and water fluxes over the canopy at this study site. It appears that the two approaches using PAR provide closer matches to the dates for growth onset and cessation estimated by the dendrological information. While the smoothing splines method seem more accurate with growth onset dates, it is not able to produce cessation dates. Moreover, this method requires the highest data quality for PAR to be trustworthy. The use of gapfilling when this quality is not met (data gaps) can result in additional uncertainties if performed during the critical period for onset and cessation dates determination. The cumulated PAR method has the advantage of being able to provide both onset and cessation dates. It also seems more robust when only few missing data points are present but will still provide inaccurate date estimate when data gaps are occuring during the potential period for onset or cessation of wood growth. However, using the smoothing splines method or the cumulated method provide significant differences in the dates of growth onset (Wilcoxon rank-sum test, p value < 0.01).

Finally, using the 10 °C temperature threshold or the 435 μmol m^{-2} s^{-1} PAR threshold to build the onset dates using microcore measurements does not make significant differences (Wilcoxon non parametric test, p value = 0.45). Therefore, three sets of onset dates and two sets of cessation dates can be tested to provide the best wood growth estimate for climate correlation.

Table 4.23: *Onset and cessation dates estimated via the different methods tested in this study. Dates followed by (D) are estimated via dendrometer measurements or (M) via microcore measurements*

Hyytiälä

Year	Dendrometers	Microcores	NEE method	ET method	Recurrent Environment	Cumulative variables
Onset (DOY)						
2007	125	151	82	107	125 (D) 151 (M)	108 (D) NA (M)
2008	120	142	93	97	120 (D) 141 (M)	119 (D) NA (M)
2009	115	134	104	110	115 (D) 132 (M)	114 (D) NA (M)
Cessation (DOY)						
2007	210	228	291	262	NA (D) 246 (M)	223 (D) NA (M)
2008	235	230	294	275	NA (D) 244 (M)	235 (D) NA (M)
2009	220	231	286	260	NA (D) 259 (M)	219 (D) NA (M)

Norunda

Year	Dendrometers	Microcores	NEE method	ET method	Recurrent Environment	Cumulative variables
Onset (DOY)						
2010	105	NA	NA	NA	139	119
2011	107	NA	NA	NA	NA	NA
Cessation (DOY)						
2010	265	NA	NA	NA	NA	238
2011	265	NA	NA	NA	NA	NA

Loobos

Year	Dendrometers	Microcores	NEE method	ET method	Recurrent Environment	Cumulative variables
Onset (DOY)						
2009	105	NA	NA	NA	104	106
2010	107	NA	NA	NA	103	106
Cessation (DOY)						
2009	265	NA	NA	NA	NA	261
2010	265	NA	NA	NA	NA	267

4.3.7 Inter-site variability of the growing season properties

When using the dendrometer records to provide growth dates and then extend the period of study to 1997-2009 by using PAR thresholds, the three sites can be compared in terms of estimated onset and cessation of wood growth. The onset dates at Hyytiälä are found to be significantly similar to onset dates at Loobos while Norunda dates are significantly greater than at the two other study sites (Wilcoxon rank-sum test, p value < 0.01). However, when using the cumulated PAR approach, the onset dates at Hyytiälä are found to be significantly similar to onset dates at Norunda while onset dates at Loobos are significantly set earlier than at the two other study sites (Wilcoxon rank-sum test, p value < 0.01). This result appears to be in better agreement with the expectation that the climate at Loobos is being more permissive for growth and would allow earlier dates of growth onset. Therefore, only this set of dates will be used further for dendrometers measurements.

For cessation dates, a symmetric response can be observed at Hyytiälä and Norunda cessation dates being significantly greater than the dates at Loobos (Wilcoxon rank-sum test, p value < 0.01). This pattern also seems in better agreement with the weather observations that show earlier drops in temperature at northern locations while Loobos shows higher temperature longer during autumn. Therefore, the growth formation dates obtained by the cumulated PAR in better agreement with the expectation that weather forcing is stronger in northern latitudes and act by limiting the growing period at both onset and cessation dates.

4.3.8 Summary

The use of different methods to estimate the occurrence of radial growth onset and cessation produced a range of dates that have been statistically tested (Section 4.3.6). The use of fluxes to determine the growing season detects the start of the photosynthetic activity and not the radial wood increment. By using a method based on temperature and PAR thresholds, the estimated dates were closer to those found by using the dendrological measurements. However, the limited period of time where dendrological data are available at the study sites does not permit to conclude on the accuracy of this method. Despite the uncertainties on its precision, this method is selected to produce the dates of wood formation, permitting to estimate radial growth at each site. The selected wood growth dates by the cumulated PAR method present a pattern where generally Hyytiälä and Norunda show late onset and early cessation compared to Loobos which seems to agree with the weather forcing expectations. When using microcore records,

a statistically different set of wood growth dates have been produced, it is then possible to carry out the climate analysis on both sets at Hyytiälä to observe if matching weather at the inter-annual and intra-annual scale will correlate better using a particular type of wood growth information.

4.4 Using the Gompertz equation to Model the rate of wood growth

The Gompertz model developed by Rossi *et al.* (2003) to model cell number increase, estimate rate of growth and periods of cell differentiation was adapted in this study to predict wood growth during years when dendrological information are unavailable. For that purpose, the Gompertz model was constrained by using the number of isotope measurements as the maximum growth limit while estimated onset and cessation dates were used to delimit the period of growth. The Gompertz equation is then run with fixed parameters to obtain a growth curve that can be used to match isotope values with a date of wood formation. The evolution of the growth rate through the year shows a first period with no growth before the estimated date for the growing season onset, followed by a short period with a slow increase in the rate of growth until the Gompertz curve reaches its maximum rate for the centre period of the growing season. Finally, the rate of growth is slowly decreasing in the second part of the growing season until it reaches the estimated cessation date where the growth decreases again to zero for the winter period (Studhalter *et al.*, 1963). Therefore, the distance between two dates of wood formation is greater at the beginning and at the end of the growth period while the central period is characterised by rapid growth and greater distance in days between two isotope measurements. When matching weather and isotope time series on the same scale, the integration of climate information will be then occurring on different time spans depending on the position of the isotope values in the tree-rings.

When comparing the Gompterz fit with the initial wood increment measurements at the study sites, the Gompertz method does not always fit perfectly the dendrological data. For microcore mesurements, when comparing both the fitted Gompertz curve and the dendrological information in percentage of growth, the Gompertz curve fits quite well the microcore measurements during 2009 at Hyytiälä (Figure 4.56). The curve is nearly always within the confidence intervals represented by the standard deviation from the mean measurements calculated over the four trees analysed for cell growth. However, during 2007 and 2008, the

Gompertz fit is less accurate. For 2008, the first five values are correctly fitted but the following observations do not follow a similar slope with a decrease in growth rate and cause the Gompertz curve to overestimate the percentage of growth in the central period of the growing season until it reaches DOY 216 where the data points and the Gompertz curve start again to be similar (Figure 4.57). The worst adjustment occurs during 2007 with the Gompertz curve underestimating wood growth during the first microcore measurements until DOY 176 where the fit will then overestimate wood growth until DOY 215 when the fit starts finally to be satisfying for the last measurements (Figure 4.58). For dendrometer measurements, the Gompertz curve fitted to the wood growth of 2009 overestimate the rate of growth between DOY 135 to DOY 185 (Figure 4.59). However, growth during year 2008 is correctly fitted by the Gompertz procedure (Figure 4.60). A mismatch between the Gompertz curve and the dendrometer records during 2007 seems to occur essentially due to an earlier onset date estimated via the method of cumulated PAR (DOY 108 instead of DOY 125) (Figure 4.61). However, if the Gompertz curve is shifted to the true onset location, the rate of growth is correctly predicted.

Therefore, the procedure adopted to predict wood growth seems not to always provide the best estimate of growth rate and the determination of wood growth. However, it is noticeable that if all years were recorded with dendrological information, it would be possible to fit correctly the Gompertz function according to the wood growth properties. It is then not the Gompertz method that fails to predict wood growth but the procedure to obtain realistic onset and cessation dates via the available dendrological data for each year by using common environmental characteristics occuring during these events. Therefore, the procedure proposed in this work provides an approximate technique to characterise wood growth when dendrological data are absent leaving scope for further improvements. The consequences to such deviation between modeled wood growth and the dendrological measurements are that weather variables and isotope measurements will be mismatched when the relationship between these time series will be assessed and therefore may cause a lower degree of fit than expected between climate forcing and isotope variation.
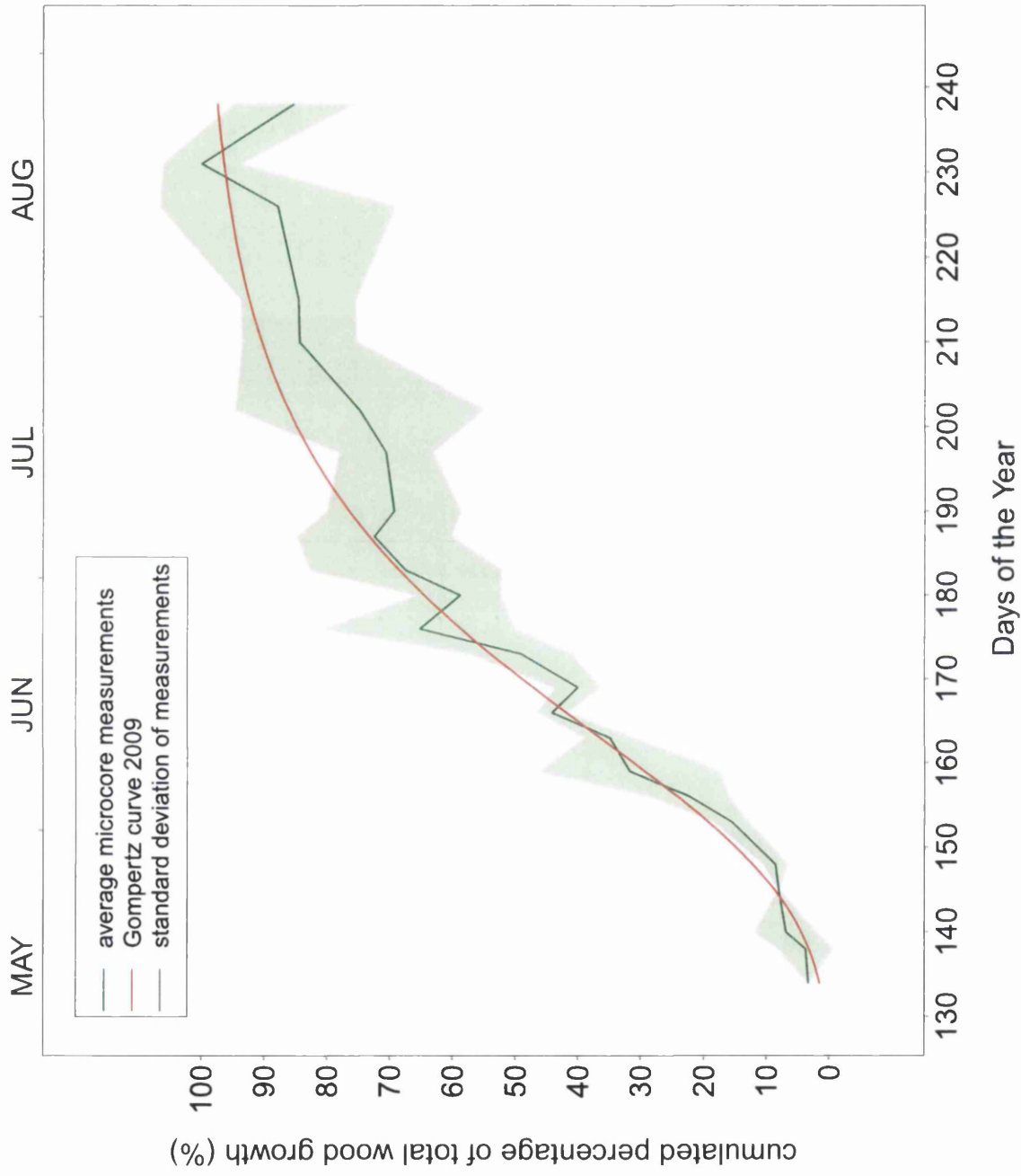
Figure 4.56: *Microcore measurements at Hyytiälä for 2009 expressed in cumulated percentage of total wood growth (green line) with confidence intervals (standard deviation) for each measurement. The Gompertz curve (red solid line) is fitted with the estimated growth onset and cessation dates.*
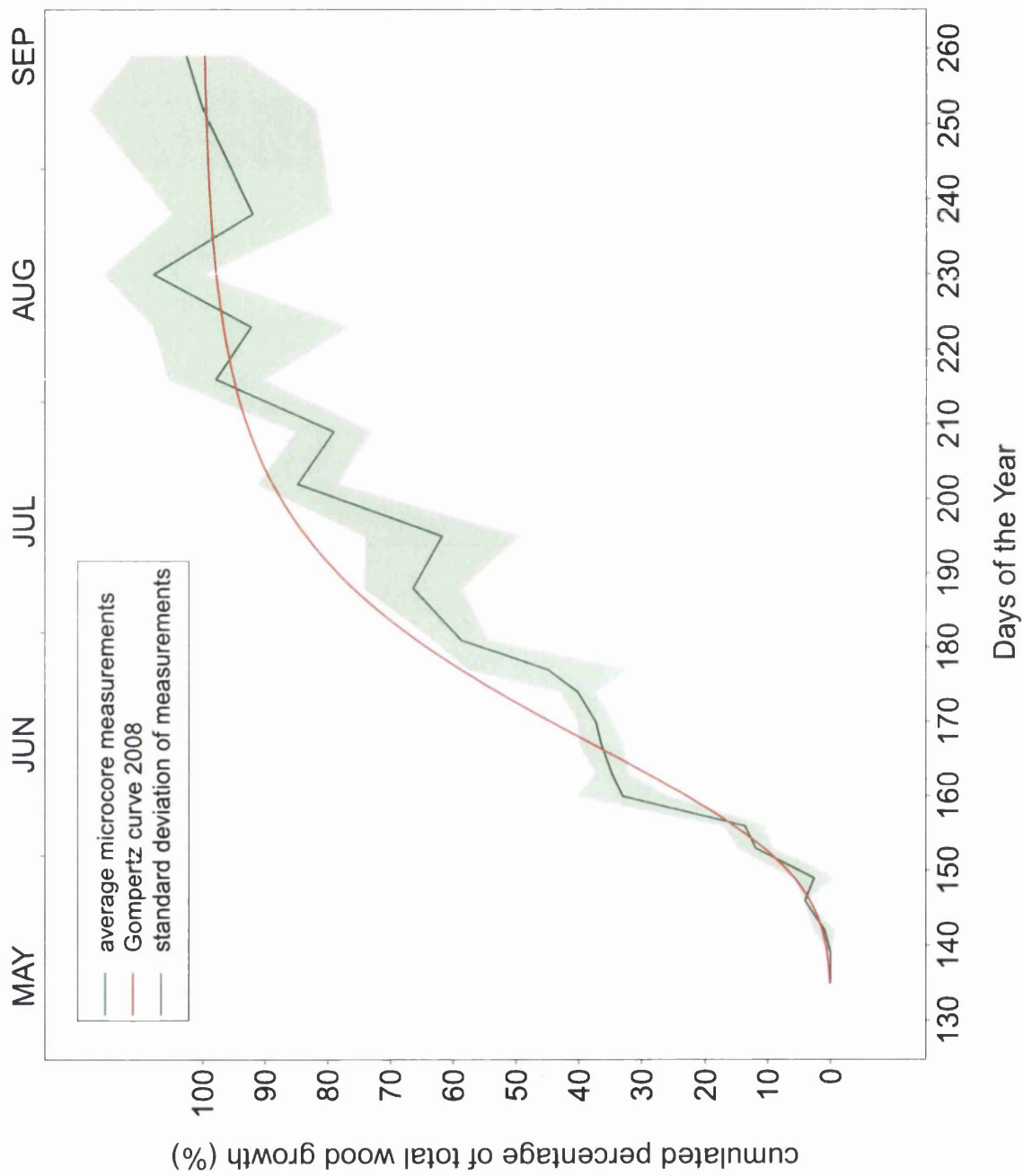
Figure 4.57: *Microcore measurements at Hyytiälä for 2008 expressed in cumulated percentage of total wood growth (green solid line) with confidence intervals (standard deviation) for each measurement. The Gompertz curve (red solid line) is fitted with the estimated growth onset and cessation dates.*
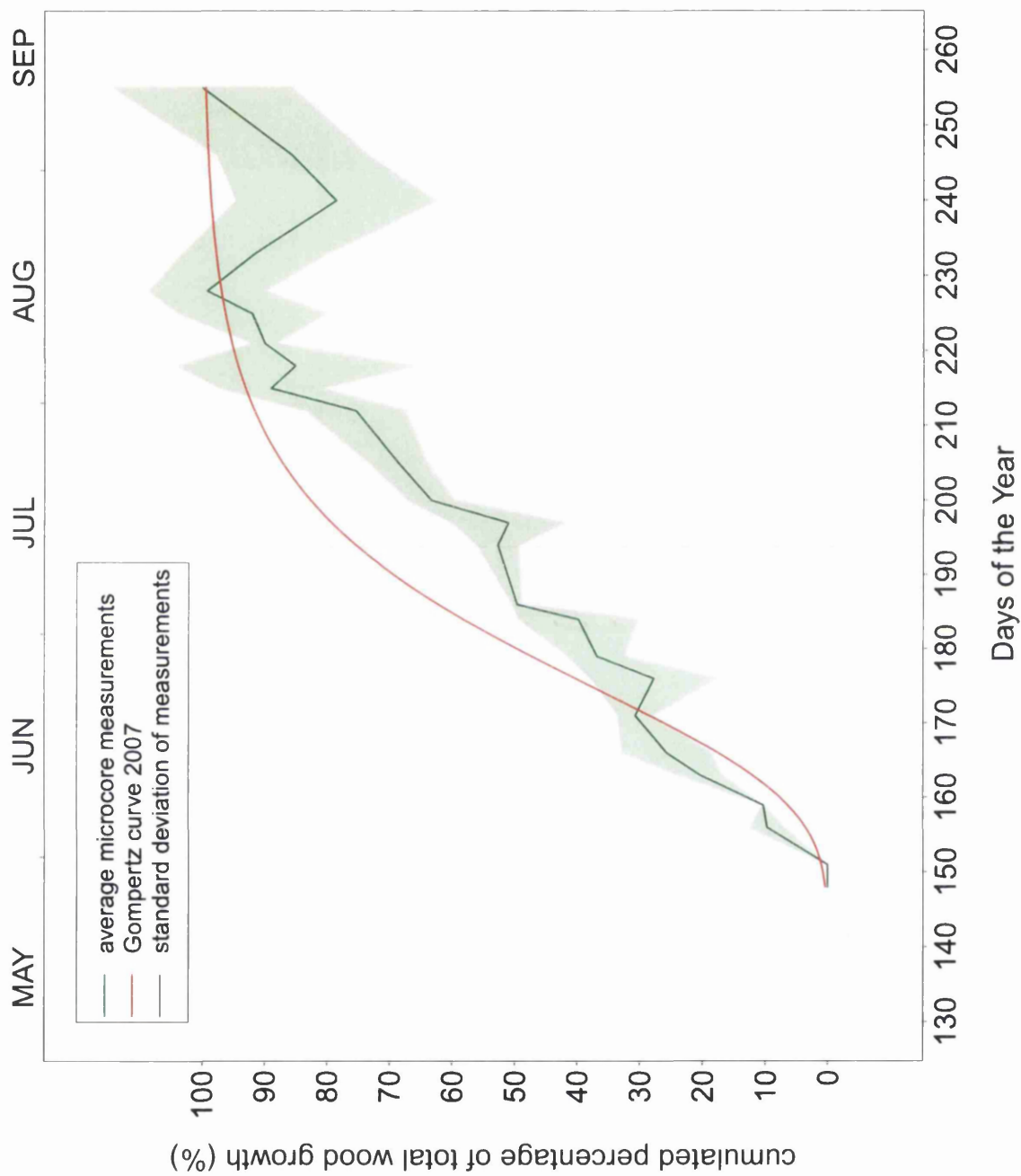
Figure 4.58: *Microcore measurements at Hyytiälä for 2007 expressed in cumulated percentage of total wood growth (green solid line) with confidence intervals (standard deviation) for each measurement. The Gompertz curve (red solid line) is fitted with the estimated growth onset and cessation dates.*
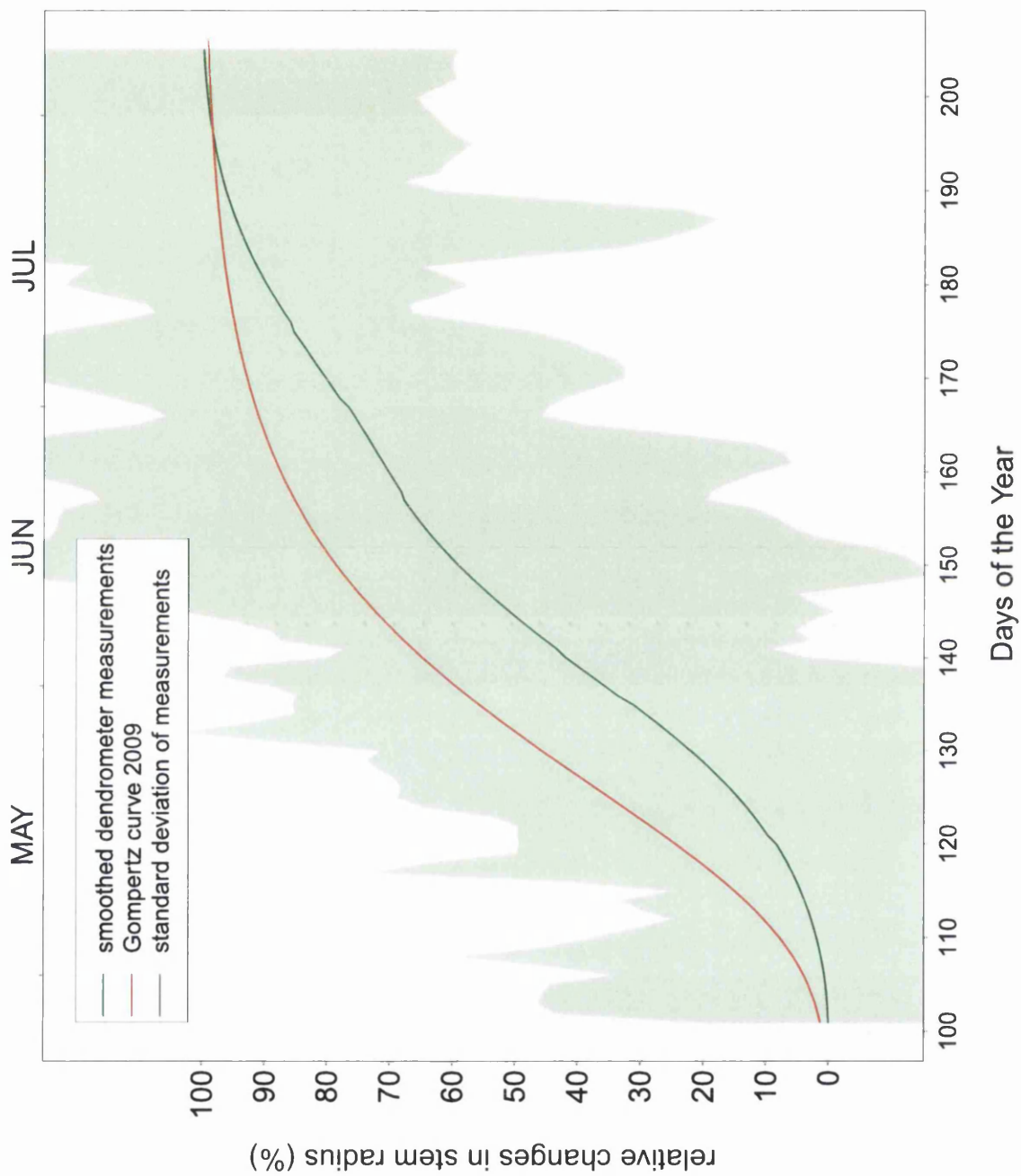
Figure 4.59: *dendrometer measurements at Hyytiälä for 2009 expressed in relative stem radius (green solid line) with confidence intervals (standard deviation) for each seven days of growth. The Gompertz curve (red solid line) is fitted with the estimated growth onset and cessation dates.*
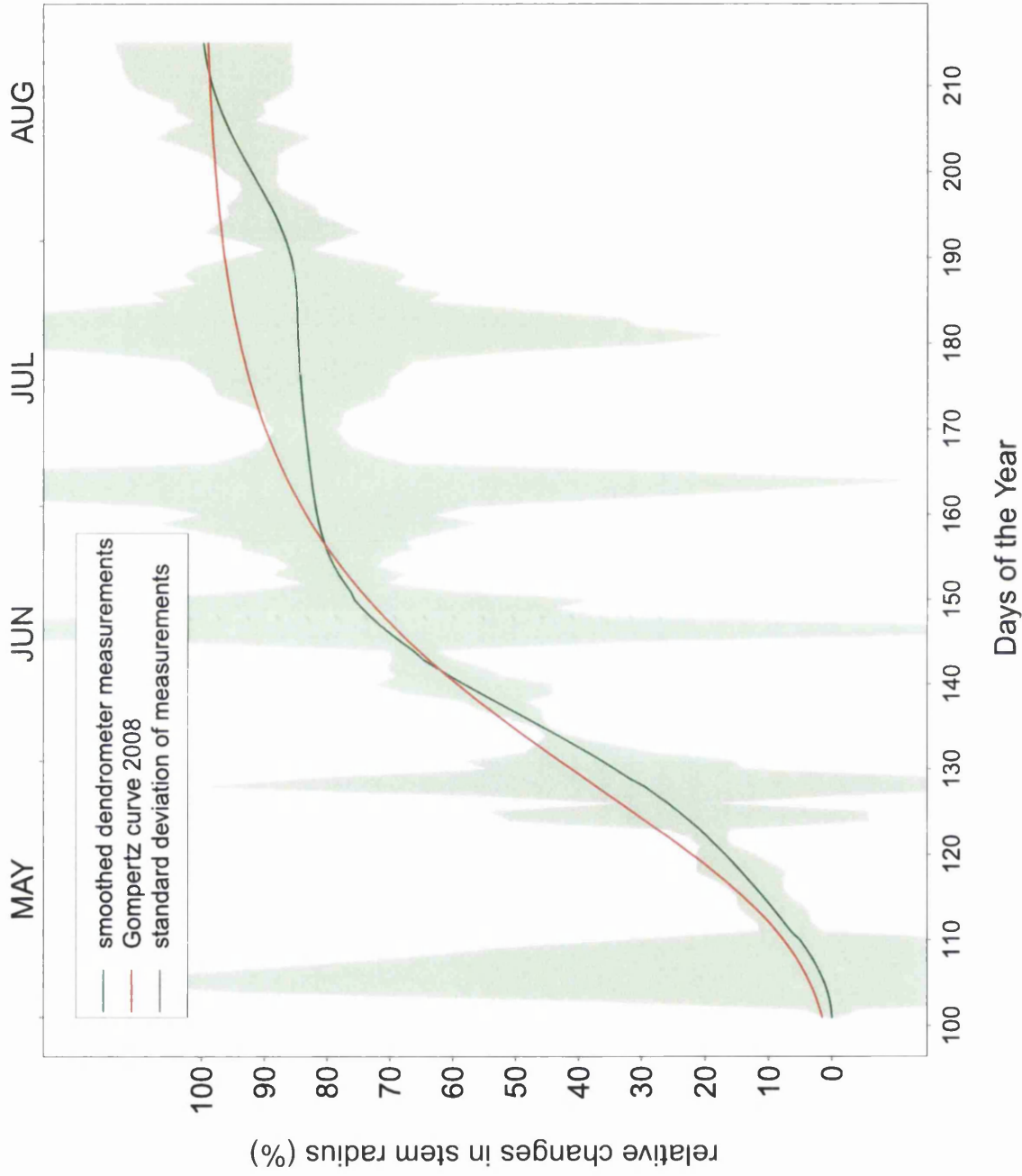
Figure 4.60: *dendrometer measurements at Hyytiälä for 2008 expressed in relative stem radius (green solid line) with confidence intervals (standard deviation) for each seven days of growth. The Gompertz curve (red solid line) is fitted with the estimated growth onset and cessation dates.*
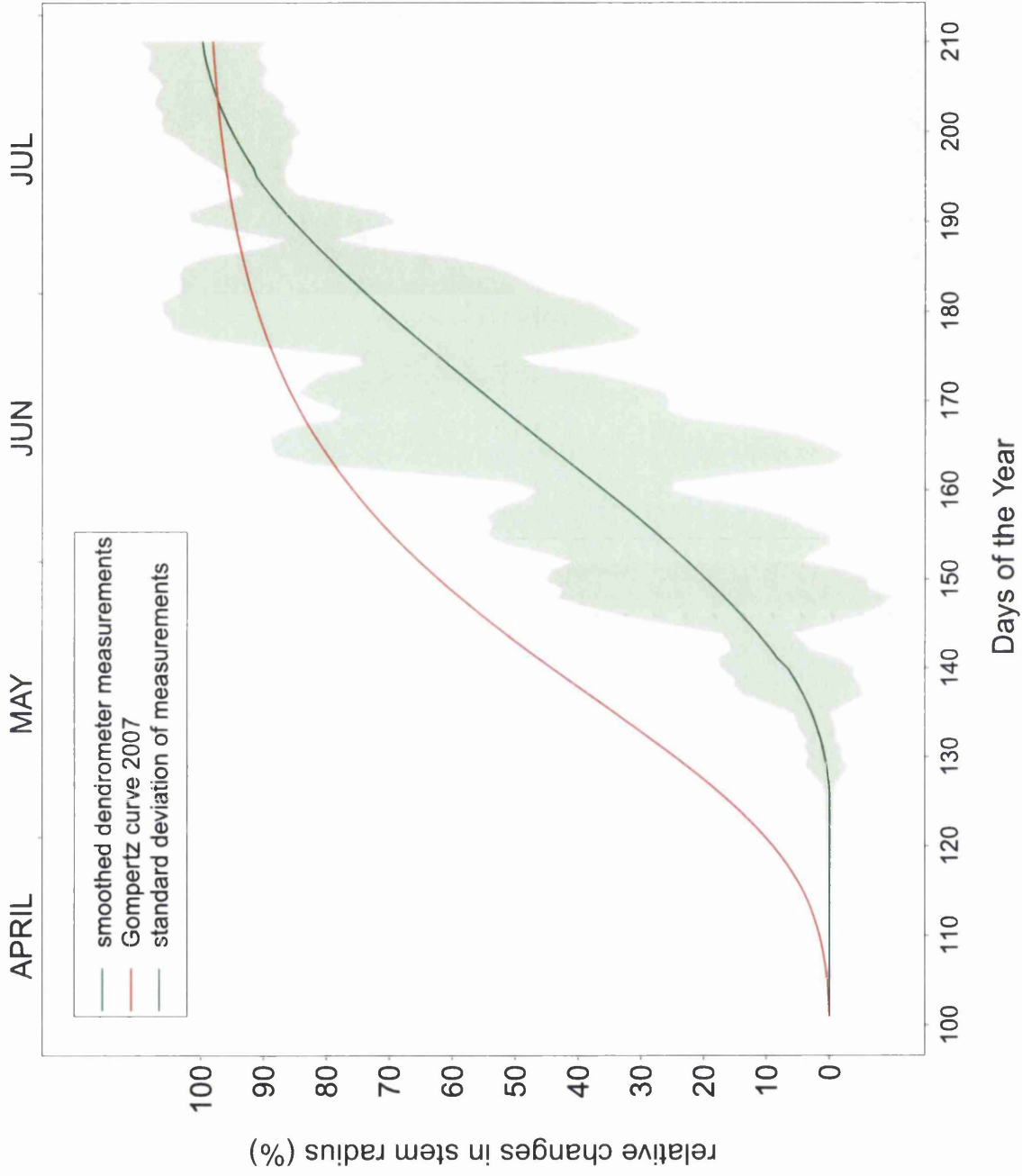
Figure 4.61: *dendrometer measurements at Hyytiälä for 2007 expressed in relative stem radius (green solid line) with confidence intervals (standard deviation) for each seven days of growth. The Gompertz curve (red solid line) is fitted with the estimated growth onset and cessation dates.*

4.5   Cell life time

The final consideration to characterise wood growth properties is to possibly include the duration of the wood cell life in the procedure to match weather variables with isotope measurements. As proposed by Schollaen *et al.* (2014), wood cells can integrate climate information over a variable period after the formation of cells which should match the time when the cells are alive and active. Therefore, a theoretical time of life when cells will be affected by weather variation can be estimated by using the wood properties. It is known that wood cells live a different time span depending on their position in the tree-rings due to the transition from soft and short living earlywood cells to hard and long living latewood cells. The range of variation proposed by Schollaen *et al.* (2014) starts from five days of cell life for the earliest cells to 50 days for the last latewood cells with a regular increment during the growing season. This current study will use these suggestions to test if the life span of cells influences the integration of climate forcing in isotope time series. Figure 4.62 shows a possible evolution of the tree cell life span during an average year of growth and the quantity of days that will be used to integrate weather information against the relative wood growth in percentage. To analyse the effect of the addition of cell life time in the evaluation of the relationship between isotope time series and climate forcing, the integration of weather variables will be performed both with and without the additional life time generated by this method.
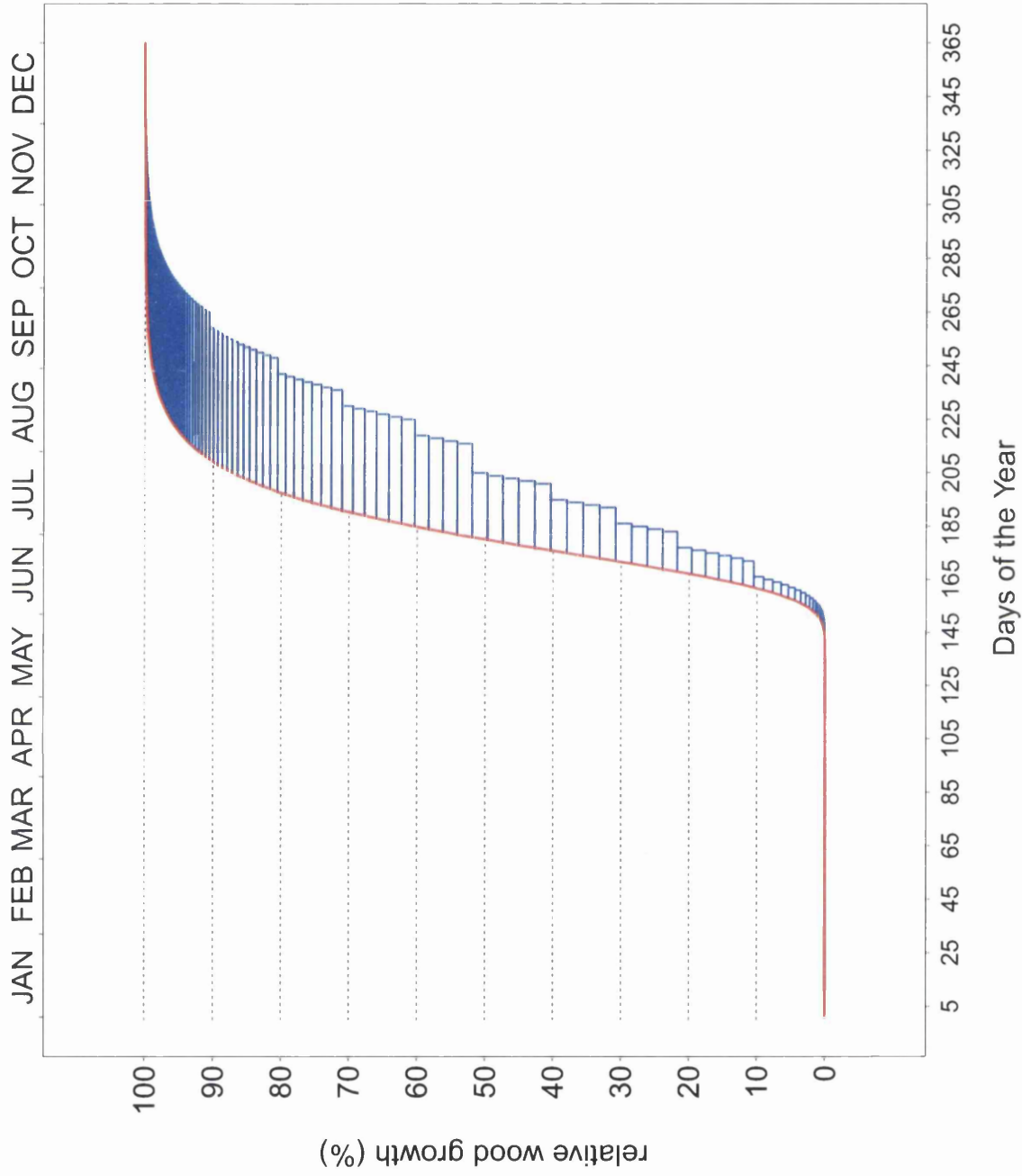
Figure 4.62: *Evolution of the additional integration period for weather forcing due to cell life time by percentage of growth (blue bars) applied at a Gompertz curve (red line) for a typical year of growth at Hyytiälä.*

4.6 Conclusion

By normalising dendrological measurements, two different sets of dates for onset and cessation of wood growth have been produced. Dendrometer measurements present at the three study sites can serve to obtain comparable growth information while microcore measurements only present at Hyytiälä record the cell number increase and provide a different set of onset and cessation dates. Different methods have been tested to predict wood growth in the absence of dendrometer measurements with better results found when cumulating PAR and determining thresholds values for onset and cessation events. However, for microcore measurements only a combination of smoothed PAR and temperature can be used to estimate wood growth, but with questionable confidence. The fit of the Gompertz curve to each year of wood growth is not optimal when using estimated dates of onset and cessation and would benefit from improvements in the determination of wood growth. Consequently, the match between weather variables and isotope measurements on the same time scale can be impaired by non representative growth rates during the growing season. Finally, the consideration of implementing cell life time has been described to increase the integration period of weather information for each isotope measurement with the addition from 5 to 50 days depending on the position of isotope measurements in the tree-ring width. Chapter V will present the correlation between the weather variables and the isotope measurements at the inter-annual resolution depending on the onset and cessation dates estimated via dendrometers or microcores and the inclusion of cell life time in the integration period of weather information.

Chapter V : Linear relationships between weather and isotope measurements at the inter-annual resolution

5.1 Introduction

The carbon stable isotope time series show seasonal variations that contain a climatic signal of past weather change. By matching the weather information with the stable carbon isotopes at the inter-annual resolution, it is possible to evaluate the validity of the dates chosen to delimit the wood growth period. Therefore, both set of dates built from dendrometer and microcore measurements will be used to match weather information to isotope values. It is expected that a stronger relationship will be present if the growing season selection is more accurate which will help determine if the use of a particular set of dates provide a more realistic match between weather and $\delta^{13}C$ time series. Addition of cell life time in the integration period for weather information will also be evaluated. The potential improvement of the strength of the relationship between weather variables and $\delta^{13}C$ may indicate that the cell life time theory is worth applying when matching weather information to $\delta^{13}C$ values. Finally, the influence from the combination of light, temperature and precipitation will be assessed by a multiple linear regression.

This chapter will present:

- the relationship between weather variables and stable carbon isotopes at the inter-annual resolution;

- the effect of cell life time addition in the integration of weather information;

- the use of a multiple linear regression model combining the three tested weather variables to interpret the stable carbon isotope variation at the inter-annual scale.

5.2 Correlation of weather variables at Hyytiälä at the inter-annual resolution

5.2.1 δ^{13}C time series over the period of wood growth estimated by using dendrometer measurements

5.2.1.1 Simple linear regression between δ^{13}C time series and weather variables

To compare weather variables with stable carbon isotope time series at the annual resolution, the annual weather values are integrated over the full wood growth period estimated using the method presented in Chapter IV. For temperature and PAR, the annual values represent the average of temperatures or PAR values met during the growing season, while for precipitation they represent the sum of millimetres of rain that has fallen during the growing season. The use of linear regressions present a simple approach to model the relationship between weather variables (independent) and δ^{13}C time series (dependent variable) and to determine causality.

At Hyytiälä, when dates from dendrometer measurements are used to build a growing season dataset, the relationships between δ^{13}C time series at the annual resolution and both temperature or PAR are low and not significant (p value > 0.05). However, with precipitation, the linear regression shows a significant and negative fit with the annual δ^{13}C values ($R^2 = 0.47$, p value < 0.05). Therefore, the only significant linear fit is obtained with precipitation when using growing season dates estimated via dendrometer measurements at the annual resolution (figure 5.63).

When integrating the cell life time period to the match between δ^{13}C time series and the weather variables, the linear regression scores change drastically. Both temperature and PAR linear regressions become significant and show a positive linear relationship with a R^2, respectively, equal to 0.51 and 0.52 (p value < 0.05). However, the regression with precipitation decreases in intensity while still being significant ($R^2 = 0.37$, p value < 0.05). Therefore, including the cell life time period when matching weather and isotope values provides potentially a better linear fit than without (figure 5.64). As all three weather variables are significant in the linear single relationship with annual δ^{13}C time series, a multiple linear regression from these variables may be built to evaluate if δ^{13}C values would be better predicted by the combination of all three weather variables.

Figure 5.63: *Left: Inter-annual comparison between $\delta^{13}C$ (black open circles), temperature (red open circles), PAR (green open circles) and precipitation (blue open circles) for the period 1997-2009 at Hyytiälä (dendrometer measurements). Right: The linear regression with the adjusted R^2 value and p value.*

Figure 5.64: *Left: Inter-annual comparison between $\delta^{13}C$ (black open circles), temperature (red open circles), PAR (green open circles) and precipitation (blue open circles) with cell life time at Hyytiälä (dendrometer measurements). Right: The linear regression with the adjusted R^2 value and p value.*

5.2.1.2 Multiple linear regression fit between $\delta^{13}C$ time series and weather variables

When building a multiple linear regression based on the three weather variables (temperature, PAR, precipitation) as explanatory factors by using forward step-wise regression, the linear adjustment between measured $\delta^{13}C$ time series and the modelled $\delta^{13}C$ time series is reasonably large ($R^2 = 0.51$, $p < 0.05$) at the inter-annual level (Figure 5.65). However, the increase of fit from the combination of the three variables is only slightly better than with the single regression with precipitation only ($R^2 = 0.47$, $p < 0.05$). This is due to the fact that the single linear regressions with temperature and PAR are not significant. Using the Akaike information criterion (AIC) to compare models based on the combination of the three selected variables (Table 5.24) shows a minimum value of AIC obtained when having temperature, PAR and precipitation in the multiple linear model predicting the inter-annual $\delta^{13}C$ variation. Therefore, this criterion-based method suggests that a model based on the three variables is justified when predicting $\delta^{13}C$.

When using the weather variables integrated with the cell life time period, the fit of the multiple linear model increases compared to the model without cell life time ($R^2 = 0.71$, $p < 0.05$) and provides a better fit than with the single linear regressions (figure 5.66). The Akaike information criterion suggests that a model based on precipitation only is the best in terms of balance between model size and the number of parameters used to predict the $\delta^{13}C$ variation. However, the adjusted R squared is the highest when using the three variables in the multiple linear regression for the cost of a small increase in AIC.

Table 5.24: *Akaike's information criterion (AIC) for each variable and variable combination in a multiple linear regression model at Hyytiälä for the period 1997-2009 when dendrometer measurements are used to estimate the growing season with and without cell life time (CLT).*

Variables	AIC without CLT	AIC with CLT
Temperature	17.12	26.00
PAR	20.14	24.82
Precipitation	20.35	18.20
Temperature & PAR	15.00	25.42
Temperature & Precipitation	16.74	19.28
PAR & Precipitation	15.97	20.08
Temperature & PAR & Precipitation	14.25	21.16
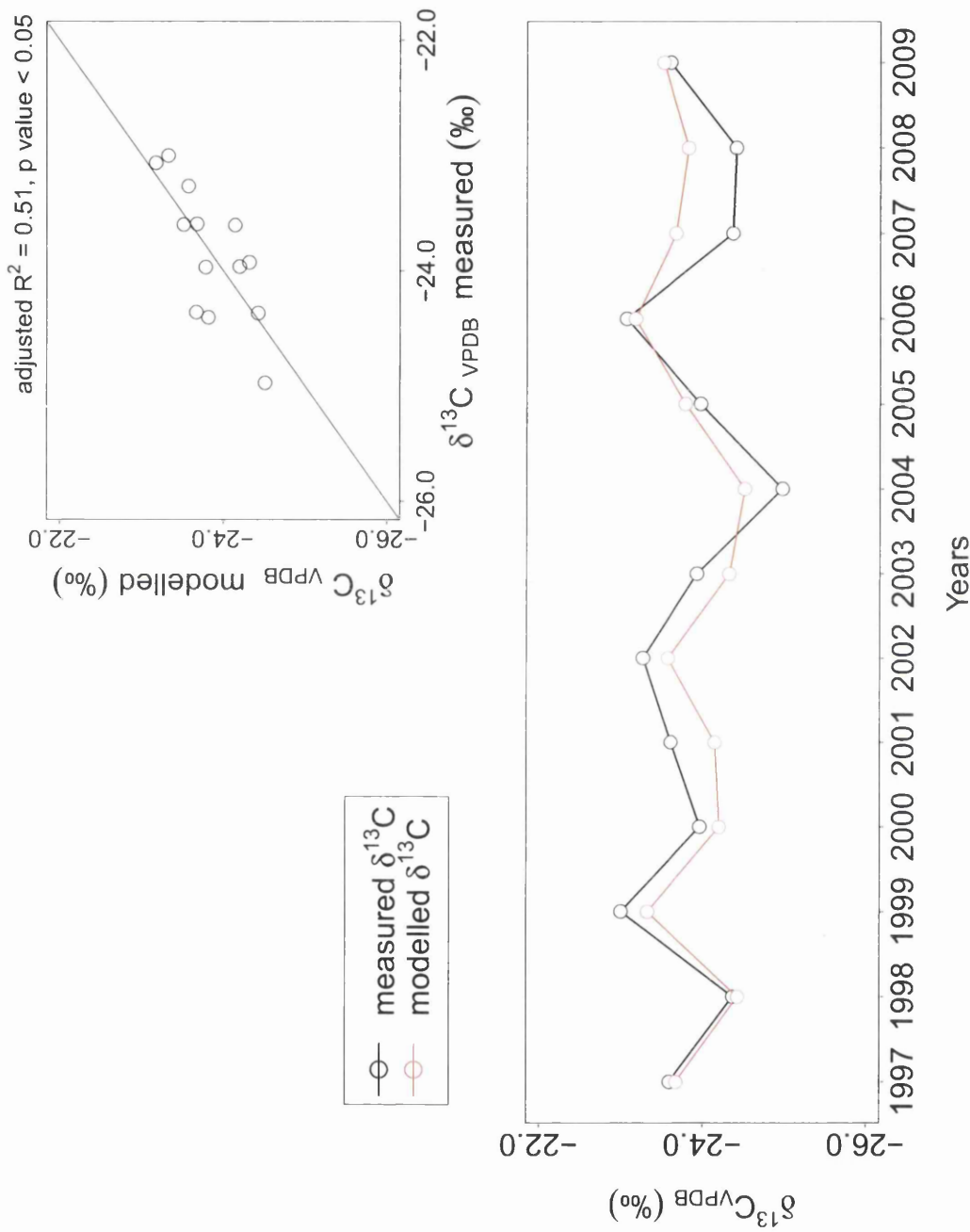
Figure 5.65: *Inter-annual comparison between measured $\delta^{13}C$ (black open circles) and modelled $\delta^{13}C$ (orange open circles) time series for the period 1997-2009 at Hyytiälä by using a multiple linear regression including temperature, PAR and precipitation as explanatory factors to the measured $\delta^{13}C$ variation (dendrometer measurements). The topright panel shows the linear behaviour between the measured and modelled $\delta^{13}C$ values with the adjusted R^2 value and p value.*
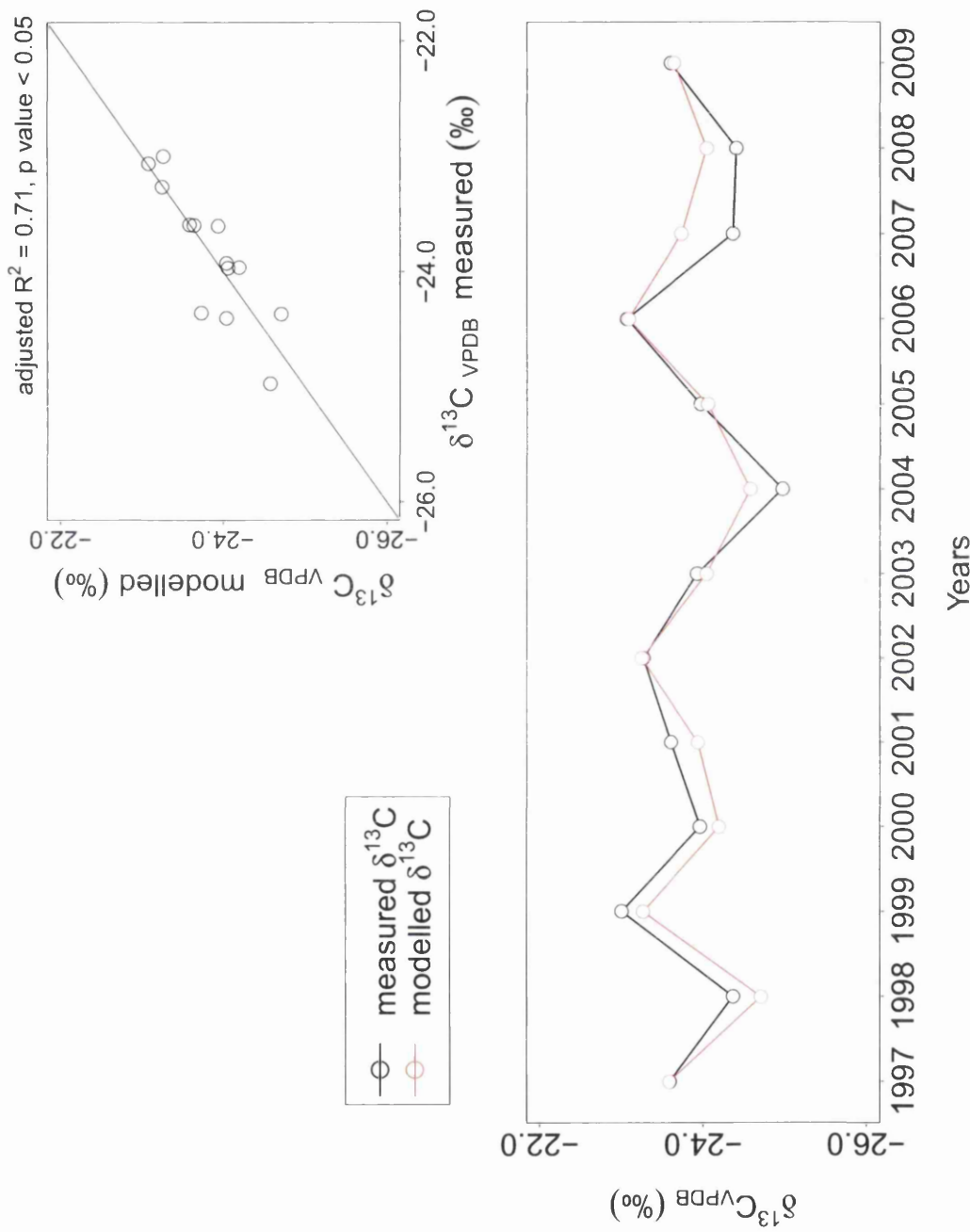
Figure 5.66: *Inter-annual comparison between measured $\delta^{13}C$ (black open circles) and modelled $\delta^{13}C$ (orange open circles) when adding cell life time at Hyytiälä by using a multiple linear regression including temperature, PAR and precipitation as explanatory factors to the measured $\delta^{13}C$ variation (dendrometer measurements). The topright panel shows the linear behaviour between the measured and modelled $\delta^{13}C$ values with the adjusted R^2 value and p value.*

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5.2.2 δ^{13}C time series over the period of wood growth estimated by using microcore measurements

5.2.2.1 Simple linear regression between δ^{13}C time series and weather variables

Similar to the previous section, an analysis of the influence of each single weather variable on annual δ^{13}C time series can be carried out when using the microcore measurements to predict the growing season at Hyytiälä. The fit suggested by the R^2 value shows great differences with the regression obtained using the dendrometer estimated growth dates. Temperature still does not presents a significant relationship with the annual δ^{13}C values but the relationship with PAR becomes strong ($R^2 = 0.73$, $p < 0.05$) while the precipitation that was previously reasonably large ($R^2 = 0.47$, $p < 0.05$) turns not significant. Therefore, the method chosen to estimate the growing season extent influences greatly the results from the single linear regressions between δ^{13}C time series and weather variables (figure 5.67).

When including the cell life time integration period for the weather variables, the results of the single linear regressions change to having a significant relationship with temperature ($R^2 = 0.25$, $p < 0.05$) with also a decrease in the fit with PAR ($R^2 = 0.51$, $p < 0.05$). However, the precipitation linear regression remains not significant. Therefore, applying the cell life time theory seems to improve the relationships for not significant variables but decreases the fit when a variable already possesses a strong relationship with the annual δ^{13}C values (figure 5.68).

Figure 5.67: *Left: Inter-annual comparison between $\delta^{13}C$ (black open circles), temperature (red open circles) and precipitation (blue open circles) at Hyytiälä (microcore measurements). Right: The linear regression with the adjusted R^2 value and p value.*
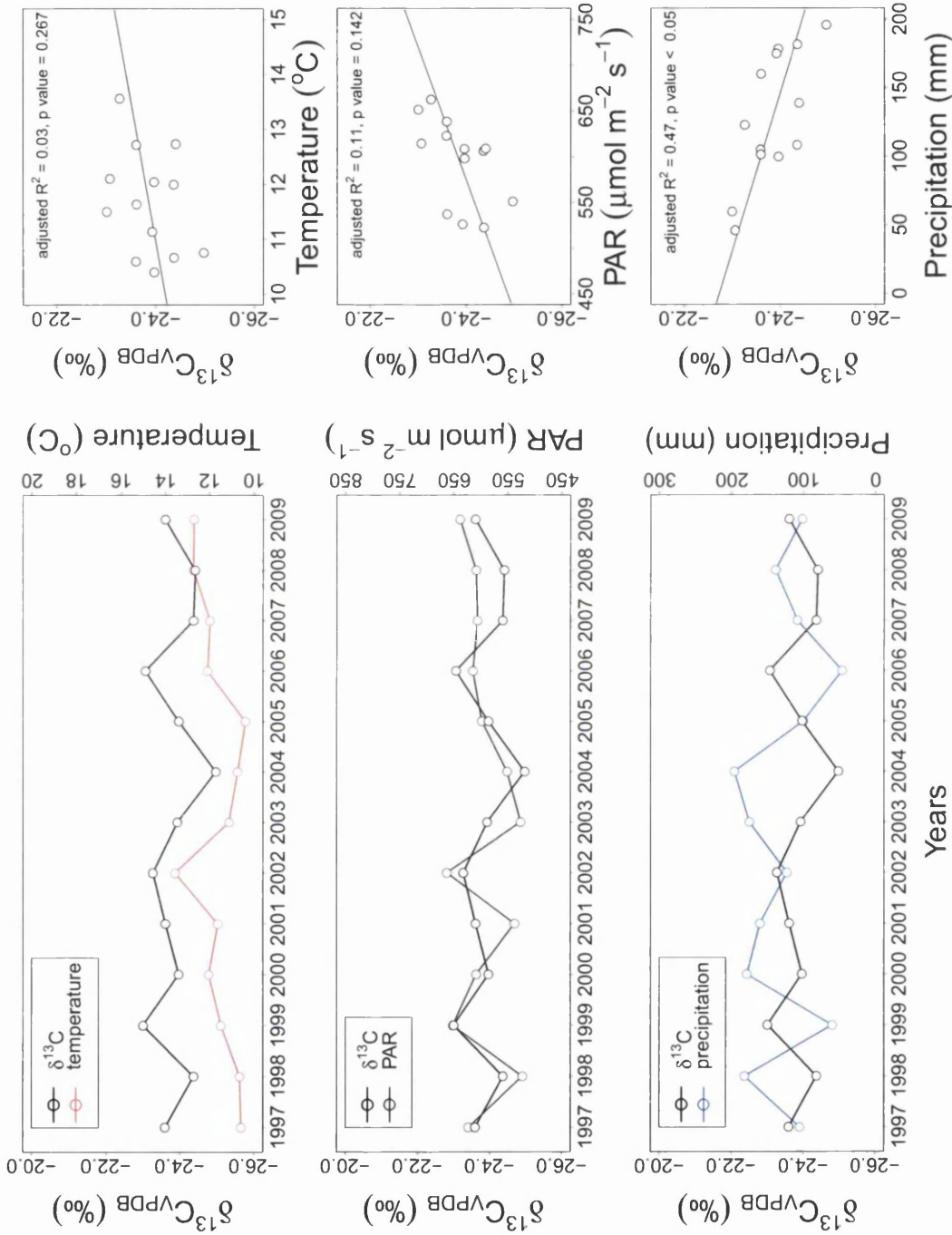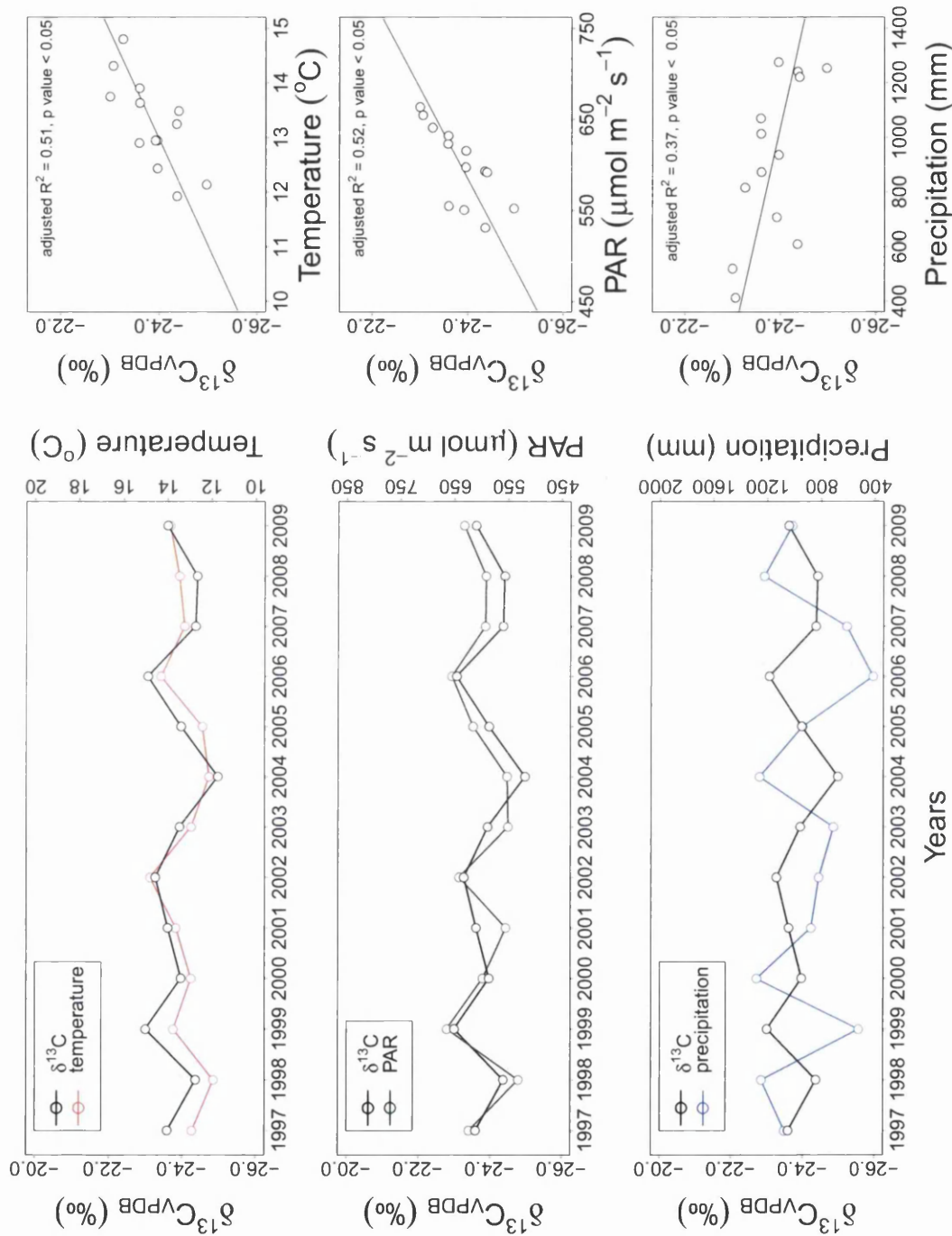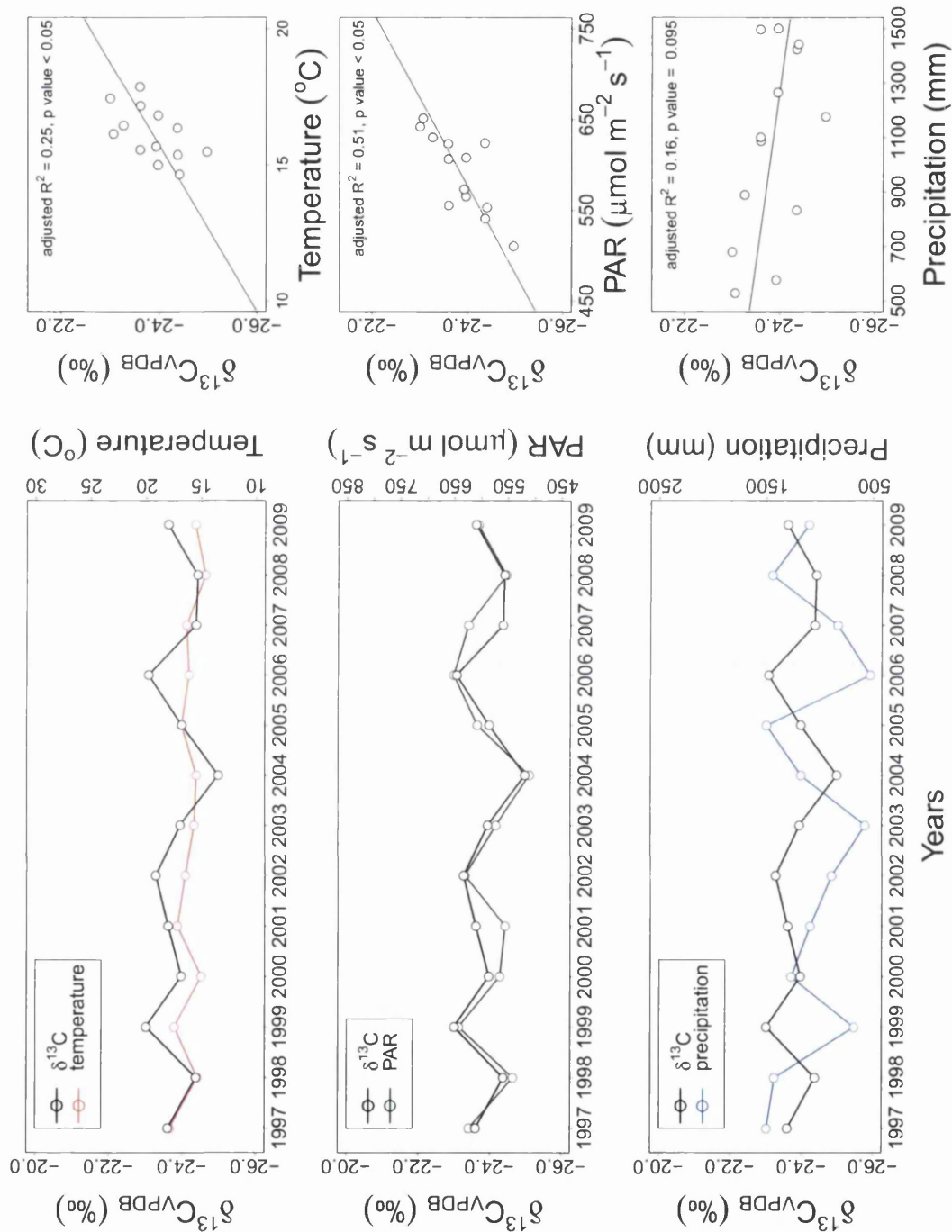
Figure 5.68: *Inter-annual comparison between $\delta^{13}C$ (black open circles), temperature (red open circles), PAR (green open circles) and precipitation (blue open circles) with the addition of cell life time at Hyytiälä (microcore measurements). Right: The linear regression with the adjusted R^2 value and p value.*

5.2.2.2 Multiple linear regression fit between $\delta^{13}C$ time series and weather variables

Building a multiple linear regression model based on the three weather variables integrated over the growing season estimated using the microcore measurements (figure 5.69) and by using forward stepwise regression, the fit between the measured and the modelled $\delta^{13}C$ annual values is dramatically high ($R^2 = 0.83$, $p < 0.05$). However, the single relationship with PAR was already high ($R^2 = 0.73$, $p < 0.05$) which then makes the increase of fit quite small and coming from the inclusion of temperature and precipitation which were first not significant with the $\delta^{13}C$ annual values. The Akaike information criterion presents a minimum value when using PAR and precipitation in a multiple linear model with PAR being the single variable having the highest adjusted R squared (Table 5.25). A PAR only model holds a quite similar AIC value and would permit to use only one variable. Therefore, using the three variables into a multiple linear model is not necessary to obtain the best model to predict $\delta^{13}C$ values at the inter-annual level.

With the inclusion of cell life time in the integration period for weather variables (figure 5.70), the fit is high ($R^2 = 0.61$, $p < 0.05$) but as previously only shows a slight increase from the single PAR relationship ($R^2 = 0.51$, $p < 0.05$). Using the Akaike information criterion to evaluate which variables provide the best model for $\delta^{13}C$ prediction shows a minimum AIC value for the combination of PAR and precipitation while the AIC for the three variable combination is in a close range (Table 5.25). Therefore, either using PAR and precipitation or all three variables allows to predict the $\delta^{13}C$ values when including cell life time in the climate analysis.

Table 5.25: *Akaike's information criterion (AIC) for each variable and variable combination in a multiple linear regression model at Hyytiälä for the period 1997-2009 when microcore measurements are used to estimate the growing season with and without cell life time (CLT).*

Variables	AIC without CLT	AIC with CLT
Temperature	22.68	24.69
PAR	17.00	9.14
Precipitation	24.08	24.66
Temperature & PAR	18.78	23.03
Temperature & Precipitation	20.85	23.03
PAR & Precipitation	16.66	5.84
Temperature & PAR & Precipitation	18.17	7.02
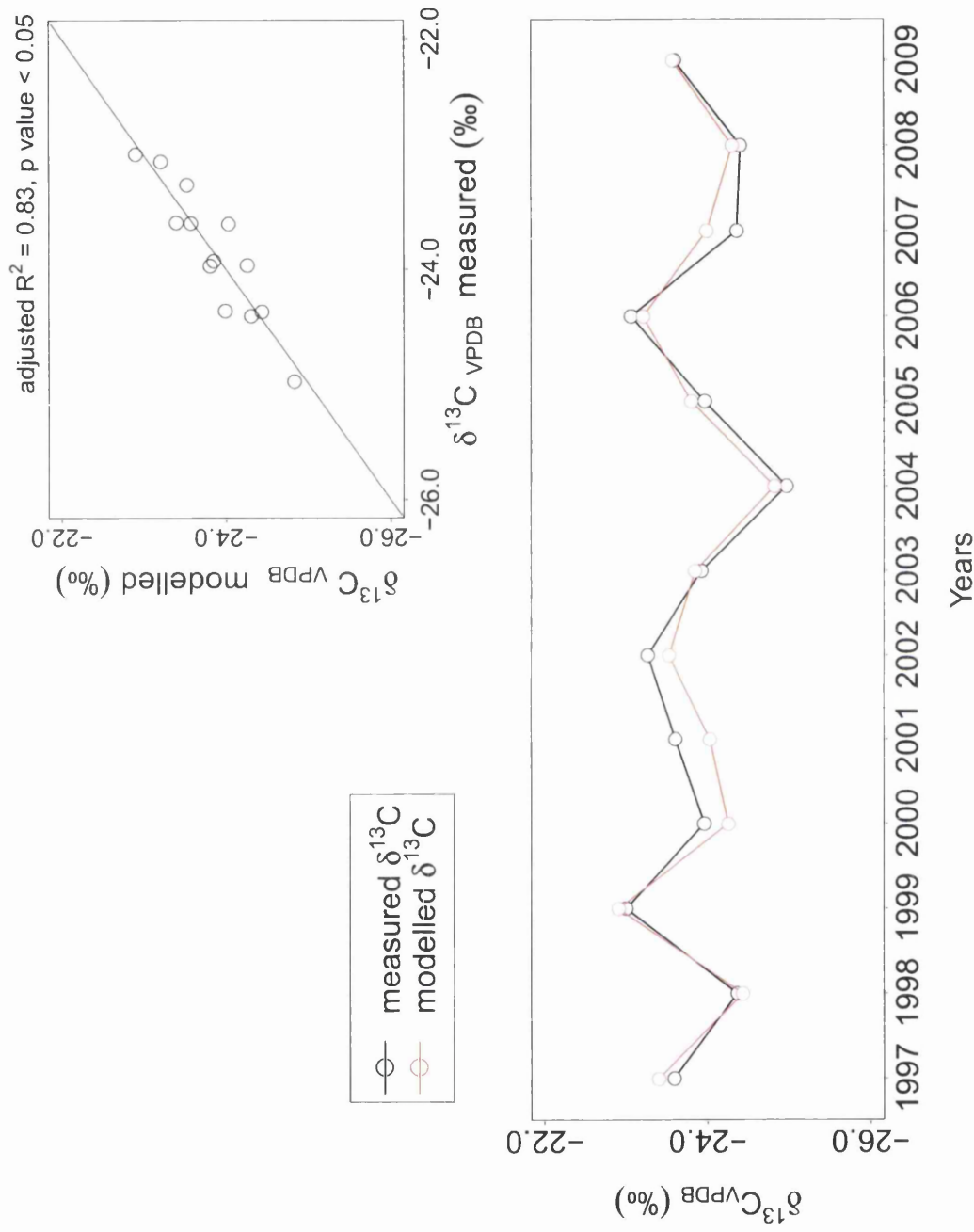
Figure 5.69: *Inter-annual comparison between measured $\delta^{13}C$ (black open circles) and modelled $\delta^{13}C$ (orange open circles) at Hyytiälä by using a multiple linear regression including temperature, PAR and precipitation as explanatory factors to the measured $\delta^{13}C$ variation (microcore measurements). The topright panel shows the linear behaviour between the measured and modelled $\delta^{13}C$ values with the adjusted R^2 value and p value.*
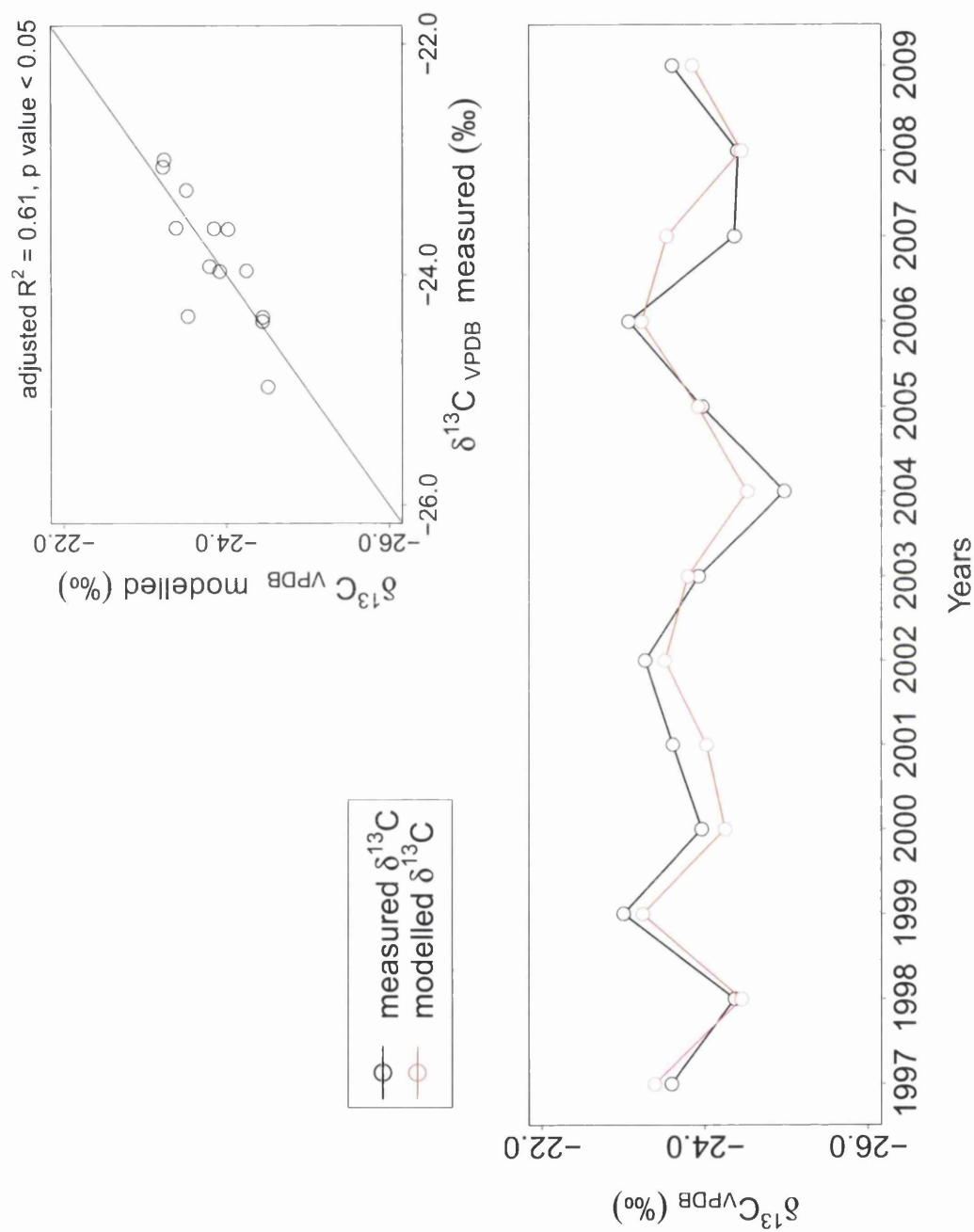
Figure 5.70: *Inter-annual comparison between measured $\delta^{13}C$ (black open circles) and modelled $\delta^{13}C$ (orange open circles) with the addition of cell life time at Hyytiälä by using a multiple linear regression including temperature, PAR and precipitation as explanatory factors to the measured $\delta^{13}C$ variation (microcore measurements). The topright panel shows the linear behaviour between the measured and modelled $\delta^{13}C$ values with the adjusted R^2 value and p value.*

5.2.3 Summary

At Hyytiälä, the availability of both dendrometer and microcore measurements allowed to compare of the linear regression performance to predict the annual $\delta^{13}C$ variation. Using one or the other type of measurements provided different results but instead of having a better linear fit in one case, the results from the single linear regressions revealed a shift in the importance of the weather variables with a greater weight of temperature and precipitation when using dendrometer measurements while the PAR linear fit is reasonably large when using micro-core measurements. Applying the cell life time theory to the time integration of weather variables causes an increase in the fit of variables that were previously not significant while it tends to decrease the fit of the ones that were already showing a strong relationship with $\delta^{13}C$ annual values. One suggestion can be that the weather variables do not influence the $\delta^{13}C$ on the same time span and that different integration periods should be used for each variable to obtain an optimal single linear fit with $\delta^{13}C$ time series. Evaluating the combination of the weather variables in a multiple linear regression model using a criterion-based method (AIC) shows that all three variables are not always necessary to predict realistically inter-annual $\delta^{13}C$ values. Using microcore measurements provides a higher adjusted R squared without cell life time while the integration of cell life time is better modelled when the climate analysis is carried out with the growing season estimated using dendrometer measurements. Therefore, it is possible that each weather variable needs to be integrated on a different time span to optimise the fit with $\delta^{13}C$ time series.

5.3 Correlation of weather variables at Norunda at the inter-annual resolution

5.3.1 δ^{13}C time series over the period of wood growth estimated by using dendrometer measurements

5.3.1.1 Simple linear regression between δ^{13}C time series and weather variables

At Norunda, only dates from dendrometer measurements are available to examine the linear regressions between annual δ^{13}C values and weather variables. All three single linear regressions show not significant fit for temperature, PAR and precipitation (p value > 0.05). Only the years 1997, 1998, 2001 and 2002 are available for precipitation. None of the variables present a significant linear relationship at the annual resolution when using the available dendrometer measurements (figure 5.71).

Adding the cell life time period to the cell formation dates when matching weather variables and annual δ^{13}C values does not improve the previous linear regression fits. All three weather variable relationships remain not significant. Therefore, including the cell life time period when matching weather and isotope values at Norunda does not provide an improvement in the understanding of the weather influence over the annual δ^{13}C values by observing single linear regressions (figure 5.72).
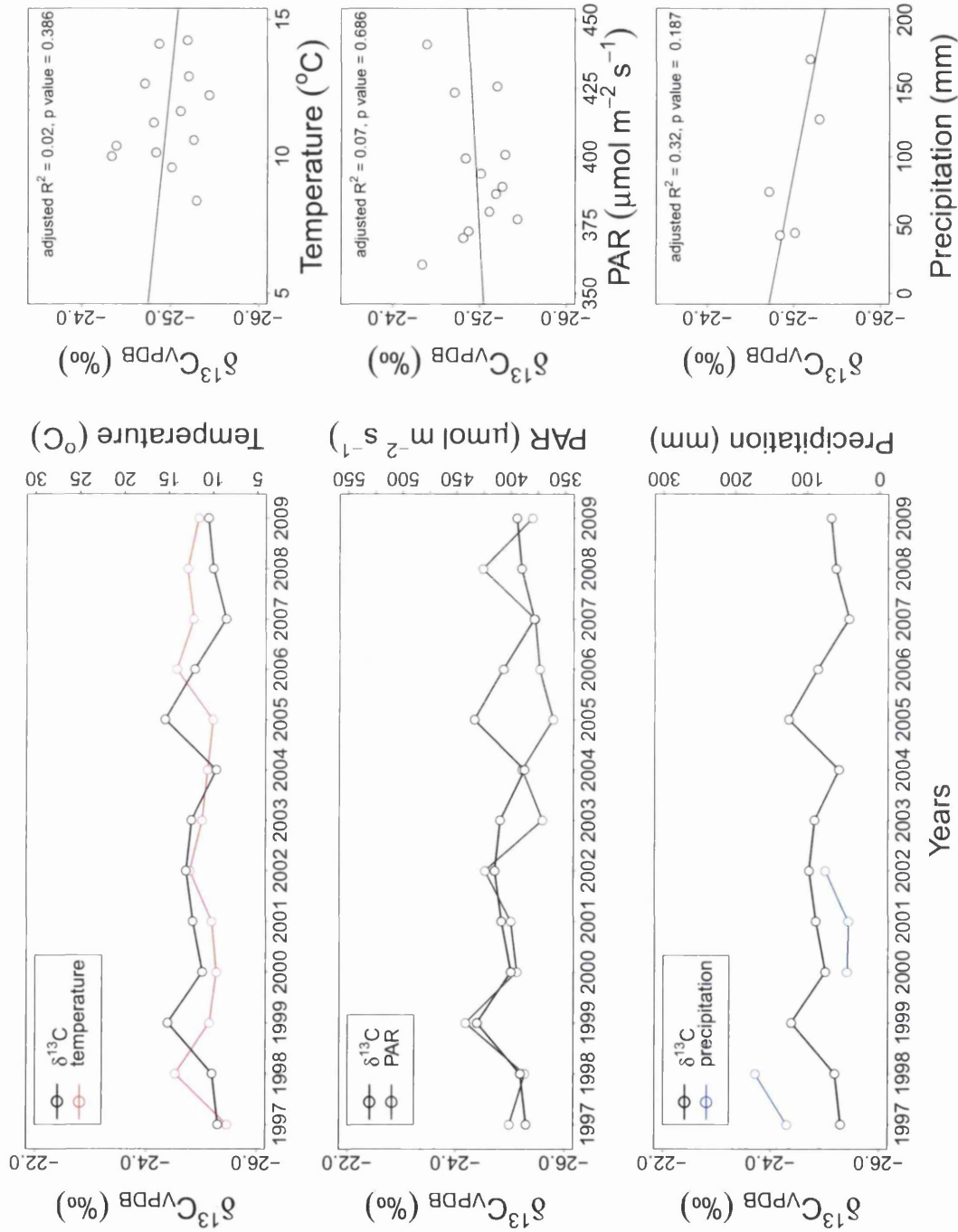
Figure 5.71: *Left: Inter-annual comparison between $\delta^{13}C$ (black open circles), temperature (red open circles), PAR (green open circles) and precipitation (blue open circles) at Norunda. Right: The linear regression with the adjusted R^2 value and p value.*
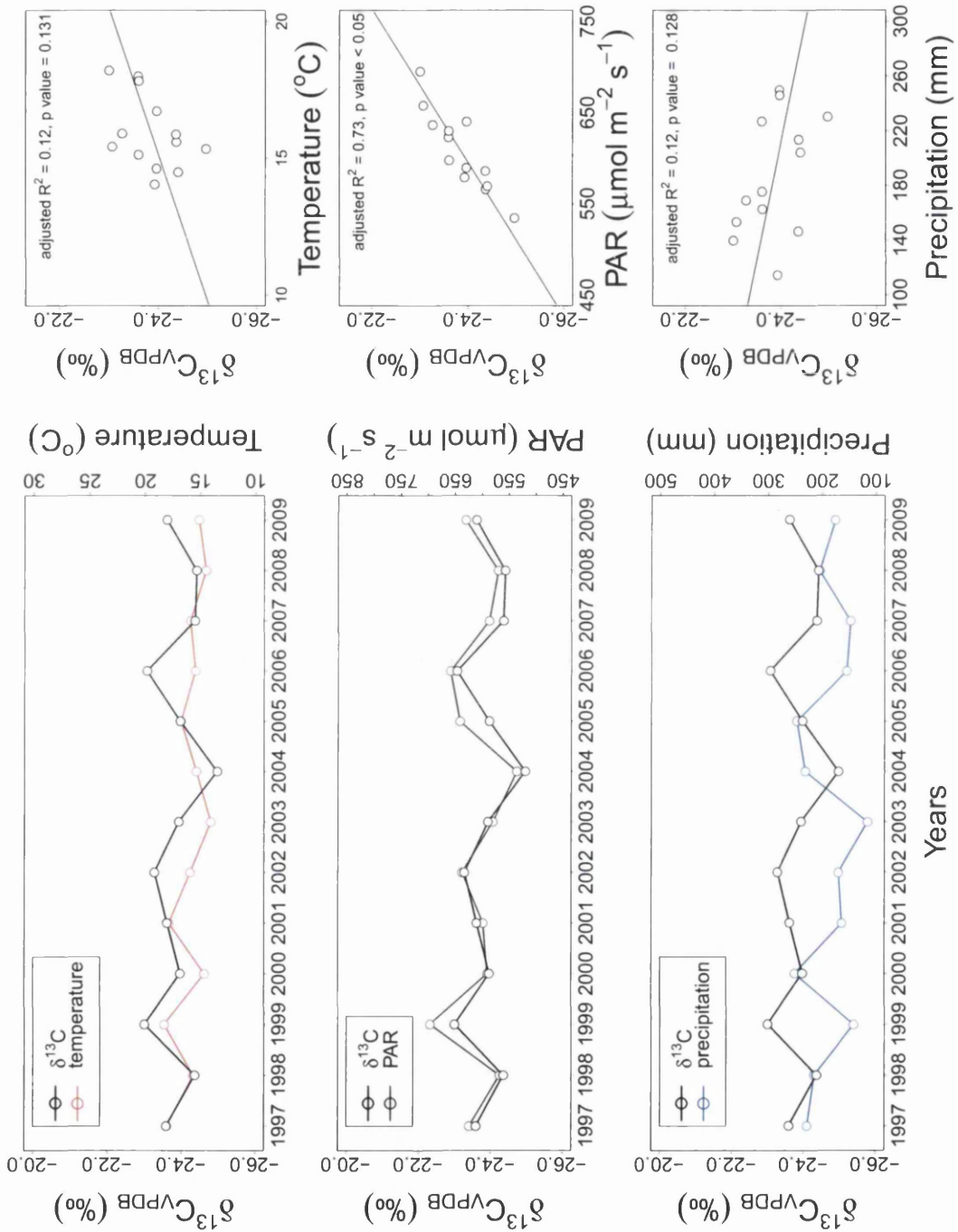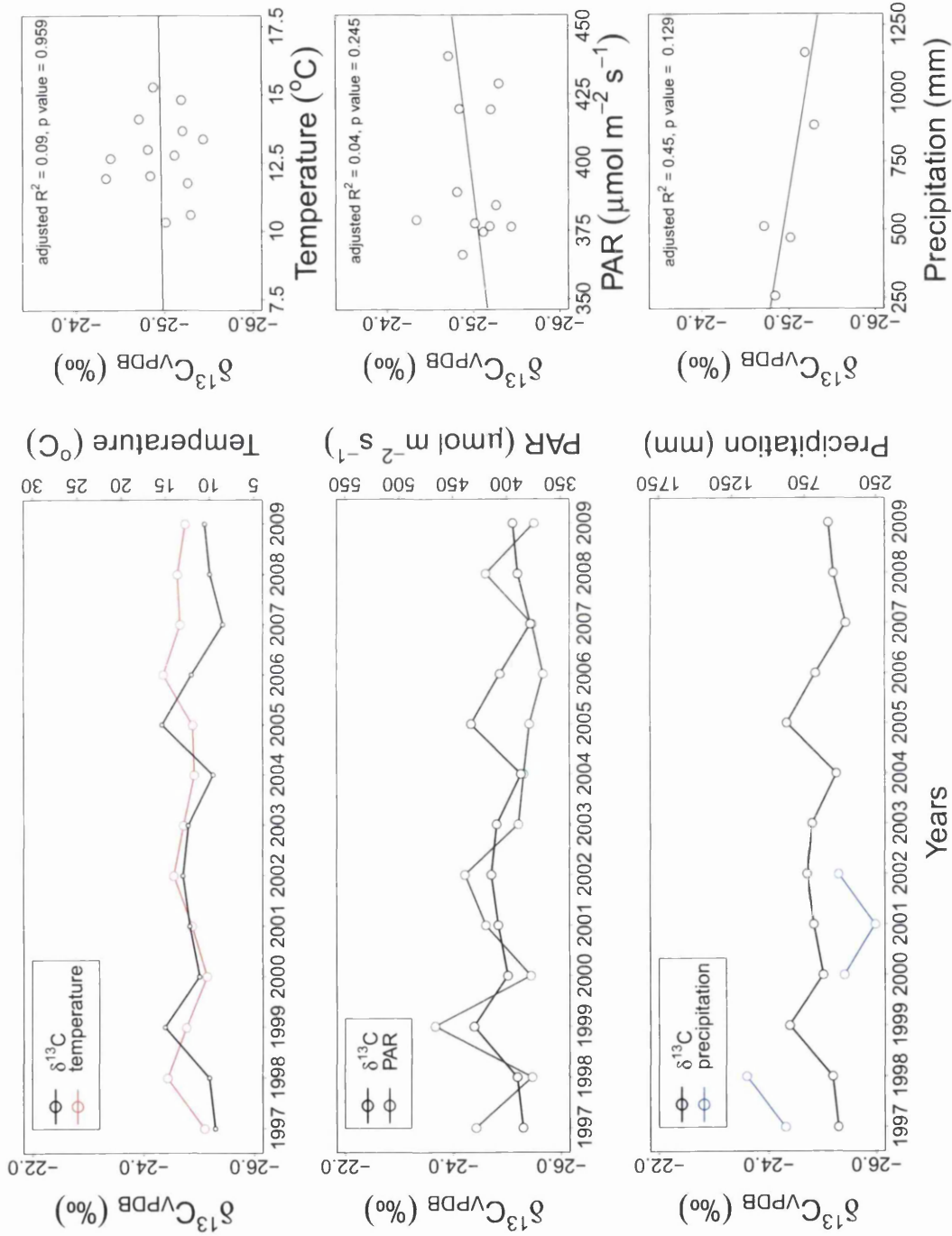
Figure 5.72: *Left: Inter-annual comparison between* $\delta^{13}C$ *(black open circles), temperature (red open circles), PAR (green open circles) and precipitation (blue open circles) with cell life time at Norunda. Right: The linear regression with the adjusted R^2 value and p value.*

5.3.1.2 Multiple linear regression fit between $\delta^{13}C$ time series and weather variables

When building a multiple linear regression based on temperature and PAR, the goodness of fit between the measured and the modelled $\delta^{13}C$ annual values is low and not significant as expected from the single relationships ($R^2 = 0.03$, $p = 0.263$). Therefore, both single and multiple linear regressions fail to predict the annual $\delta^{13}C$ values (figure 5.73).

With the inclusion of cell life time, the fit is still low and non significant ($R^2 = 0.07$, $p = 0.191$). Therefore, even with the inclusion of the cell life time in the calculation of the matching period between $\delta^{13}C$ and weather factors, the multiple linear regression model seems not to show a significant fit and presents no confidence in its capacity of predicting annual carbon isotopic variation (figure 5.74).
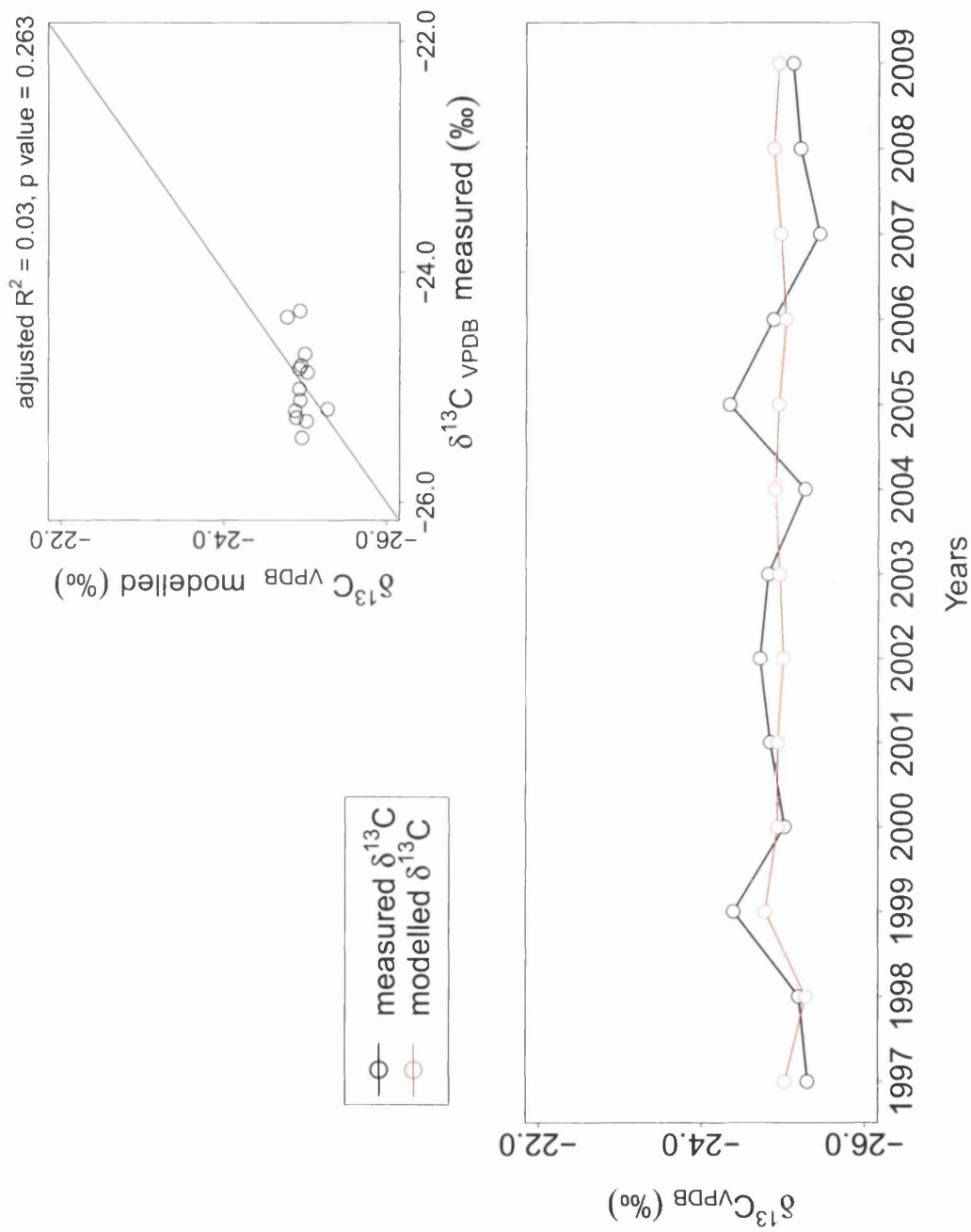
Figure 5.73: *Inter-annual comparison between measured $\delta^{13}C$ (black open circles) and modelled $\delta^{13}C$ (orange open circles) at Norunda by using a multiple linear regression including temperature, PAR and precipitation as explanatory factors to the measured $\delta^{13}C$ variation. The topright panel shows the linear behaviour between the measured and modelled $\delta^{13}C$ values with the adjusted R^2 value and p value.*
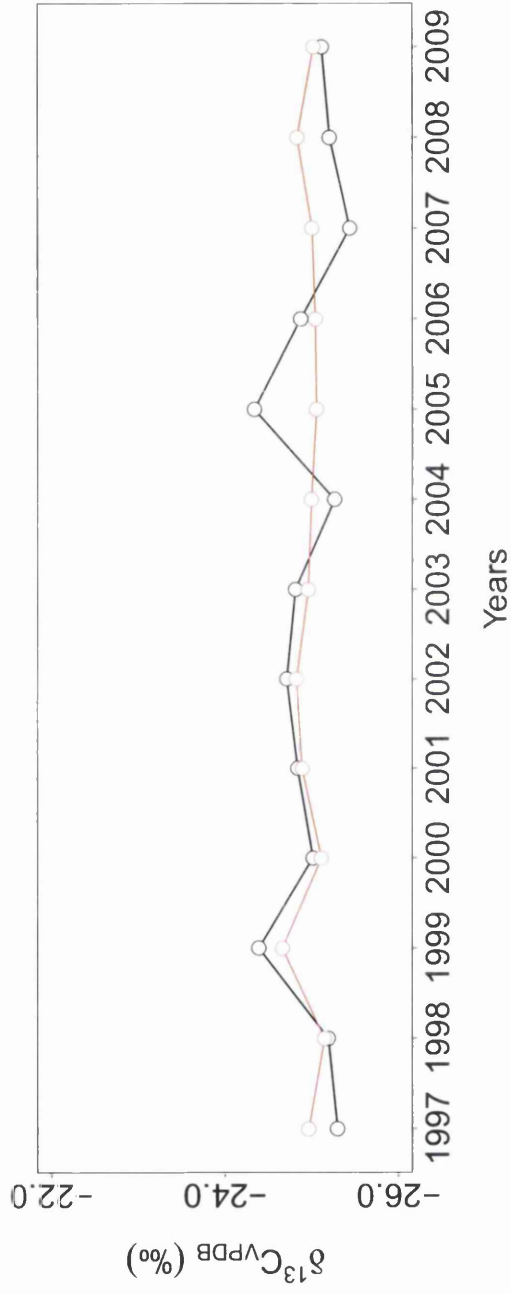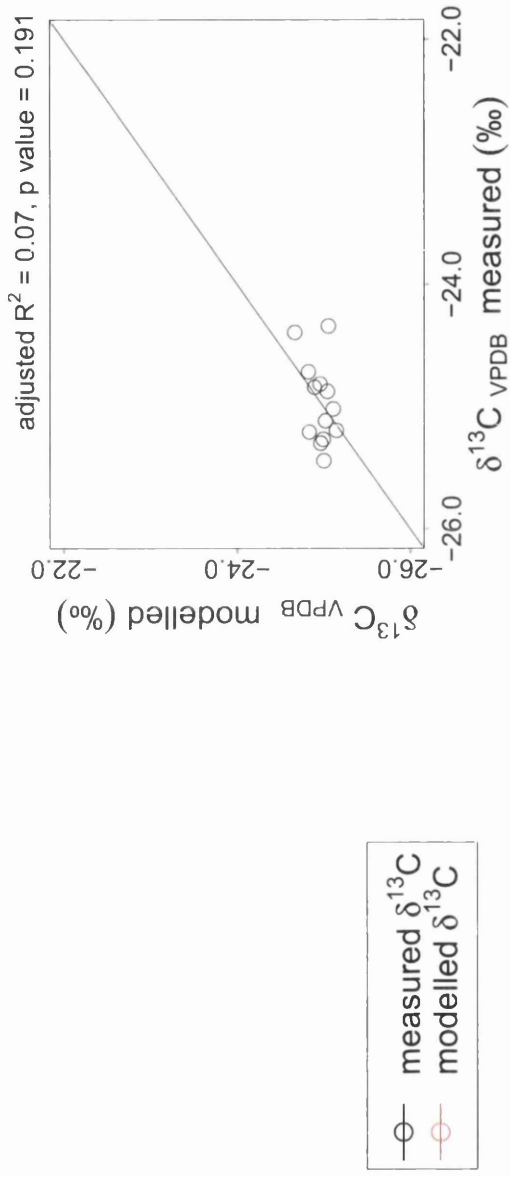
Figure 5.74: *Comparison between measured $\delta^{13}C$ (black open circles) and modelled $\delta^{13}C$ (orange open circles) with cell life time at Norunda by using a multiple linear regression including temperature, PAR and precipitation as explanatory factors to the measured $\delta^{13}C$ variation. The topright panel shows the linear behaviour between the measured and modelled $\delta^{13}C$ values with the adjusted R^2 value and p value.*

5.3.2 Summary

As none of the weather variables present significant single linear relationships with the annual δ^{13}C values, the application of a multiple linear regression to increase the prediction of the δ^{13}C variation at the inter-annual resolution is inadequate. The reasons of such a difference with the results obtained at Hyytiälä may be explained by the dates chosen to represent the growing season as only one year of dendrometer measurements was tested in Chapter IV. Investigation of the best set of dates for this study site would surely improve the matching procedure between weather variables and annual δ^{13}C values. When applying cell life time, no improvement is shown in the linear regression fits which is also unexpected when observing its influence over the δ^{13}C dataset at Hyytiälä. If the growing season was shorter than the set of dates proposed in this study, the integration of weather over a larger period due to cell life time to each δ^{13}C value would improve the linear fit by the inclusion of a realistic matching period between the weather variable and the δ^{13}C values.

5.4 Correlation of weather variables at Loobos at the inter-annual resolution

5.4.1 δ^{13}C time series over the period of wood growth estimated by using dendrometer measurements

5.4.1.1 Simple linear regression between δ^{13}C time series and weather variables

At Loobos, the linear regression between annual δ^{13}C values and weather variables are examined based on the growing season estimated by using dendrometer measurements. Temperature and precipitation present not significant single linear regressions with the annual δ^{13}C values (p value > 0.05). Years 1997 to 2000 are missing for the PAR variable. Nevertheless, this variable show a significant linear relationship ($R^2 = 0.45$, $p < 0.05$). However, in contrast to Hyytiälä where the PAR relationship is also significant, the linear regression presents a negative trend with lower annual values of PAR than the range met at Hyytiälä. Only the PAR variable presents a significant and negative linear fit at the annual resolution when using the available dendrometer measurements at Loobos (figure 5.75).

When adding the cell life time period to the cell formation dates to match weather variables and annual δ^{13}C values, the previous linear regression fits are not improved. Temperature and precipitation still present not significant relationships while the fit of PAR decreases ($R^2 = 0.38$, $p < 0.05$). Therefore, including the cell life time period when matching weather and isotope values at Loobos does not provide an improvement in the understanding of the weather influence over the annual δ^{13}C values when analysing single linear regressions (figure 5.76).

Figure 5.75: *Left: Inter-annual comparison between* $\delta^{13}C$ *(black open. circles), temperature (red open circles), PAR (green open circles) and precipitation (blue open circles) for the period 1997-2009 at Loobos. Right: The linear regression with the adjusted R^2 value and p value.*

Figure 5.76: *Left: Inter-annual comparison between $\delta^{13}C$ (black: open circles), temperature (red open circles), PAR (green open circles) and precipitation (blue open circles) with cell life time at Loobos. Right: The linear regression with the adjusted R^2 value and p value.*

5.4.1.2 Multiple linear regression fit between $\delta^{13}C$ time series and weather variables

When building a multiple linear regression based on the three weather variables (figure 5.77), the fit between the measured and the modelled $\delta^{13}C$ annual values is average and significant as carried out mainly by the single relationships from PAR ($R^2 = 0.51$, $p < 0.05$). Using the Akaike information criterion to evaluate if a combination of variables provides a better model to predict $\delta^{13}C$ values shows that a single regression based on PAR represents the best model due to its low AIC value. The addition of temperature is also an option as the increase in the AIC is minimal (Table 5.26).

The inclusion of cell life time does not significantly improve the fit of the linear regression than without it ($R^2 = 0.58$, $p < 0.05$). The use of the Akaike information criterion shows a similar result than without cell life time with the best model being based on PAR only due to its low AIC value. Therefore, in both cases the use of the three variables in a multiple linear regression model is not necessary to predict inter-annual $\delta^{13}C$ values at Loobos (Table 5.26).

Table 5.26: *Akaike's information criterion (AIC) for each variable and variable combination in a multiple linear model at Loobos for the period 1997-2009 with and without cell life time (CLT).*

Variables	AIC without CLT	AIC with CLT
Temperature	19.70	19.97
PAR	2.87	3.92
Precipitation	20.03	20.55
Temperature & PAR	2.99	4.46
Temperature & Precipitation	20.99	21.97
PAR & Precipitation	4.78	4.96
Temperature & PAR & Precipitation	4.98	4.38

Figure 5.77: *Inter-annual comparison between measured $\delta^{13}C$ (black open circles) and modelled $\delta^{13}C$ (orange open circles) at Loobos by using a multiple linear regression including temperature, PAR and precipitation as explanatory factors to the measured $\delta^{13}C$ variation. The top-right panel shows the linear behaviour between the measured and modelled $\delta^{13}C$ values with the adjusted R^2 value and p value.*

Figure 5.78: *Inter-annual comparison between measured $\delta^{13}C$ (black open circles) and modelled $\delta^{13}C$ (orange open circles) with cell life time at Loobos by using a multiple linear regression including temperature, PAR and precipitation as explanatory factors to the measured $\delta^{13}C$ variation. The topright panel shows the linear behaviour between the measured and modelled $\delta^{13}C$ values with the adjusted R^2 value and p value.*

5.4.2 Summary

Only the PAR variable shows a significant single linear regression at Loobos during the period 2001 to 2009 at the inter-annual resolution. However, this relationship with the annual $\delta^{13}C$ values is negative and with lower values of PAR than for Hyytiälä. The application of a multiple linear regression model to increase the prediction of the $\delta^{13}C$ variation at the inter-annual resolution shows only a slight improvement to the single PAR linear regression. The reasons for the non significance of the relationships with the annual $\delta^{13}C$ values may be explained by the uncertainties linked to the method producing growing season dates as only two years of dendrometer measurements where available to build a growing season model. However, this does not explain why PAR shows a negative linear relationship with a lower range of PAR values than at Hyytiälä. A shift in the trend of the relationship between $\delta^{13}C$ values and PAR at the inter-annual resolution may be explained by a different water status of the trees during the growing season. The multiple linear regression model shows only a slight improvement to the single linear model using PAR and is possibly not necessary for improving the prediction of annual $\delta^{13}C$ values. When applying the cell life time theory, the single linear fit decreases for PAR while the multiple linear model shows an equivalent fit. Therefore, there is no improvement in the prediction of annual $\delta^{13}C$ values when adding the cell life time period to the time integration of weather variables at Loobos.

5.5 Conclusion

Depending on the study site where weather variables and annual $\delta^{13}C$ values have been matched by the estimation of growing season dates, the fit of both single and multiple linear regressions change drastically. Hyytiälä presents the best results in terms of the significance of the linear regressions and the improvement of the different relationships by the application of cell life time. However, at Norunda the results are poor when using linear regressions to evaluate the weather forcing on annual $\delta^{13}C$ values. Different factors can be involved in the lack of fit from the weather variables : the methodology to match growing season dates to the $\delta^{13}C$ time series suffers from the lack of confidence in the procedure due to the absence of dendrological information for most years studied and the quality of the data collected at the flux-tower site. Finally, at Loobos the only significant relationship is present with PAR and both multiple regression and the addition of cell life time do not improve the relationship with $\delta^{13}C$ values. However, this relationship shows a negative trend which is in contrast to the relation observed at Hyytiälä. To understand this shift in the relationship between PAR and annual $\delta^{13}C$ values, it would be interesting to evaluate the water status of the trees and observe if water stressed trees would present a negative relationship with light variables because of the stress induced by an increase in the rate of photosynthesis.

Chapter VI will present a similar approach using linear regressions to establish the causality between weather variables and $\delta^{13}C$ time series at the intra-annual resolution.

Chapter VI : Linear relationships between weather and isotope measurements at the intra-annual resolution

6.1 Introduction

Following the inter-annual analysis between climate forcing and annual $\delta^{13}C$ values, a similar analysis can be carried out at intra-annual resolution. The previous results show reasonably large variance explained by the linear regressions tested at Hyytiälä which could be an indication that the selection of the radial growth dates in Chapter IV is accurate and that the trees show a response to climate forcing which can be quantified via the $\delta^{13}C$ variation. However, these results were not verified at Norunda and Loobos not displaying significant linear regressions and so presumably dates used to predict the growing season may be inaccurate. Therefore, the expectations to observe the effect of climate forcing on intra-annual $\delta^{13}C$ time series are high at Hyytiälä but are low for Norunda and Loobos.

This chapter will present:

- the relationship between weather and stable carbon isotopes at the intra-annual resolution;

- the effect of cell life time addition in the integration of weather information at this resolution;

- the use of a multiple linear regression model combining the three tested weather variables to interpret stable carbon isotope variation at the intra-annual scale.

6.2 Correlation of weather variables at Hyytiälä at the intra-annual resolution

6.2.1 δ^{13}C time series over the period of wood growth estimated by using dendrometer measurements

6.2.1.1 Simple linear regression between δ^{13}C time series and weather variables

At the intra-annual resolution, each isotope value of 80 μm is matched with a weather component integrated via the Gompertz function as presented in Chapter IV. For temperature and PAR, the intra-annual values represent the average of temperatures or PAR values calculated over the time of wood formation of the 80 μm sampled via the laser system, while for precipitation they represent the sum of millimetres of rain that has fallen during this same period.

At Hyytiälä, when dates from dendrometer measurements are used to build the growing season dataset, the relationships between δ^{13}C time series and temperature is zero and not significant (p value $= 0.240$) while PAR ($R^2 = 0.02$, p value < 0.05) and precipitation ($R^2 = 0.06$, p value < 0.05) show weak relationships at a significant level. Similarly, only weak significant linear regressions are observed with PAR and precipitation while the temperature influence is not significant when using growing season dates estimated via dendrometer measurements at the intra-annual resolution (Figure 6.79).

When integrating the cell life time period to the match between δ^{13}C time series and the weather variables, the linear regression fit changes slightly. All three linear relationships are now significant but temperature ($R^2 = 0.05$, p value < 0.05) and precipitation ($R^2 = 0.03$, p value < 0.05) still present a weak fit, while the relationship with PAR is stronger ($R^2 = 0.19$, p value < 0.05). Therefore, including the cell life time period when matching weather and intra-annual isotope values provides potentially a better linear fit for PAR (Figure 6.80).
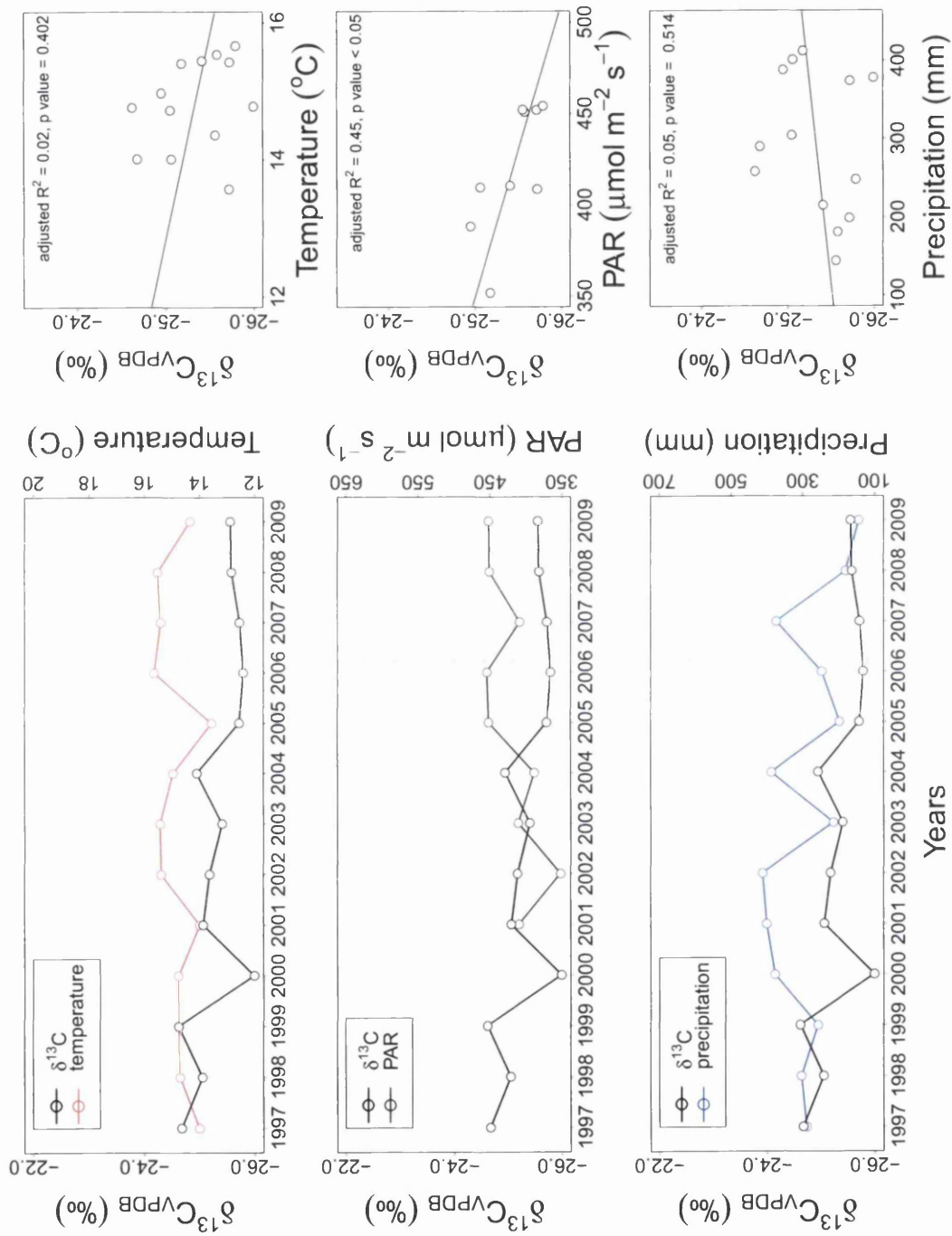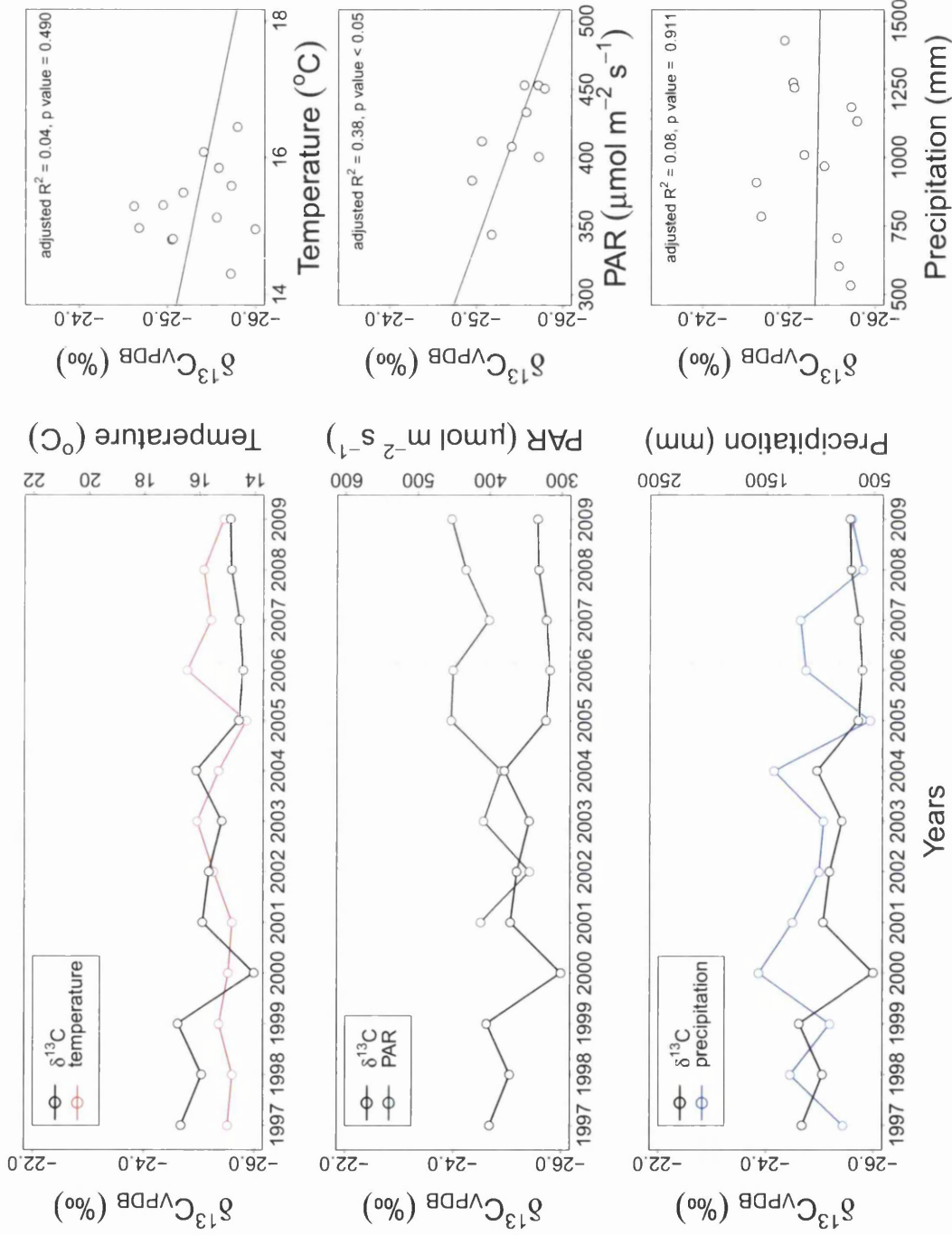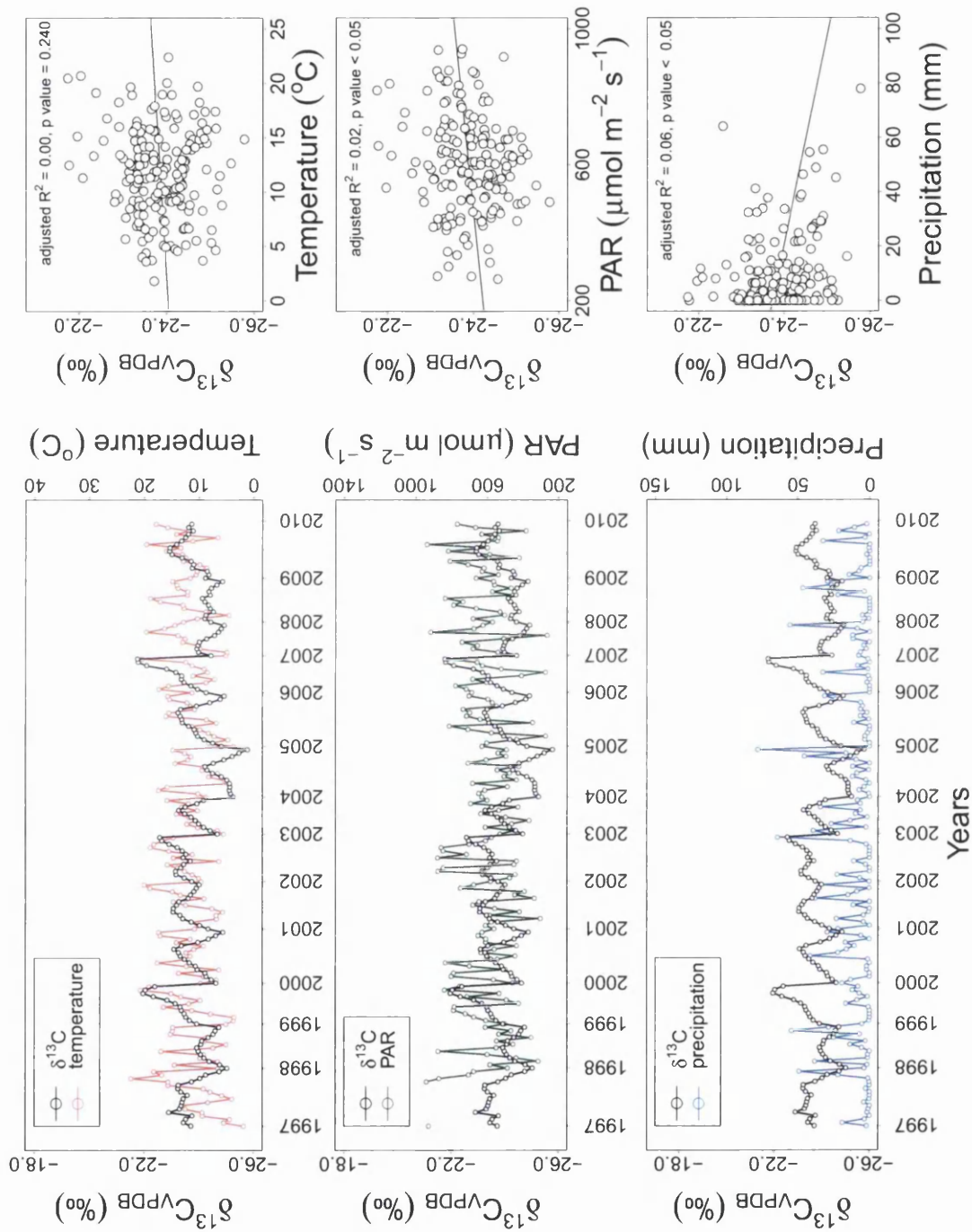
Figure 6.79: *Left: Intra-annual comparison between $\delta^{13}C$ (black open circles), temperature (red open circles), PAR (green open circles) and precipitation (blue open circles) at the intra-annual resolution at Hyytiälä (dendrometer measurements). Right: The linear regression with the adjusted R^2 value and p value.*

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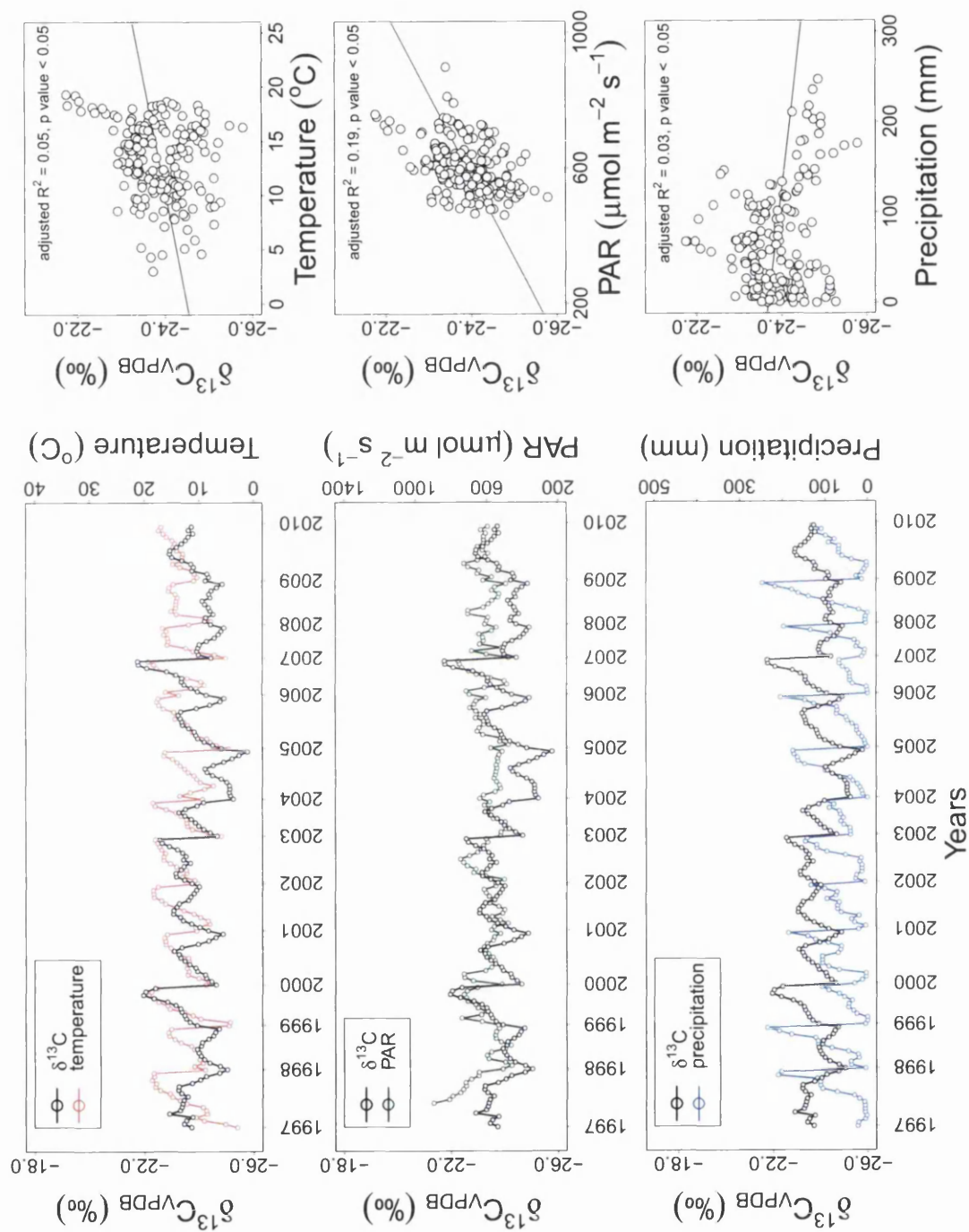
Figure 6.80: *Left: Intra-annual comparison between $\delta^{13}C$ (black open circles), temperature (red open circles), PAR (green open circles) and precipitation (blue open circles) with the addition of cell life time at Hyytiälä (dendrometer measurements). Right: The linear regression with the adjusted R^2 value and p value.*

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6.2.1.2 Multiple linear regression of δ^{13}C time series and weather variables

When all three weather variables (temperature, PAR and precipitation) are used as explanatory factors into a multiple linear regression model at Hyytiälä, the linear behaviour between measured δ^{13}C time series and the modelled δ^{13}C time series is not significant ($R^2 = 0.00$, $p = 0.758$) at the intra-annual level. This is due to the single linear regressions with temperature while PAR being not significant while the precipitation relationship is too weak to provide a strong fit. Therefore, it is unwise to use a multiple linear regression model as displayed in Figure 6.81 to predict δ^{13}C variation at this resolution.

When using the weather variables integrated with the cell life time period, the fit of the multiple linear regression model increases slightly compared to the model without cell life time ($R^2 = 0.09$, $p < 0.05$) but provides a weaker fit than with the PAR linear regression alone (Figure 6.82). By running a criterion-based method (AIC) to evaluate which variable is worth including into a multiple linear regression model (Table 6.27), the combination of the three weather variables provides the lowest AIC value when considering wood growth independently of the inclusion of cell life time. Therefore in both cases, this method would suggest to combine the three variables to predict δ^{13}C intra-annual values.

Table 6.27: *Akaike's information criterion (AIC) for each variable and variable combination in a multiple linear regression model at Hyytiälä for the period 1997-2009 when dendrometer measurements are used to estimate the growing season with and without cell life time (CLT).*

Variables	AIC without CLT	AIC with CLT
Temperature	393.20	384.39
PAR	369.38	355.49
Precipitation	383.01	387.46
Temperature & PAR	370.90	352.64
Temperature & Precipitation	382.48	349.48
PAR & Precipitation	365.40	355.44
Temperature & PAR & Precipitation	364.68	335.60

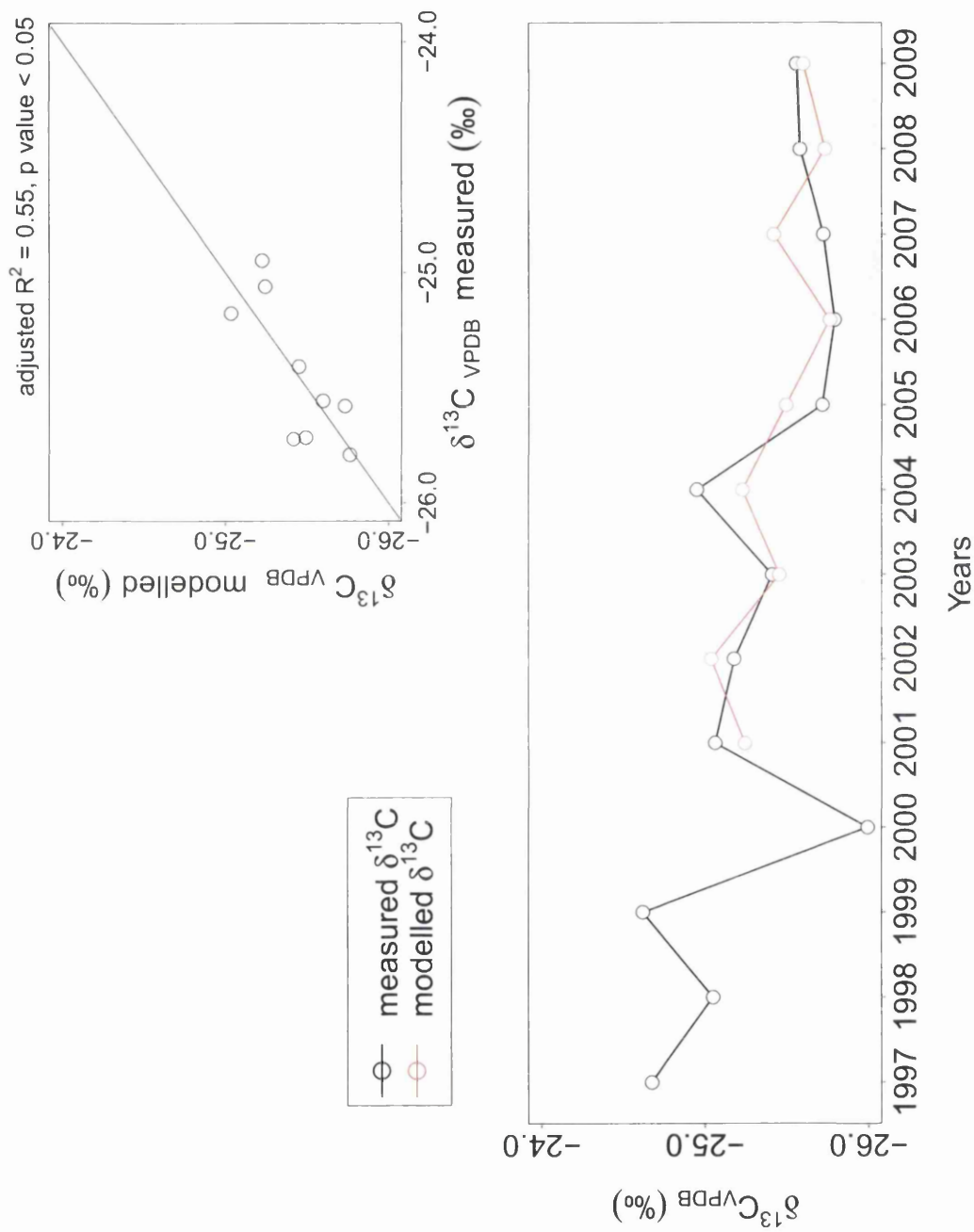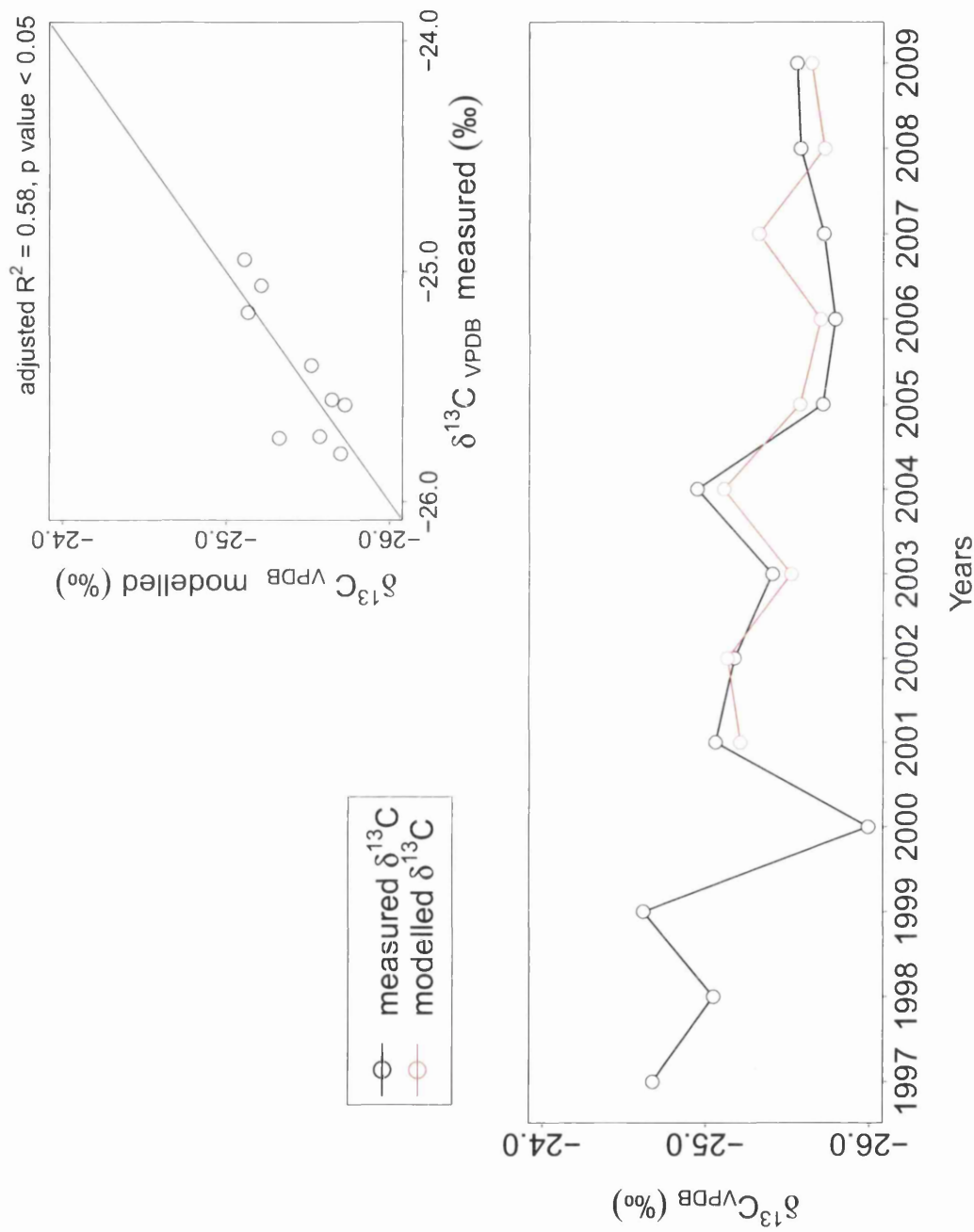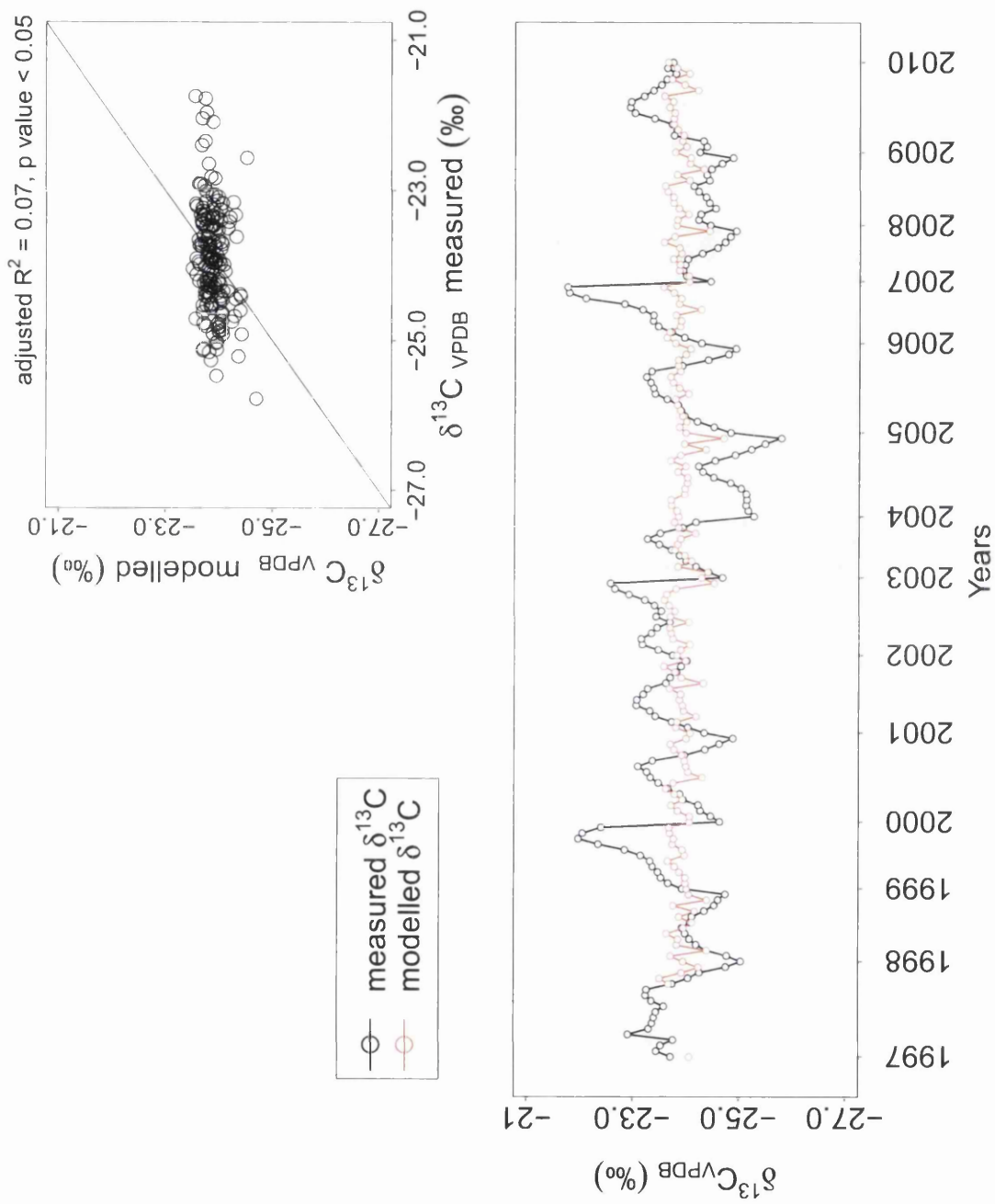**Figure 6.81:** *Intra-annual comparison between measured $\delta^{13}C$ (black open circles) and modelled $\delta^{13}C$ (orange open circles) time series at the intra-annual resolution for the period 1997-2009 at Hyytiälä by using a multiple linear regression including temperature, PAR and precipitation as explanatory factors to the measured $\delta^{13}C$ variation (dendrometer measurements). The topright panel shows the linear behaviour between the measured and modelled $\delta^{13}C$ values with the adjusted R^2 value and p value.*
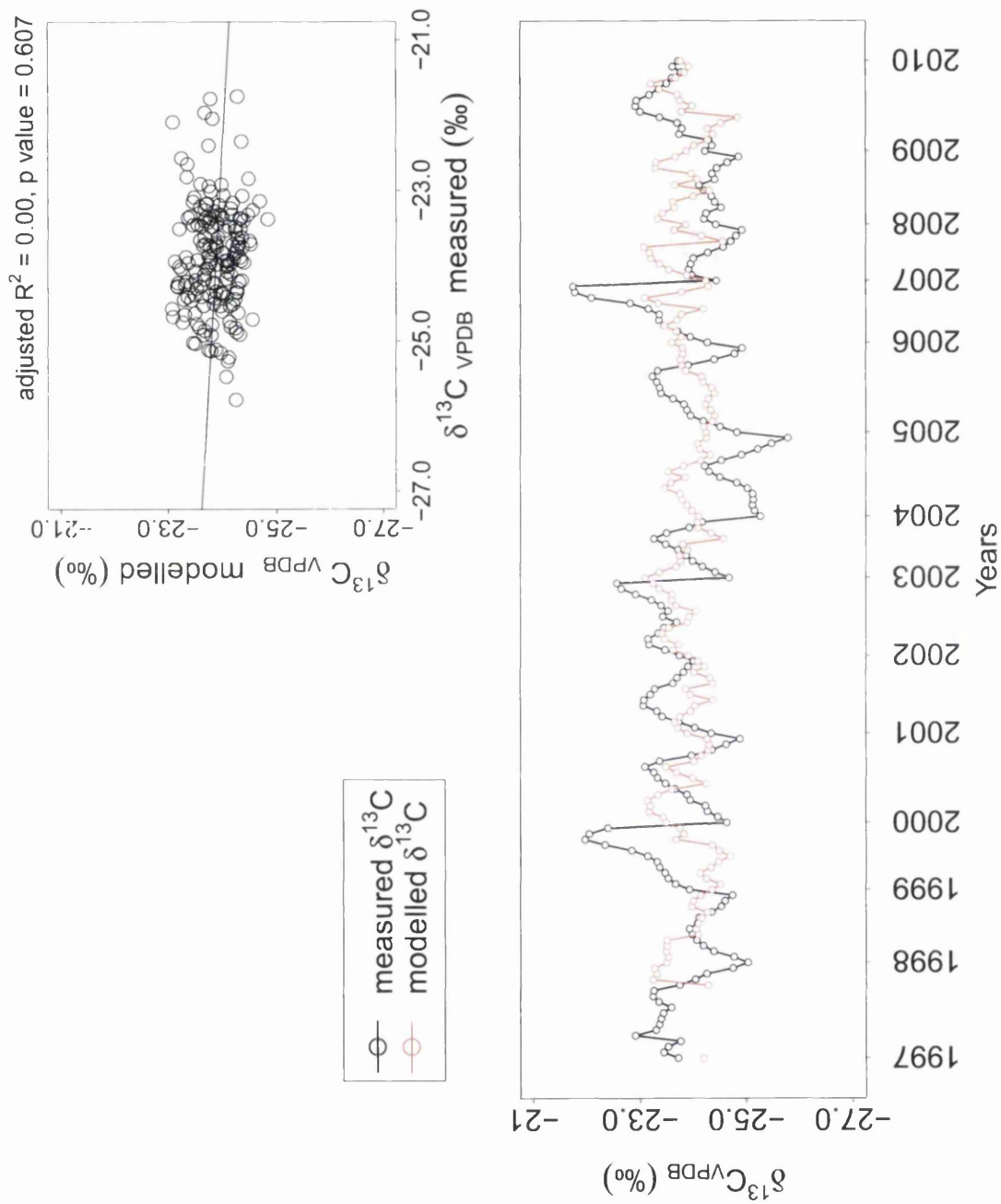
Figure 6.82: *Intra-annual comparison between measured $\delta^{13}C$ (black open circles) and modelled $\delta^{13}C$ (orange open circles) when adding cell life time at Hyytiälä by using a multiple linear regression including temperature, PAR and precipitation as explanatory factors to the measured $\delta^{13}C$ variation (dendrometer measurements). The topright panel shows the linear behaviour between the measured and modelled $\delta^{13}C$ values with the adjusted R^2 value and p value.*

6.2.2 δ^{13}C time series over the period of wood growth estimated by using microcore measurements

6.2.2.1 Simple linear regression between δ^{13}C time series and weather variables

Similar to the previous section, an analysis of the separate influence of each weather variable on intra-annual δ^{13}C time series can be carried out when using the microcore measurements to predict the growing season. The goodness of fit described by the R^2 value shows slight differences with the dendrometer estimated growth dates. Temperature presents a weak but significant relationship with the intra-annual δ^{13}C values ($R^2 = 0.07$, $p < 0.05$) while the relationship with PAR becomes slightly higher ($R^2 = 0.12$, $p < 0.05$) and the precipitation stays low ($R^2 = 0.09$, $p < 0.05$). Therefore, the choice of which method to estimate the growing season dates influences the results from the single linear regressions between δ^{13}C time series and weather variables at the intra-annual resolution (Figure 6.83).

When using the cell life time integration period for the weather variables, the results of the temperature linear regression change to having a relatively small variance explained ($R^2 = 0.25$, $p < 0.05$) with also a slight increase in the goodness of fit with PAR ($R^2 = 0.17$, $p < 0.05$). However, the precipitation linear regression remains weak ($R^2 = 0.03$, $p < 0.05$). Therefore, applying the cell life time theory seems to improve the linear relationships for temperature and PAR while the precipitation fit stays low (Figure 6.84).
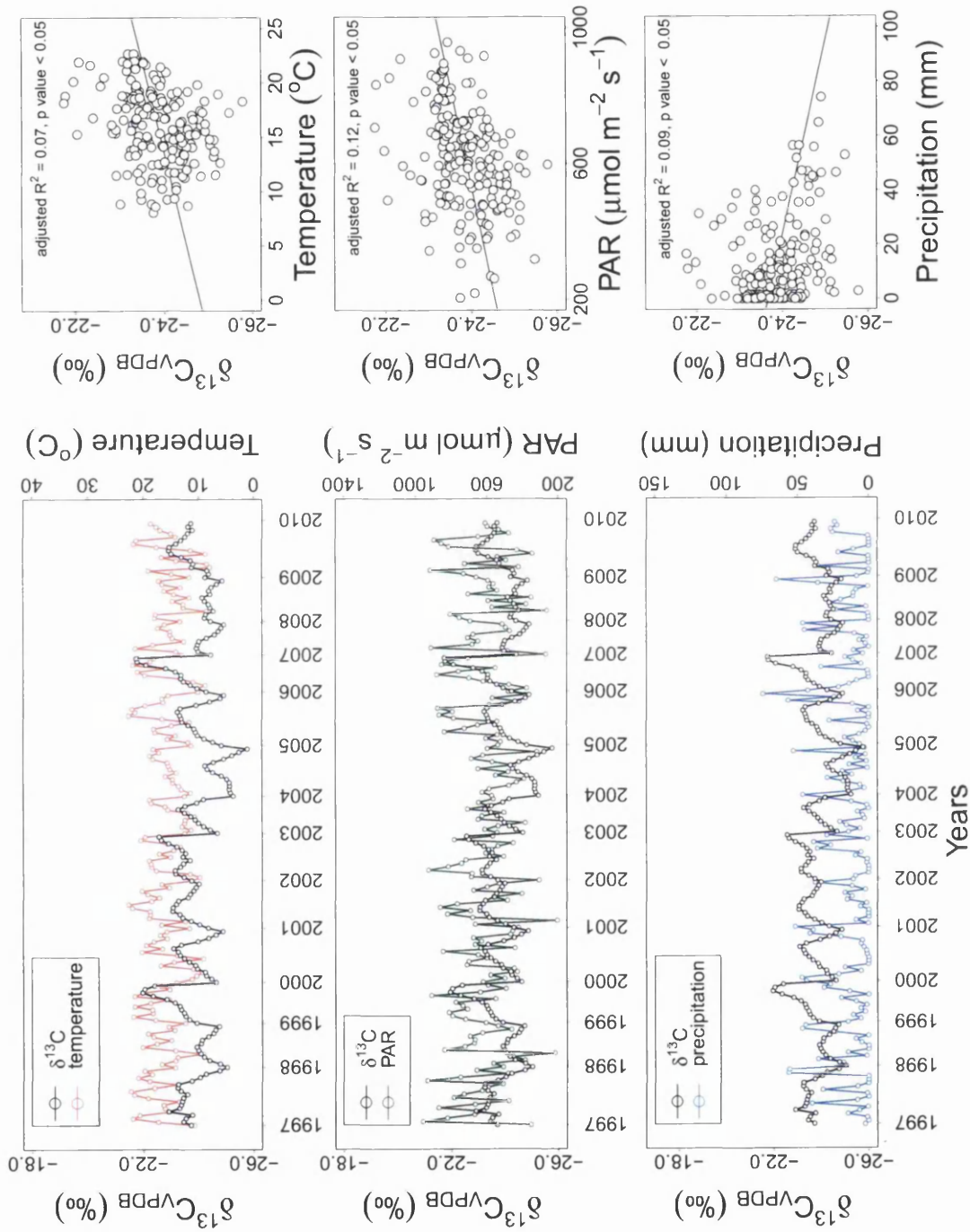
Figure 6.83: *Left: Intra-annual comparison between $\delta^{13}C$ (black open circles), temperature (red open circles), PAR (green open circles) and precipitation (blue open circles) at Hyytiälä (microcore measurements). Right: The linear regression with the adjusted R^2 value and p value.*

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Figure 6.84: *Left: Intra-annual comparison between $\delta^{13}C$ (black: open circles), temperature (red open circles), PAR (green open circles) and precipitation (blue open circles) with the addition of cell life time at Hyytiälä (microcore measurements). Right: The linear regression with the adjusted R^2 value and p value.*

6.2.2.2 Multiple linear regression fit between $\delta^{13}C$ time series and weather variables

When building a multiple linear regression model based on the three weather variables integrated over the growing season estimated by using microcore measurements (Figure 6.85), the fit between the measured and the modelled $\delta^{13}C$ intra-annual values is weak ($R^2 = 0.16$, $p < 0.05$). However, the single relationship with PAR is quite similar in terms of variance explained ($R^2 = 0.12$, $p < 0.05$) which then makes the increase of fit quite small. The use of the Akaike information criterion shows that the combination of the three variables provides the lowest AIC value when cell life time is not included (Table 6.28). Therefore, a multiple linear regression based on these three weather variables represents the best model to predict $\delta^{13}C$ intra-annual values.

With the inclusion of cell life time in the integration period for weather variables (Figure 6.86), the fit is greater ($R^2 = 0.29$, $p < 0.05$) but as previously shown, it only provides a slight increase from the temperature only relationship ($R^2 = 0.25$, $p < 0.05$). In this case, the Akaike information criterion suggests that a model based on temperature and PAR is the best to predict the $\delta^{13}C$ variation (Table 6.28).

Table 6.28: *Akaike's information criterion (AIC) for each variable and variable combination in a multiple linear regression model at Hyytiälä for the period 1997-2009 when microcore measurements are used to estimate the growing season with and without cell life time (CLT).*

Variables	AIC without CLT	AIC with CLT
Temperature	63.68	342.60
PAR	65.60	361.90
Precipitation	62.24	388.70
Temperature & PAR	64.72	334.62
Temperature & Precipitation	58.20	335.41
PAR & Precipitation	64.20	361.96
Temperature & PAR & Precipitation	57.17	335.34
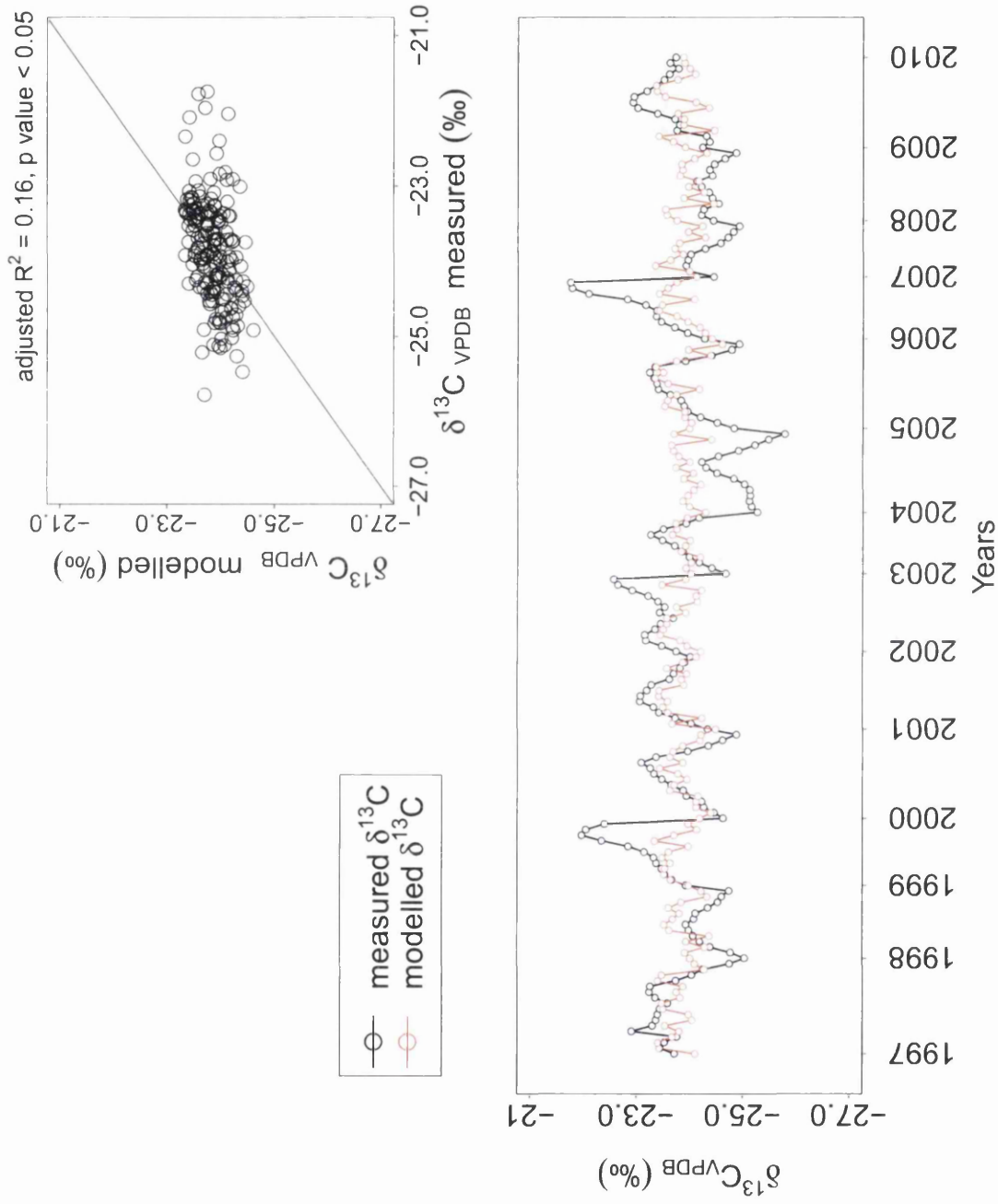
Figure 6.85: *Intra-annual comparison between measured $\delta^{13}C$ (black open circles) and modelled $\delta^{13}C$ (orange open circles) at Hyytiälä by using a multiple linear regression including temperature, PAR and precipitation as explanatory factors to the measured $\delta^{13}C$ variation (microcore measurements). The topright panel shows the linear behaviour between the measured and modelled $\delta^{13}C$ values with the adjusted R^2 value and p value.*
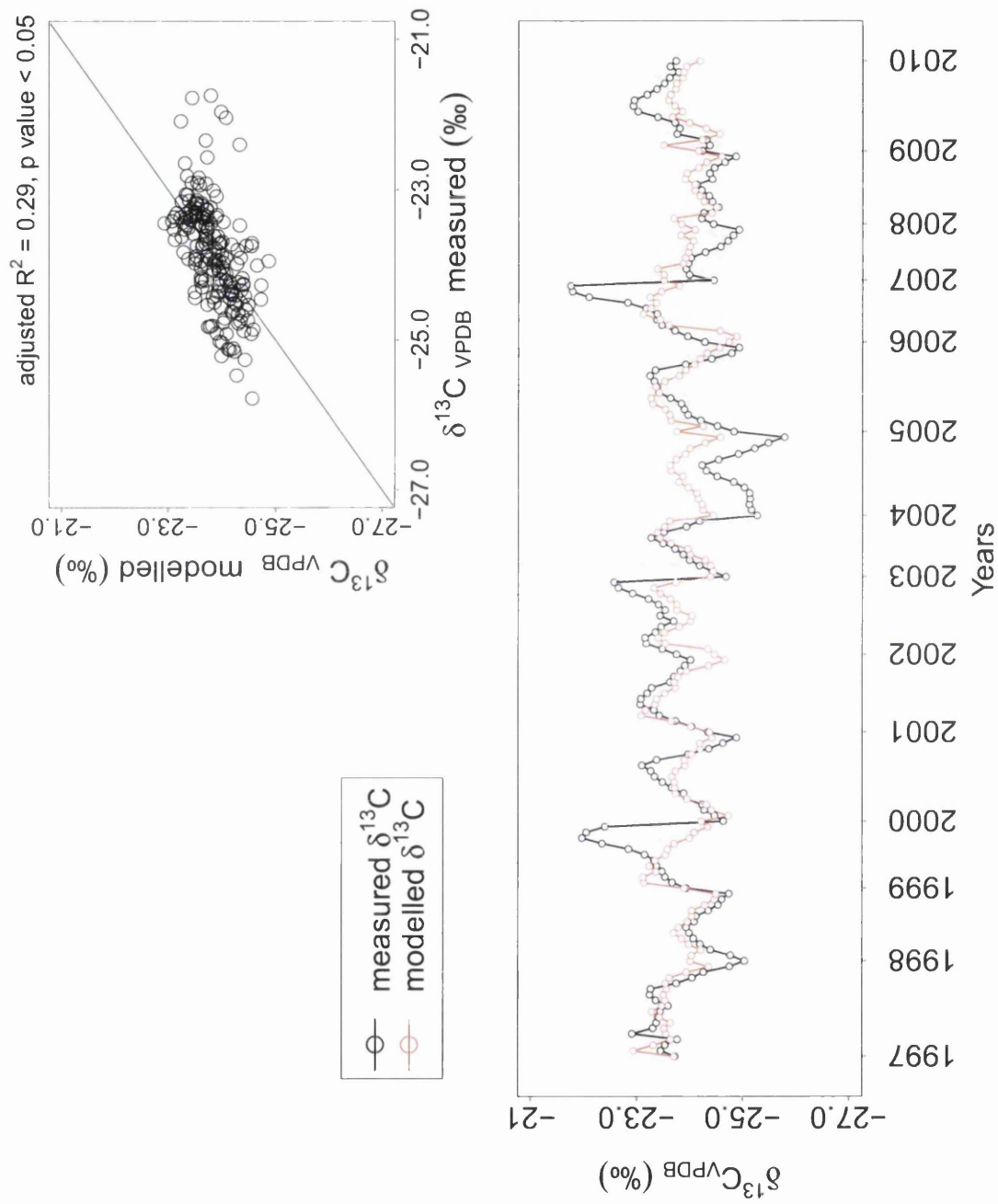
Figure 6.86: *Intra-annual comparison between measured $\delta^{13}C$ (black open circles) and modelled $\delta^{13}C$ (orange open circles) with the addition of cell life time at Hyytiälä by using a multiple linear regression including temperature, PAR and precipitation as explanatory factors to the measured $\delta^{13}C$ variation (microcore measurements). The topright panel shows the linear behaviour between the measured and modelled $\delta^{13}C$ values with the adjusted R^2 value and p value.*

6.2.3 Application of smoothed splines to measured and modelled δ^{13}C time series

To attenuate the small time scale variation, smoothing splines can be applied with a low smoothing power (span $= 0.2$) to the modelled and measured δ^{13}C time series (Figure 6.87). With the attenuation of high frequency variability, the R^2 value increases from 0.29 to to 0.35 which is not a considerable increase. However,the smoothed modelled δ^{13}C time series predict correctly the direction of the variation (towards more negative or more positive δ^{13}C values) for most years while the lack of fit occurs when a sharp variation is present in the measured δ^{13}C time series usually during the late section of the tree-rings with either higher values (years 1999, 2000, 2006 and 2009) or lower values (years 2003 and 2004) than predicted by the multiple linear regression model.
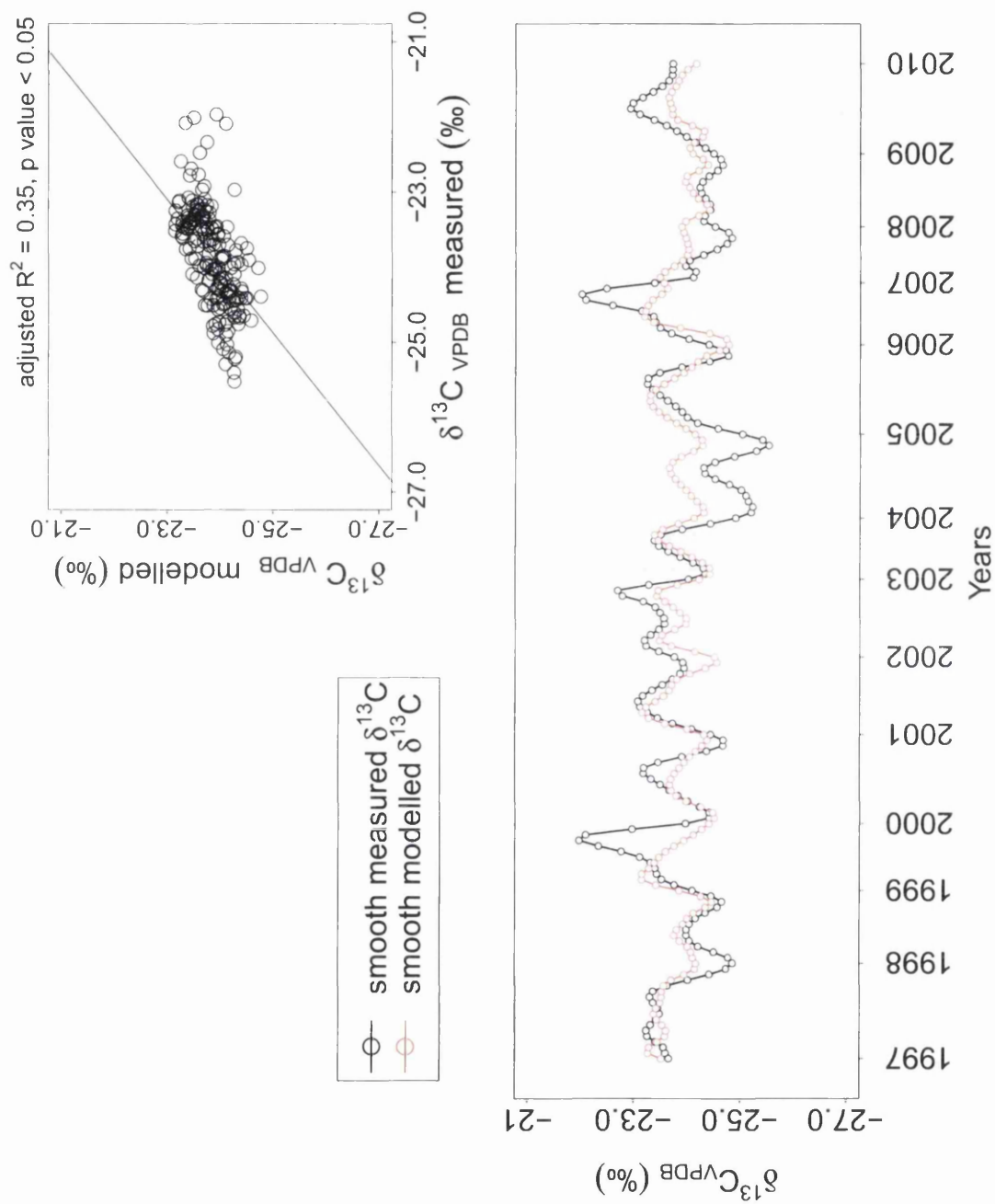
Figure 6.87: *Intra-annual comparison between measured $\delta^{13}C$ (black open circles) and modelled $\delta^{13}C$ (orange open circles) with the application of smooth splines at Hyytiälä by using a multiple linear regression including temperature, PAR and precipitation as explanatory factors to the measured $\delta^{13}C$ variation (microcore measurements). The topright panel show the linear behaviour between the measured and modelled $\delta^{13}C$ values with the adjusted R^2 value and p value.*

6.2.4 Summary

Similar to the inter-annual resolution, testing growing season dates from dendrometer or microcore measurements do change the fit from the linear regressions at the intra-annual resolution (Table 6.29). Using microcore measurements improve slightly the results of the single linear regression from PAR and precipitation while providing significance to the temperature regression. Although the increase in the fit of each single regression is small, when comparing the multiple linear regression the fit from the dataset using the dendrometer measurements is not significant while using microcores to predict the growing season provides a low but significant fit ($R^2 = 0.16$, $p < 0.05$). When applying the cell life time to the dataset, the temperature single linear regression changes dramatically between the two dendrological measurements. For dendrometer measurements, only the PAR linear regression benefits from the addition of cell life time ($R^2 = 0.19$, $p < 0.05$), while for temperature ($R^2 = 0.05$, $p < 0.05$) and for precipitation ($R^2 = 0.03$, $p < 0.05$) the fit stays low. For microcore measurements, the temperature regression benefits the most from the cell life time ($R^2 = 0.25$, $p < 0.05$) while PAR ($R^2 = 0.17$, $p < 0.05$) and precipitation ($R^2 = 0.03$, $p < 0.05$) are equivalent to the fits obtained with dendrometer measurements. When the multiple linear regressions are compared, the addition of cell life time provides a significant improvement ($R^2 = 0.29$, $p < 0.05$) for the microcore measurements. However, only temperature and PAR are selected by the Akaike criterion-based method to form the best model predicting $\delta^{13}C$ intra-annual values. The increase in the fit when including cell life time when dendrometer measurements are used is more modest ($R^2 = 0.09$, $p < 0.05$) but the Akaike information criterion suggest the use of the three variables to predict $\delta^{13}C$ intra-annual values. Therefore, at Hyytiälä and at the intra-annual resolution, using microcore measurements to estimate the growing season with the addition of the cell life time provides the best linear fits to predict $\delta^{13}C$ intra-annual values (Table 6.29). Applying smooth splines to attenuate the high frequency variation in the $\delta^{13}C$ time series results in a small but significant improvement to the fit.

Table **6.29**: *Summary of adjusted R squared and Akaike information criterion (AIC) at Hyytiälä for the linear regressions for the period 1997-2009 when using dendrometers or microcores with and without cell life time (CLT).*

	Hyytiälä							
	dendrometers				microcores			
	without CLT		with CLT		without CLT		with CLT	
Variables	adj R^2	AIC	adj R^2	AIC	adj R^2	AIC	adj R^2	AIC
Temperature	0.00	393.20	0.05	384.39	0.07	63.68	0.25	342.60
PAR	0.02	369.38	0.19	355.49	0.12	65.60	0.17	361.90
Precipitation	0.06	383.01	0.03	387.46	0.09	62.24	0.03	388.70
Temperature & PAR	0.02	370.90	0.20	352.64	0.12	64.72	0.28	334.62
Temperature & Precipitation	0.07	382.48	0.26	349.48	0.14	58.20	0.28	335.41
PAR & Precipitation	0.05	365.40	0.19	355.44	0.14	64.20	0.17	361.96
Temperature & PAR & Precipitation	0.06	364.68	0.27	335.60	0.16	57.17	0.29	335.34

6.3 Correlation of weather variables at Norunda at the intra-annual resolution

6.3.1 δ^{13}C time series over the period of wood growth estimated by using dendrometer measurements

6.3.1.1 Simple linear regression between δ^{13}C time series and weather variables

At Norunda, only dates from dendrometer measurements are available to examine the linear regressions between intra-annual δ^{13}C values and weather variables. All three single linear regressions present not significant fits from temperature, PAR and precipitation (p value > 0.05). Precipitation data are only recorded during year 1997, 1998, 2001 and 2002. None of the variables present a significant linear fit at the intra-annual resolution when using the available dendrometer measurements (Figure 6.88).

Adding the cell life time period to the cell formation dates to match weather variables and intra-annual δ^{13}C values does not improve the previous linear regression fits. All three weather variables relationships remain not significant. Therefore, including the cell life time period when matching weather and isotopes values at Norunda does not improve the understanding of the weather influence over the intra-annual δ^{13}C values for single linear regressions (Figure 6.89). As for the single weather variables presenting no significant relationship with the δ^{13}C values, the multiple linear regression is also not significant and will not be displayed as its capacity in the prediction of δ^{13}C values is negligible.
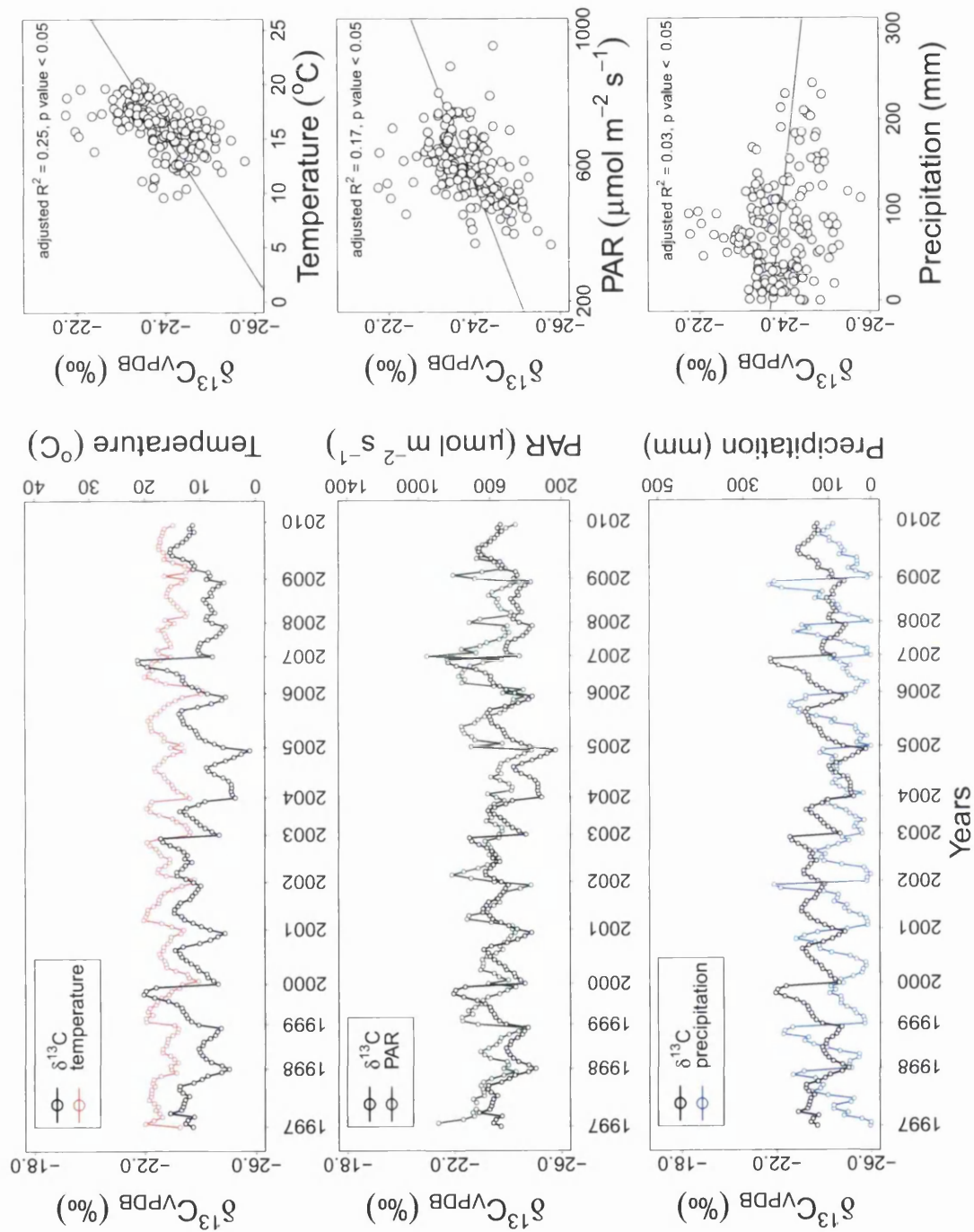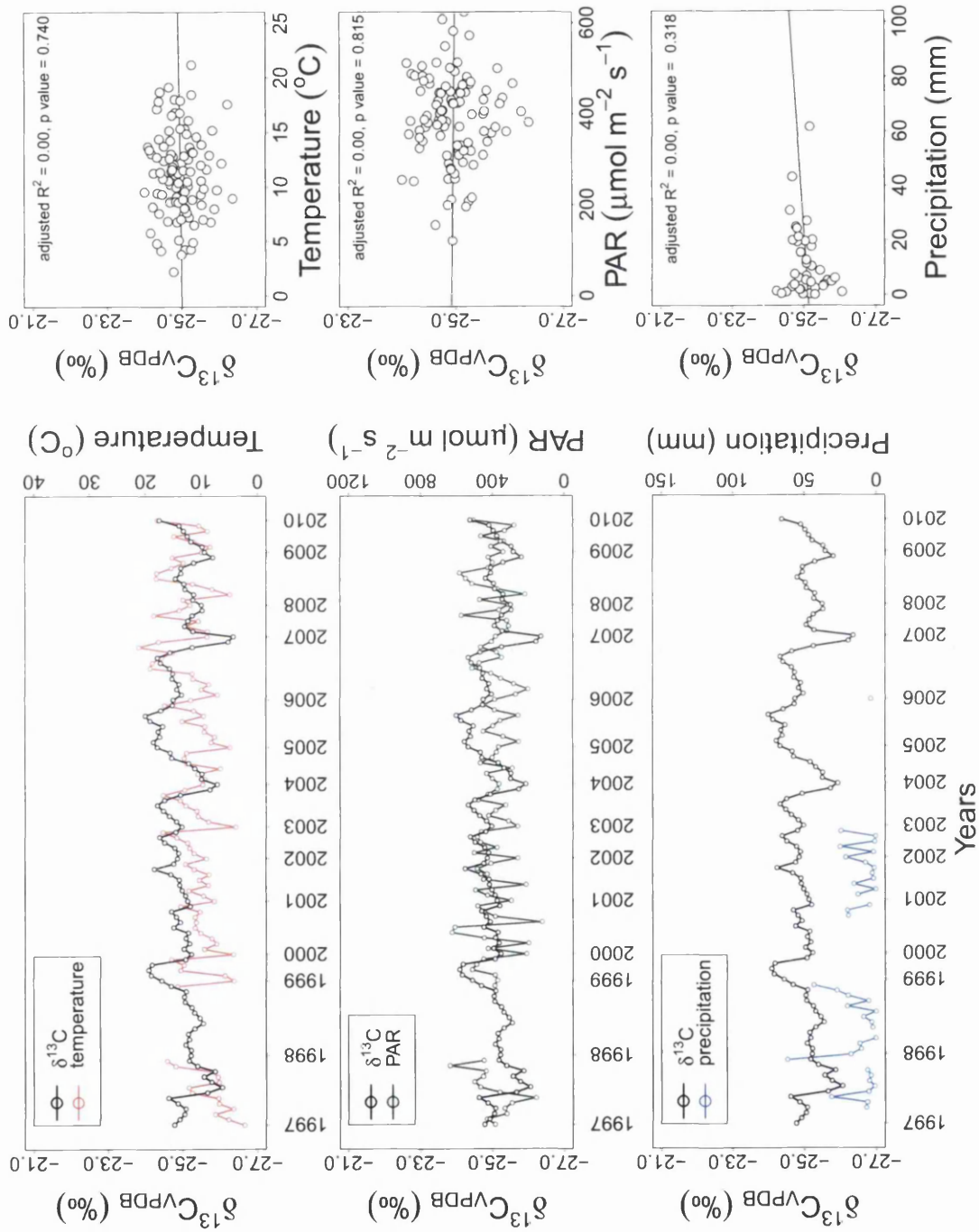
Figure 6.88: *Left: Intra-annual comparison between $\delta^{13}C$ (black open circles), temperature (red open circles), PAR (green open circles) and precipitation (blue open circles) for the period 1997-2009 at Norunda. Right: The linear regression with the adjusted R^2 value and p value.*

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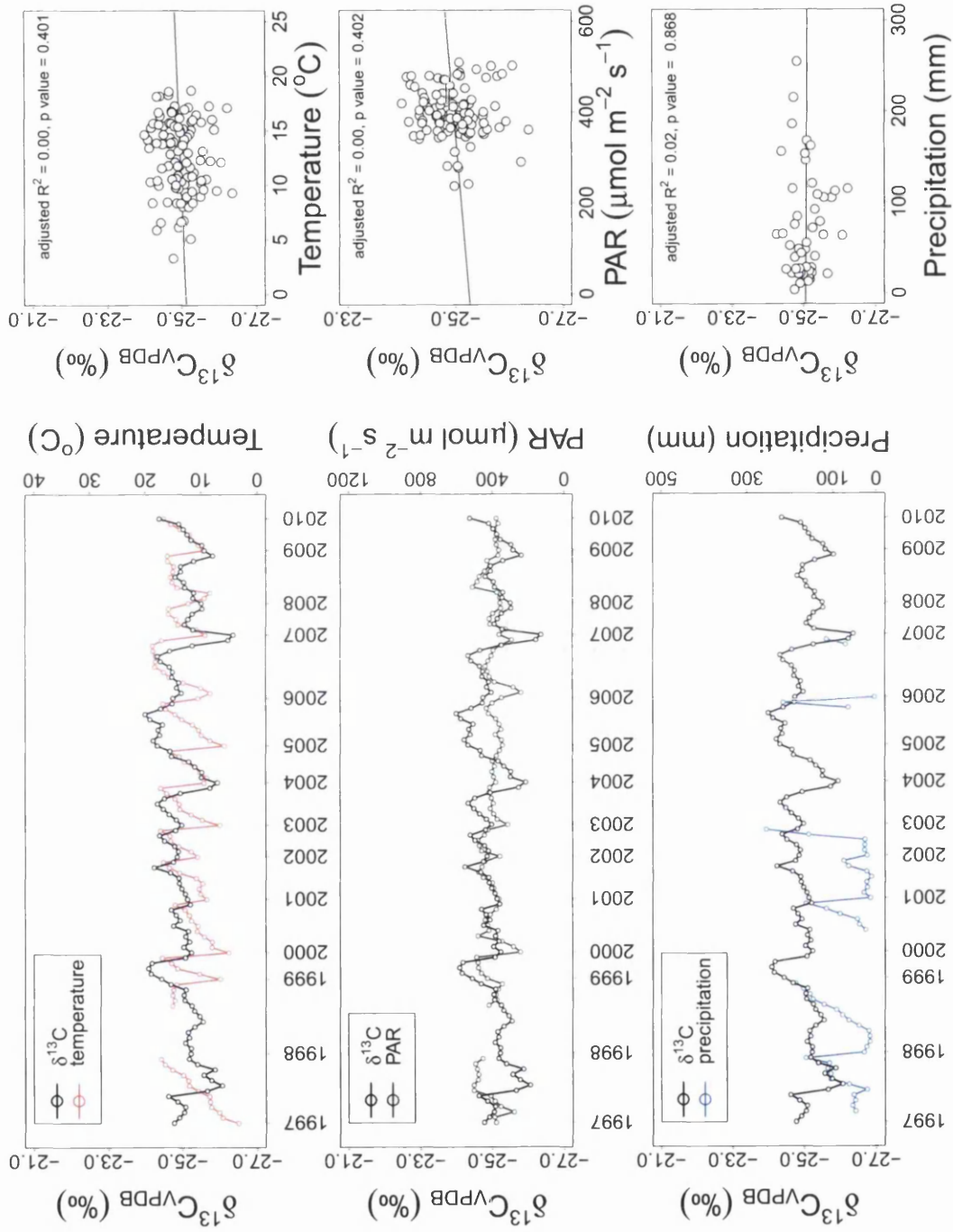
Figure 6.89: *Left: Intra-annual comparison between $\delta^{13}C$ (black open circles), temperature (red open circles), PAR (green open circles) and precipitation (blue open circles) with cell life time. Right: The linear regression with the adjusted R^2 value and p value.*

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6.4 Correlation of weather variables at Loobos at the intra-annual resolution

6.4.1 δ^{13}C time series over the period of wood growth estimated by using dendrometer measurements

6.4.1.1 Simple linear regression between δ^{13}C time series and weather variables

At Loobos, the application of linear regressions between intra-annual δ^{13}C values and weather variables provides similar results to the ones observed at Norunda with the three single linear regressions being not significant (Figure 6.90).

Including the cell life time period when matching weather and δ^{13}C values at Loobos does not provide an improvement in the understanding of the weather influence over the intra-annual δ^{13}C values by observing single linear regressions (Figure 6.91). As none of the weather variables presents a significant relationship with the δ^{13}C values, the multiple linear regression will also be not significant and will not be displayed as its capacity in the prediction of δ^{13}C values is negligible.

Figure 6.90: *Left: Intra-annual comparison between $\delta^{13}C$ (black open circles), temperature (red open circles), PAR (green open circles) and precipitation (blue open circles) for the period 1997-2009 at Loobos. Right: The linear regression with the adjusted R^2 value and p value.*

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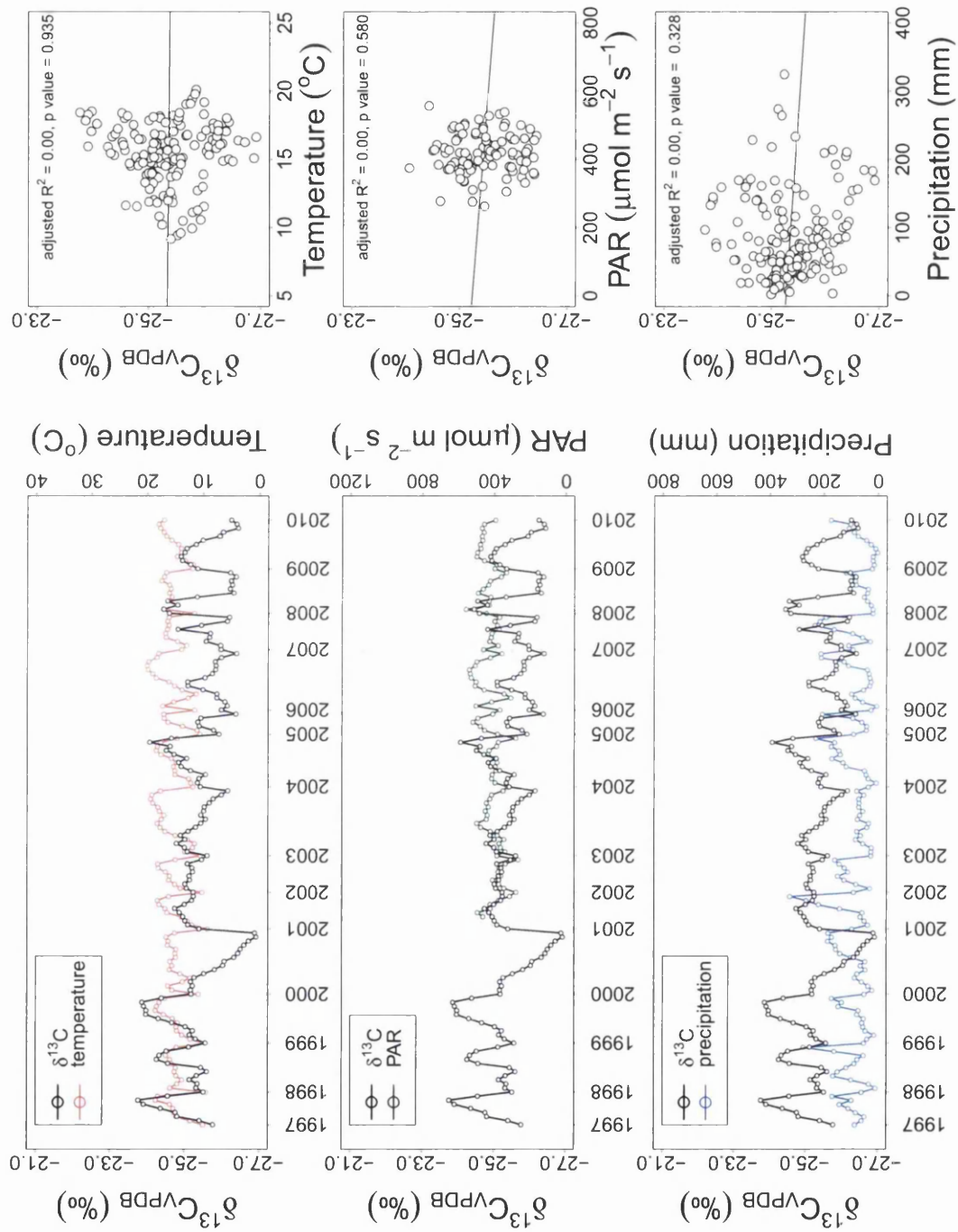
Figure 6.91: *Left: Intra-annual comparison between $\delta^{13}C$ (black open circles), temperature (red open circles), PAR (green open circles) and precipitation (blue open circles) with cell life time. Right: The linear regression with the adjusted R^2 value and p value.*

6.5 Conclusion

At the intra-annual resolution, the linear regression fits between $\delta^{13}C$ and weather time series show weaker relationships than at the inter-annual resolution. At Hyytiälä, the linear regressions still present the best fits compared to Norunda and Loobos that show no significance in the linear relationships between the weather variables and $\delta^{13}C$ values (see Section 6.2.4, Table 6.29). The dataset based on the microcore measurements still produces better fits than the ones based on the dendrometer measurements. The application of cell life time also provides an improvement in the fit of both single and multiple linear regressions. The match between the measured and modelled $\delta^{13}C$ values can be further improved when applying light intensity smooth splines to the $\delta^{13}C$ time series which decreases the low frequency variation. It can then be seen that the smoothed modeled time series struggles mainly to predict the $\delta^{13}C$ values at the end of each tree-ring section. However, the smoothing procedure also change the climate signal property and the increase in the adjustment of the linear regression cannot be directly linked to an increase in the quality of the signal. Measured $\delta^{13}C$ values can be either overestimated or underestimated by the modelled $\delta^{13}C$ values in the late tree-ring section depending on the years. However, when referring to Figure 3.21 in Chapter III, it seems unlikely that a difference between modelled and measured $\delta^{13}C$ values that greater than 1 ‰ could be explained by the difference in air $\delta^{13}C$ values between August and September that has an amplitude less than 0.5 ‰. Therefore, physiological influences are to be considered to explain this unpredicted variation in latewood as the weather influence seems out of cause. Chapter VII will now present the discussion for this study.

Chapter VII : Discussion

7.1 Evaluation of the method for estimating wood formation dates

Wood formation is the product of the cambial cell differentiation during a short time window where environmental factors and the physiological activity can influence the cell formation process into a final tree-ring (Frankenstein *et al.*, 2005). Therefore, researchers are trying to track these influences by analysing tree-ring width, carbon pools and isotope composition of the wood. How relatively short weather events are recorded by trees during the growing season is still a new field to explore (Rossi *et al.*, 2012). As the time frame for the calibration between climate and wood formation is changing from one year to another, it is critical to understand the onset of wood formation as well as the cessation and rate of growth during each year.

Previous studies have investigated the link between tree growth and climate; they are usually focusing on either tree height growth by observing phenological changes (apical activity, leaves sprouts) or radial growth by the use of radial increment measurements (dendrometers, microcores). Interestingly, the same climatic controls are mentioned in the literature for both growth processes: temperature (Moser *et al.*, 2010) and photoperiod (Chuine, 2010; Körner & Basler, 2010). Most studies have focused on estimating dates for the onset of either height or radial growth formation while the cessation of growth has been left aside (Gričar *et al.*, 2007; Rossi & Deslauriers, 2007; Seo *et al.*, 2008; Turcotte *et al.*, 2009). The reason for the lack of knowledge on the radial growth cessation is principally due to its poor correlation with climate or physiological activity. There are only few studies on radial growth cessation estimation procedures (Menzel *et al.*, 2006).

The first investigation was conducted by Garner & Allard (1923) on the effect of the photoperiod on height growth cessation. The cessation of height growth has then been characterised by the co-occurrence of critical short photoperiod

(Weiser, 1970; Kramer, 1936). However, no equivalent link was established in the current study between estimated dates of radial growth cessation and PAR. A second hypothesis based upon temperature made the observation that height cessation in boreal forest was induced by sudden cold nights (Korpilahti, 1988). More recent studies seem to agree on the combined effect of night length and air temperature (Hanninen & Kramer, 2007). Kalcsits *et al.* (2009) also insisted on the importance of cold night time temperature having a greater impact on growth cessation than day time temperature. However, the importance of warm temperature co-occurring with short photoperiod was also pointed out in a range of latitudes for different tree species (Tanino *et al.*, 2010; Dormling, 1989; Heide, 2003). For Scots pine, another method using temperature sum accumulation seems to have been a valid method to estimate height growth cessation (Koski & Sievanen, 1985). Interestingly, an early start of height growth seems to be generally followed by an early growth cessation (Koski & Sievanen, 1985; Vihera-Aarnio *et al.*, 2005). This pattern would suggest that the temperature sum accumulation method could be used to characterise both onset and cessation dates, an early onset provoked by the effect of higher temperature sum in spring being carried over to determine an early cessation in autumn (Hänninen & Tanino, 2011). Recent investigations tried to verify the possible control on the cessation of growth indirectly by the date of wood onset which would set the time that is available for cells to form during the growing season (Lupi *et al.*, 2010). However, this hypothesis was not verified when correlating directly onset and cessation dates (Rossi *et al.*, 2012). The correlation between each stage of the growth process makes sense when considering that the effect of warm night temperature tends to diminish the time to achieve growth (earlier date of growth cessation). Therefore, the cessation date may not be set up by a specific climate factor or physiological process but could be the result of the weather conditions affecting the rate of growth during the growing season.

These findings could not be confirmed at the three selected study sites of the current study. The simple approach using direct temperature and PAR effect on growth onset provided more accurate estimates assessed by dendrological records. However, radial growth cessation dates did not seem to co-occur in a consistent manner with weather in late summer. Therefore the method proposed in this study with threshold values still constitutes an improvable technique. A method using cumulative temperature degree days has been tested at the study sites and seems to be relatively accurate in estimating wood growth when using dendrometer measurements. However, this method did not succeed in predicting onset and cessation dates estimated when using the microcore measurements. The use of this method for deriving the radial growth onset could be inappropriate as the sum

of degree days is not coupled with an active and co-occurring biological process constrained by temperature or light (Bonhomme, 2000).

Despite altitude or latitude changes, the time range in which the onset and cessation are occurring seems to be quite short. Rossi *et al.* (2012) states onset dates from mid-May to mid-June (DOY 138–177) and cessation dates from mid-July to beginning of September (DOY 189–250) for black spruce (*Picea mariana*) of the boreal forest of Quebec, Canada. For the year 2010 in the central Swiss Alps, Simard *et al.* (2013) calculated mean onset dates within a range from mid-May (DOY 138 ±3.0, altitude 1300m, *Larix decidua*) to start of June (DOY 159 ±3.5, altitude 2200m, *Larix decidua*) and mean cessation dates from end of October (DOY 302 ±6.0, altitude 2200m, *Larix decidua*) to beginning of November (DOY 311 ±0.0, altitude 1300m, *Larix decidua*). Despite the difference in location and tree species, the dates for growth onset and cessation are in a similar range than the ones estimated at the study sites based on the methods presented in Chapter IV. Therefore, the approach selected in this study can provide a realistic range of wood growth dates while the inter-annual variation may not be reproduced correctly.

Canopy level carbon dioxide and water fluxes also seem to be uncorrelated from the tree-ring δ^{13}C variation over the period 1997-2009 at both annual and intra-annual scales. This has been previously observed by Offermann *et al.* (2011). They suggest that storage compounds are characterised by a different δ^{13}C signature than the one from the current photosynthates and can be integrated in the tree-ring at the same time. Therefore, the final tree-ring δ^{13}C signature is resulting from the combination of the different carbon compounds. The post-photosynthetic fractionation processes can also alternate the δ^{13}C signature from the phloem stable isotopes ratio to the final tree-ring (Offermann *et al.*, 2011). While the above approach is not detailed in the present study, preliminary results showed no potential to use atmospheric carbon dioxide and water fluxes to predict intra-annual δ^{13}C variations.

A study from Tanja *et al.* (2003), focusing on the determination of the onset of the photosynthesis by the mean of NEE measurements found that air temperature was the best predictor at northern locations in Scandinavia. The study site from Norunda was selected and did not present a significant relationship between temperature and photosynthesis onset. This information ties-in with the results presented in Sections 5.3 and 6.3. Another approach tested in Tanja *et al.* (2003) was to correlate the photosynthesis onset with soil temperature and the

snow melt. However, no relationship was found which could indicate that these two environmental variables cannot be used to predict the photosynthetic onset. The availability of records from these variables at a study site may then not be an essential feature to predict wood growth.

The use of Gompertz curve to model wood growth when dendrological data are available show a good adequation with the normalised wood growth from dendrometers or microcores. However, due to the uncertainties in the determination of onset and cessation dates by the method of the thresholds on temperature or PAR presented in Chapter IV, the Gompertz curve can mismatch the realistic period of growth when dendrological data are unavailable. An alternative approach to this method may lie with the application of existing models such as the Vaganov-Shashkin model (VS) (Vaganov *et al.*, 2006), the simple biosphere model (SIB) (Sellers *et al.*, 1986) or the TREERING model applied to isotopes (Hemming *et al.*, 2001).

7.2 δ^{13}C variation as a link to physiological activities

As the weather amplitude during the year is becoming greater when moving towards the northern latitudes in Europe, trees need to be able to endure the cold and dark season and restart growth and physiological processes each year at the onset of the warm and sunny season (Leavitt, 1969; Heide *et al.*, 1985; Leinonen & Hanninen, 2002). Therefore, trees rely on an annual development cycle to survive in unfavorable weather conditions in winter and perform growth in favorable weather conditions in summer (Weiser, 1970; Perry, 1971; Sarvas, 1972; Fuchigami *et al.*, 1982). This cycle has to be synchronised with the weather variation of each year to trigger growth when the potential conditions causing frost damage are no longer occurring (Koski & Sievänen, 1982). Evergreen species keep old needles from one year to the next and do not need to produce fresh leaves before the start of photosynthesis and stem growth. While the cycle for growth is occurring, the concentration of sugars in the cambial zone increases. These sugars in a soluble state can either come from previous year remobilised starch or from the early photosynthesis production and are essential to growth. Highest concentration co-occur at the end of the radial increment, matching the peak in the lignification process (Simard *et al.*, 2013). Previous studies investigated the relationship between the concentration of sugars (or pool of carbon compounds) and the altitude / latitudes of trees. The hypothesis being that greater concentration of sugars or

larger pools of carbon reserves would be an adaptation of trees to survive harsh conditions in high elevations / latitudes (Fajardo *et al.*, 2013). However no link between the variation through the season of the available sugars and the gradient of altitude / latitude was found (Hoch *et al.*, 2002; Pomeroy *et al.*, 1970; Fischer & Höll, 1991, 1992). Therefore, the growth process seems not to be limited by the carbon supply (Körner, 2003b) and could be more sensitive to environmental controls when one wants to explain the variation in growth performance of the trees between low and high altitude / latitude (Simard *et al.*, 2013). Another study by Uggla *et al.* (2001) reported no correlation between the availability of carbon compounds and the latewood initiation suggesting that the wood formation cycle could also be internally independent on the carbon pool.

These studies support the hypothesis that trees, even at the limit of their geographic distribution, are not limited by carbon supplies (Körner, 2003b; Fajardo *et al.*, 2013). Other control factors on the cambial activity may be involved like the conversion from the carbon compounds to the tissues and a temperature limitation at the highest altitude/ latitudes limiting growth processes below 5 °C (James *et al.*, 1994; Körner, 2006; Solfjeld & Johnsen, 2006; Alvarez-Uria & Körner, 2007). This would suggest that at the thermal treeline, growth is controlled by temperature restrictions preventing the formation of wood tissues under the 5 °C treshold (Fajardo *et al.*, 2013). However, the trees growing at the selected study sites are not experiencing temperatures that could critically impair their probability of survival during the growing season but still show annual patterns of growth with winter cessations. If the carbon pool is not limiting for trees and the weather is permissive to growth for most of the year, it is still necessary to find the appropriate controls on the radial growth cycle for the studied trees. These controls could vary for the different locations depending on which environmental variables are limiting the conversion of carbon compounds to tree tissues. Therefore, more studies on physiological processes at the intra-annual resolution are needed to understand how the tree-ring δ^{13}C time series can be influenced by non-climatic factors and permit the extraction of climate driven only δ^{13}C variation.

7.3 Interpretation of the δ^{13}C variation at different time resolutions for the three study sites

The common wood compound used for isotope analysis is cellulose despite a high correlation between wholewood and cellulose carbon isotope signal (Leavitt &

Long, 1986; Schleser, 1990; Livingston & Spittlehouse, 1996). Some studies also analysed earlywood / latewood isotope ratios instead of the whole-ring as a possible correlation from the earlywood to the previous year isotope values could be present in some tree species (Hill *et al.*, 1995; Rebetez *et al.*, 2003; Saurer *et al.*, 2000). Variation between tree species is also a factor to take into consideration when analysing the differences in carbon isotope ratio. Previous publications cover a vast range of locations and the comparison of the δ^{13}C time series from this study with previous studies can help to understand how the isotope ratio varies accordingly with its location. Vaganov *et al.* (2009) found a strong latitudinal effect in $\delta^{13}C$ annual time series of *Picea abies* when comparing values coming from Italy, Germany and Sweden. When restricting the range of publications to carbon isotope analysis on wood from Scots pines, most study sites were selected in northern Scandinavia. Therefore, the effect of latitude on δ^{13}C time series from Scots pine trees has not been assessed at the European scale. Brendel *et al.* (2002) did a study in Scotland natural stands of Scots pine trees varying in altitude and landscape. No differences in the mean wood cellulose δ^{13}C values were found despite significantly different weather conditions at the stand locations. The results presented in the current study show a similar range of annual values of δ^{13}C time series from Scots pines over the period 1997 to 2009 for the study sites. However, the year to year variation in the mean annual value of δ^{13}C shows a gradual pattern where Hyytiälä has the greatest variation in δ^{13}C inter-annual time series followed by Norunda and finally Loobos. If climate is to be considered to be the main driver of the δ^{13}C variation, a common variation between δ^{13}C and climate records at the inter-annual scale would have been detected at the three study sites while the procedure including cell life time should have provided an improvement in the quality of the signal. However, during the growing season at Hyytiälä average temperature and average PAR values are less variable inter-annually in the period 1997 to 2009 than at the two other sites. Only the mean precipitation sum is varying in a larger proportion during these years. One possible explanation is that Hyytiälä holds the lowest mean temperature and mean PAR of the three study sites and that even a small variation in limiting weather conditions can have a considerable effect on the δ^{13}C variation.

7.4 Determining the link between carbon isotope and climate at the three study sites: model assessment

Kozlowski & Pallardy (2002) identified that the tree growth requirements are carbon dioxide and oxygen from the atmosphere, water and minerals from the soil, light and temperature as catalysts of the growth process. Considering that the carbon pool is not limiting for trees at the study sites in northern Europe, the construction of a model to predict growth should focus on these environmental factors as constraints on the speed of conversion from carbon compounds to tree tissues. The variation in the $\delta^{13}C$ time series should reflect how the combined effect of these factors are impacting the growth processes. However, comparing single environmental variables with the $\delta^{13}C$ time series provided only a limited explanation of the $\delta^{13}C$ intra-annual variation in this work at Hyytiälä. Moreover, the combination of the three tested weather variables only provided a small improvement in the prediction of the $\delta^{13}C$ variation.

Rigling *et al.* (2002) showed that the relationship between a single variable and the $\delta^{13}C$ time series can vary from a positive to a negative relationship when a second variable is causing a strong limitation to tree growth. Barbour *et al.* (2002) also reported a shift in the importance of environmental variables when correlating carbon stable isotopes at different study sites. $\delta^{13}C$ time series can present a significant correlation with a single environmental variable at a specific study site but the same relationship will not be significant at another study site. In the current study, the $\delta^{13}C$ time series show significant linear relationships with the three selected climate factors (temperature, PAR and precipitation) at Hyytiälä while the relationships are not significant at Norunda and Loobos. Therefore, it is essential to consider a wider range of environmental influences to be able to explain the climatic variation contained in the $\delta^{13}C$ time series. As the combination between water, temperature and light availability presumably is key to understanding the relationship of $\delta^{13}C$ time series with other environmental variables, it is surprising that none of the tested weather variables present a significant relationship with $\delta^{13}C$ time series. Light limitation of photosynthesis has been reported to affect the $\delta^{13}C$ values (Leavitt & Long, 1986; McCarroll & Pawellek, 2001) as well as the combined effect of water and light availability (Geßler *et al.*, 2001; Farquhar *et al.*, 1989). The nitrogen availability in the soil has also been reported to enhance the impact of water stress in the variation of $\delta^{13}C$ (Högberg *et al.*, 1995; Livingston *et al.*, 1999). These results suggest that an appropriate use of multiple

linear regression models could explain seasonal $\delta^{13}C$ variation at the study sites presenting significant relationships with environmental variables.

When applying the cell life theory to the $\delta^{13}C$ time series, different results occurred depending on the resolution used to observe the $\delta^{13}C$ variation. At the inter-annual resolution, the additional time for climate integration induced by the inclusion of cell life duration provided an improvement of the linear regressions when the weather variables where not previously showing a significant relationship. Therefore, the proposition made by Schollaen et $al.$ (2014) to include cell life time in intra-annual isotopes studies seems legitimate when the goal is to obtain the best explanatory power from the combined effect of these three weather variables. However, as the integration period from each climate factor seems to vary as shown by the use of both dendrometer and microcore measurements, it is recommended to observe the climate time series integrated over different time periods and select the integration window matching best the $\delta^{13}C$ variation. At the intra-annual resolution, there is a clear improvement to the fit obtained by single and multiple linear regressions suggesting that the application of cell life time is mandatory to obtain a climatic signal from these weather variables in the intra-annual $\delta^{13}C$ time series. However, the application of the cell life time procedure at Norunda and Loobos did not present any improvement in the linear regressions. A better understanding of the non-climatic influences in the intra-annual $\delta^{13}C$ variation could then provide a clue to the weak climate signal detected at these study sites.

At the inter-annual resolution, the choice to use either dendrometer or microcore measurements to estimate the growing season influences significantly the regression fits between weather variables and annual $\delta^{13}C$ values. At Hyytiälä, when using dendrometer measurements, temperature and PAR present a higher adjusted R squared value than precipitation (temperature, $R^2 = 0.51$; PAR, $R^2 = 0.52$; precipitation, $R^2 = 0.37$) with the application of cell life time. However, when using microcore measurements, PAR is clearly showing a stronger linear regression than temperature and precipitation (temperature, $R^2 = 0.25$; PAR, $R^2 = 0.51$; precipitation, $R^2 = 0.16$). The results of Chapter V follow the pattern predicted by McCarroll & Loader (2004) for northern Europe which is more influenced by light and low moisture stress than at southern locations. Young et $al.$ (2010) also reported the $\delta^{13}C$ series to better predict sunshine or cloud cover rather than other climate variables on long scale chronologies in northern Scandinavia. This would suggest that the principal process driving the $\delta^{13}C$ signature in tree-rings at Hyytiälä is coming from the photosynthetic rate as itself is driven by the effect

of temperature and light on the enzyme production and its activity (McCarroll & Pawellek, 2001). However, these results were not confirmed at Norunda and Loobos where the relationships between the weather variables are found to be not significant at both annual and intra-annual resolutions. The fact that the temperature relationship with δ^{13}C values is weaker when using microcore measurements to predict radial growth could suggest that different time integration periods are needed to match each weather variable to annual δ^{13}C values instead of a unique set of onset and cessation dates. However, The multiple linear regression model shows that the modelled annual δ^{13}C values provide a high adjusted R squared value for both dendrological records which induce no preference for one or the other method of recording tree growth when predicting annual δ^{13}C values.

Unlike the results obtained at the inter-annual scale at Hyytiälä, the use of microcore measurements show clearly an improvement in the linear regression for temperature compared to dendrological measurements at the intra-annual resolution. It is noticeable that the adjusted R squared values are lower than the ones found at the inter-annual resolution. This can be partially explained by mismatches when modelling the seasonal growth period via the Gompertz equation due to its sensitivity to onset and cessation dates estimation. As demonstrated by using the Akaike information criterion, both temperature and PAR variables can be considered as explanatory factors to the intra-annual δ^{13}C variation when cell life time is applied. Hence, modelled Hyytiälä values (by multiple linear regression) reproduce a similar pattern of variation than measured δ^{13}C values. However, this model fails to predict the intra-annual δ^{13}C variation with confidence. The lack of relationship between intra-annual δ^{13}C values and climate was already described by Skomarkova et al. (2006) who found only the central period of the growing season to relate with the concurrent assimilation and climate. As storage processes and cell maturation are occurring at the same time during this period, non-climatic influences may be a reason for the differences between modelled and measured δ^{13}C time series. The slight improvement in the fit when smoothing the modelled and measured δ^{13}C time series can come from a resilience of the δ^{13}C time series to record small scale weather events at the intra-annual resolution.

Another clue to understand why the model applied in this study does not explain a greater part of the variability of the measured δ^{13}C time series results from the observations of the years 1999 and 2006 at Hyytiälä where the δ^{13}C values are increasing nearly till the end of the tree-ring while the weather conditions are favourable for growth during most of the estimated growing season with temperatures above 10 °C and increasing precipitation events. Therefore,

instead of showing a negative trend between $\delta^{13}C$ time series and precipitation inducing more negative $\delta^{13}C$ values during the release from water stress, the $\delta^{13}C$ values become less negative with the increase in rainfall. This phenomenon can be explained by a higher rate of photosynthesis that could be resulting from the presence of optimum conditions for growth. This would suggest the $\delta^{13}C$ time series can record undistinguishably water stress induced by a lack of rainfall and increases in the rate of photosynthesis due to the presence of favorable weather conditions. By measuring the daily wood increment and scaled $\delta^{13}C$ values over three years on *Eucalyptus nitens* in Tasmania, Drew & Downes (2009) presented a strong relationship between the rate of growth and the $\delta^{13}C$ time series. Moreover, Drew *et al.* (2009) proposed a theory showing that the trees could possibly use the stored carbon compounds accumulated during a stressed period to incorporate into the tree-ring after the release from a water stress which then show high $\delta^{13}C$ while co-occurring during the release of water stress (Chapin *et al.*, 1990). The relationship between the climate and the $\delta^{13}C$ time series can only be assumed to be direct when the tree-ring is formed from current photosynthate. When the tree uses stored photosynthate or increases its rate of growth, the $\delta^{13}C$ signature is then impaired by physiological and storage processes (Helle & Schleser, 2004; Schulze *et al.*, 2004; Skomarkova *et al.*, 2006). This kind of study may be the answer to the unexplained variance of $\delta^{13}C$ time series at the northern Europe study sites.

7.5 Research implications and further investigations

The relationship between $\delta^{13}C$ time series and weather variables at Hyytiälä presents a strong linear behaviour at the annual resolution. Therefore, the methodology seems valid to produce growing season onset and cessation. However, at the intra-annual resolution the linear fit decreases considerably while still being significant. The linear response of the $\delta^{13}C$ time series to co-occurent temperature, PAR and precipitation time series appeared to vary depending on which measurements of growth were selected to estimate the growing season. It is then a possibility that the integration period for weather variables should be individualised to obtain the highest fit with $\delta^{13}C$ time series. The application of cell life time has shown some encouraging results to improve linear fits and therefore enhance the capacity of a multiple linear regression model to predict $\delta^{13}C$ time series with good confidence at the inter-annual resolution and show a small but significant improvement at the intra-annual resolution. At Norunda and Loobos, the linear pattern between

δ^{13}C time series and weather variables is not significant at both annual and intra-annual resolution. Therefore, the use of linear regressions at these two study sites is inappropriate to inform about the relationship between climate and δ^{13}C values. Because of the possibly stronger involvement of physiological processes at these study sites, a mechanistic approach may bring a deeper understanding of the climate signal in the δ^{13}C time series at these locations. However, current stomatal models are designed to simulate the δ^{13}C from the leaves and fail to significantly correlate with measured δ^{13}C chronologies from the wood (Bodin *et al.*, 2013).

Another approach to improve the understanding of the isotope variation in wood is to produce a dual carbon and oxygen isotope chronology. As oxygen isotope time series (δ^{18}O) are being reported to be closer to precipitation and relative humidity, a dual isotope approach would provide information on the stomatal conductance variation through the growing season (Gessler *et al.*, 2009). Barbour *et al.* (2002) suggest that when the water is not limiting for the tree growth, the δ^{13}C time series would not show an enrichment in its values while the δ^{18}O time series would present large increases in relationship to the relative humidity or vapour pressure deficit. Therefore, the availability of the soil water content and vapour pressure deficit information would be essential to test a dual isotope approach at the study sites.

The consideration of additional information on the wood properties such as the microfibril angle presented in Drew & Downes (2009) show a good potential to inform on the growth rate during water stress events as variations in the microfibril angle seem to be most likely to occur during rapid growth. As a decrease in microfibril angle is characteristic of an increasing drought (Wimmer *et al.*, 2002), the co-occurrence of an increase in δ^{13}C values would be the indication of rapid growth.

Chapter VIII : Conclusion

Carbon stable isotope chronologies represent a powerful tool to reconstruct climate over different time resolutions. The current study presents an innovative approach to intra-annual $\delta^{13}C$ time series production and calibration against meteorological variables. The analysis over three study sites in Europe provided a solid basis to test this approach and the responsiveness of thirteen years of $\delta^{13}C$ values to climate forcing at both annual and intra-annual resolutions. The characteristics of the study sites in term of variation in the climate response is an essential feature allowing $\delta^{13}C$ time series from different sites to be used as climate archives. Moreover, the replicability of the approach developed at the three study sites represents a first step in developing a generic method accessible for non-specialists in dendroclimatology.

The use of laser systems still presents some technical challenges to ensure high quality when producing $\delta^{13}C$ time series at high resolution. However, no other current system can produce intra-annual $\delta^{13}C$ with a better time efficiency. The expressed population signal (EPS) calculated for many independent $\delta^{13}C$ measurements at the intra-annual scale signals a high common signal from the three $\delta^{13}C$ time series developed at Hyytiälä but not at Norunda and Loobos. However, calculating the EPS statistic over such short time series of $\delta^{13}C$ can be unsound and may only provide an approximate indication of the environmental influence on the $\delta^{13}C$ time series. To allow the correlation of co-occurrent weather variables with the $\delta^{13}C$ time series, three different methods have been compared and a considerable effort has been invested to find the best estimate of radial growth. During the years when dendrological data were available, the method using the net ecosystem exchange was found to systematically overestimate the duration of the radial growth period. The evapotranspiration method produced more realistic onset dates for the radial growth period but the cessation dates were still overestimated compared to dendrological information. Finally, a new method developed in the current study using temperature and PAR provided the closest values of radial growth onset and cessation compared to the dendrological dataset. This method, based on threshold values operating over the smoothed time series of

the weather variables and cumulated amounts of PAR, provided the final dates to estimate the radial growth period when dendrological information were unavailable at the three study sites. However, the analysis over a greater dendrological dataset is still needed to confirm the consistency of this method especially for the cessation dates where the method seems still to be imprecise. When comparing the estimated radial growth period between the study sites, Hyytiälä presents a significantly shorter length than either Norunda and Loobos. The final step to climate calibration was to set the timing of the wood formation for each intra-annual $\delta^{13}C$ values. The use of the Gompertz equation originally applied for cell growth purposes has been adapted in the current study to provide wood formation dates to the intra-annual time series. The estimated dates of the radial growth provided a constraint to the Gompertz curve parametrisation taking into account the singularity of each year of growth. Therefore, this method represents an attempt to provide the more realistic time window to calibrate co-occurrent weather variables with wood formation dates at the intra-annual resolution. The consideration of the cell life duration to estimate the co-occurring climate window provided an interesting development as the cells are theoretically able to record the climate signal during their entire life span. Application of this theory has resulted in an improvement of the prediction of measured $\delta^{13}C$ values by a multiple linear regression model using temperature, PAR and precipitation. The use of dendrometer or microcore measurements to estimate the growing season has shown to influence greatly the results of the linear regressions. At the inter-annual resolution, despite a shift of importance between temperature and PAR, both types of measurements lead to a similar variance explained for the multiple linear regression model. However, at the intra-annual resolution, microcore measurements are clearly advisable to use as the growing season determination using dendrometer measurements do not lead to significant linear regressions when matching weather variables and $\delta^{13}C$ time series.

Very different climate characteristics were identified at the three sites as controls on the annual and intra-annual isotope signal. At the annual resolution, Hyytiälä can be identified to be the study site with the lowest temperatures, Norunda receiving the less rainfall with the lowest PAR input while Loobos receives the highest rainfall with the highest temperatures. However, during the growing season, the temperature at Hyytiälä and Norunda are quite similar while the PAR input is larger at Norunda. Finally at Loobos, the precipitation input is similar to Hyytiälä and is smaller than at to Norunda. Therefore, a realistic estimate of the radial growth period is critical to achieve climate calibration.

The choice of linear regressions to characterise the relationship between weather variables and $\delta^{13}C$ time series seems to be justified at Hyytiälä despite a lower fit at the intra-annual resolution. The main climate influence found at this study site is PAR at the inter-annual scale while temperature becomes more influencing at the intra-annual scale. The potential to reconstruct climate information using a linear regression model seems to be greater at the annual resolution than at the intra-annual resolution. The procedure to smooth the $\delta^{13}C$ values has proved to be effective to increase the fit of the model at the intra-annual resolution but is not enough to bring the relationship with climate to high R squared values. Therefore, the use of linear regressions as a predictive tool at the intra-annual resolution is valid only when the relationship between $\delta^{13}C$ values and climate forcing is direct and dominant.

At Norunda and Loobos, the $\delta^{13}C$ time series do not respond linearly to the tested weather variables. To improve the understanding of this lack of response, other climate influences would need to be evaluated. An evaluation of the water stress via the soil water content and the vapour pressure deficit would be a useful complement to this study. The development of a $\delta^{18}O$ chronology on the same period as well as the microfibrille angle would also bring insight on the relation between the trees and the climate forcing at these sites. Finally, the development of a mechanistic approach to model the wood $\delta^{13}C$ response to climate forcing would be a major development to make in the coming years.

Bibliography

ALVAREZ-URIA, P., & KÖRNER, C. 2007. Low temperature limits of root growth in deciduous and evergreen temperate tree species. *Functional Ecology*, **21**(2), 211–218.

ANDERSON, D. E., VERMA, S. B., & ROSENBERG, N. J. 1984. Eddy correlation measurements of CO_2, latent heat and sensible heat fluxes over a crop surface. *Boundary-Layer Meteorology*, **29**, 263–272.

ANTONOVA, G. F., & SHEBEKO, V. V. 1981. Formation of xylem in conifers. II. Seasonal dynamics of processes determining formation of annual wood rings. *Lesovedenie*.

ANTONOVA, G. F., SHEBEKO, V. V., & MALYUTINA, E. S. 1983. Seasonal dynamics of cambial activity and tracheid differentiation in the stem of Scots pine. *Khimiya Drevesiny*, 16–22.

ARANDA, I., PARDOS, M., PUÉRTOLAS, J., JIMÉNEZ, M. D., & PARDOS, J. A. 2007. Water-use efficiency in cork oak (*Quercus suber*) is modified by the interaction of water and light availabilities. *Tree physiology*, **27**(5), 671–677.

ARENS, N. C., JAHREN, A. H., & AMUNDSON, R. 2009. Can C3 plants faithfully record the carbon isotopic composition of atmospheric carbon dioxide? *Paleobiology*.

BALDOCCHI, D., FALGE, E., GU, L., OLSON, R., HOLLINGER, D., RUNNING, S., ANTHONI, P., BERNHOFER, C., DAVIS, K., EVANS, R., FUENTES, J., GOLDSTEIN, A., KATUL, G., LAW, B., LEE, X., MALHI, Y., MEYERS, T., MUNGER, W., OECHEL, W., PAW, K. T., PILEGAARD, K., SCHMID, H. P., VALENTINI, R., VERMA, S., VESALA, T., WILSON, K., & WOFSY, S. 2001. FLUXNET: A New Tool to Study the Temporal and Spatial Variability of Ecosystem–Scale Carbon Dioxide, Water Vapor, and Energy Flux Densities. *Bulletin of the American Meteorological Society*, **82**, 2415–2434.

BALDOCCHI, D. D. 2003. Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present and future. *Global Change Biology*, **9**(4), 479–492.

BALDOCCHI, D. D., HICKS, B. B., & MEYERS, T. P. 1988. Measuring biosphere-atmosphere exchanges of biologically related gases with micrometeorological methods. *Ecology*, **69**(5), 1331–1340.

BARBOUR, M. M., ANDREWS, T. J., & FARQUHAR, G. D. 2001. Correlations between oxygen isotope ratios of wood constituents of *Quercus and Pinus* samples from around the world. *Functional Plant Biology*, **28**(5), 335–348.

BARBOUR, M. M., WALCROFT, A. S., & FARQUHAR, G. D. 2002. Seasonal variation in $\delta^{13}C$ and $\delta^{18}O$ of cellulose from growth rings of *Pinus radiata*. *Plant, Cell & Environment*, **25**(11), 1483–1499.

BATTIPAGLIA, G., DE MICCO, V., BRAND, W. A., LINKE, P., ARONNE, G., SAURER, M., & CHERUBINI, P. 2010. Variations of vessel diameter and $\delta^{13}C$ in false rings of *Arbutus unedo L.*reflect different environmental conditions. *New Phytologist*, **188**(4), 1099–1112.

BÄUCKER, E., BUES, C-T., & VOGEL, M. 1998. Radial growth dynamics of spruce (*Picea abies*) measured by micro-cores. *Iawa Journal*, **19**, 301–310.

BAUMGARTNER, A. 1969. Meteorological approach to the exchange of CO_2 between atmosphere and vegetation, particularly forests stands. *Photosynthetica*, **3**, 127–149.

BERT, D., LEAVITT, S. W., & DUPOUEY, J-L. 1997. Variations of wood $\delta^{13}C$ and water-use efficiency of *Abies alba*during the last century. *Ecology*, **78**(5), 1588–1596.

BODIN, P. E., GAGEN, M., MCCARROLL, D., LOADER, N. J., JALKANEN, R., ROBERTSON, I., SWITSUR, V. R, WATERHOUSE, J. S., WOODLEY, E. J., & YOUNG, G. H. F. 2013. Comparing the performance of different stomatal conductance models using modelled and measured plant carbon isotope ratios ($\delta^{13}C$): implications for assessing physiological forcing. *Global change biology*.

BONHOMME, R. 2000. Bases and limits to using 'degree. day'units. *European Journal of Agronomy*, **13**(1), 1–10.

BORELLA, S., LEUENBERGER, M., SAURER, M., & SIEGWOLF, R. 1998. Reducing uncertainties in $\delta^{13}C$ analysis of tree rings: pooling, milling, and cel-

lulose extraction. *Journal of Geophysical Research: Atmospheres (1984–2012)*, **103**(D16), 19519–19526.

BOWLING, D. R., McDOWELL, N. G., BOND, B. J., LAW, B. E., & EHLERINGER, J. R. 2002. ^{13}C content of ecosystem respiration is linked to precipitation and vapor pressure deficit. *Oecologia*, **131**(1), 113–124.

BRADLEY, R. S. 1999. *Paleoclimatology: reconstructing climates of the Quaternary.* Academic Press.

BRADLEY, R. S., HUGHES, M. K., & DIAZ, H. F. 2003. Climate in Medieval time. *Science*, **302**, 404–405.

BRENDEL, O., HANDLEY, L., & GRIFFITHS, H. 2002. Differences in δ^{13}C and diameter growth among remnant Scots pine populations in Scotland. *Tree physiology*, **22**(14), 983–992.

BRIFFA, K. R. 2000. Annual climate variability in the Holocene: interpreting the message of ancient trees. *Quaternary Science Reviews*, **19**, 87–105.

BRIFFA, K. R., & JONES, P. D. 1990. Basic chronology statistics and assessment. *Methods of dendrochronology: applications in the environmental sciences*, 137–152.

BRIFFA, K. R., JONES, P. D., PILCHER, J. R., & HUGHES, M. K. 1988. Reconstructing summer temperatures in northern Fennoscandinavia back to A. D. 1700 using tree-ring data from Scots pine. *Arctic and Alpine Research*, **20**, 385–394.

BRODRIBB, T. J., & McADAM, S. A. M. 2011. Passive origins of stomatal control in vascular plants. *Science*, **331**(6017), 582–585.

BUHAY, W. M., EDWARDS, T. W. D., & ARAVENA, R. 1996. Evaluating kinetic fractionation factors used for ecologic and paleoclimatic reconstructions from oxygen and hydrogen isotope ratios in plant water and cellulose. *Geochimica et Cosmochimica Acta*, **60**, 2209–2218.

BURBA, G., & ANDERSON, D. 2007. *Introduction to the eddy-covariance method.*

CAMARERO, J. J., GUERRERO-CAMPO, J., & GUTIÉRREZ, E. 1998. Tree-ring growth and structure of *Pinus uncinata* and *Pinus sylvestris* in the Central Spanish Pyrenees. *Arctic and Alpine Research*, 1–10.

CERNUSAK, L. A., MARSHALL, J. D., COMSTOCK, J. P., & BALSTER, N. J. 2001. Carbon isotope discrimination in photosynthetic bark. *Oecologia*, **128**(1), 24–35.

CERNUSAK, L. A., WINTER, K., & TURNER, B. L. 2009. Physiological and isotopic (δ^{13}C and δ^{18}O) responses of three tropical tree species to water and nutrient availability. *Plant, Cell & Environment*, **32**(10), 1441–1455.

CHAPIN, F. S., SCHULZE, E-D., & MOONEY, H. A. 1990. The ecology and economics of storage in plants. *Annual review of ecology and systematics*, **21**, 423–447.

CHUINE, I. 2010. Why does phenology drive species distribution? *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**(1555), 3149–3160.

COCOZZA, C., GIOVANNELLI, A., LASSERRE, B., CANTINI, C., LOMBARDI, F., & TOGNETTI, R. 2012. A novel mathematical procedure to interpret the stem radius variation in olive trees. *Agricultural and Forest Meteorology*, **161**, 80–93.

COOK, E. R, & KAIRIUKSTIS, L. A. 1990. *Methods of dendrochronology: applications in the environmental sciences*. Kluwer Academic Print on Demand.

COOK, E. R, & PETERS, K. 1981. The smoothing spline: a new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. *Tree-Ring Bulletin*.

COOK, E. R., BRIFFA, K. R., & JONES, P. D. 1994. Spatial regression methods in dendroclimatology: a review and comparison of two techniques. *International Journal of Climatology*, **14**, 379–402.

COPLEN, T. B. 1995. Discontinuance of SMOV and PDB. *Nature*, **375**, 285.

COPLEN, T. B. 2006. After two decades a second anchor for the VPDB $\delta^{13}C$ scale. *Rapid Communication in Mass spectrometry*, **20**, 3165–3166.

COWAN, I. R. 1982. Regulation of water use in relation to carbon gain in higher plants. *Pages 589–613 of: Physiological Plant Ecology II*. Springer.

CRAIG, H. 1954. Carbon-13 variations in Sequoia rings and the atmosphere. *Science*, **119**(3083), 141–143.

CRAIG, H., & GORDON, L. I. 1965. Deuterium and oxygen 18 variations in the ocean and the marine atmosphere. *Stable Isotopes in Océanographie Studies and Paleotemperatures, Spoleto*, 9–130.

DAMESIN, C., & LELARGE, C. 2003. Carbon isotope composition of current-year shoots from *Fagus sylvatica* in relation to growth, respiration and use of reserves. *Plant, Cell and Environment*, **26**, 207–219.

DE LAETER, J. R., BÖHLKE, J. K., DE BIÈVRE, P., HIDAKA, H., PEISER, H. S., ROSMAN, K. J. R., & TAYLOR, P. D. P. 2000. Atomic weights of the elements: review 2000. *Pure Applied Chemistry*, **75**(683).

DENMEAD, O. T. 1969. Comparative micrometeorology of a wheat field and a forest of *Pinus radiata*. *Agricultural and Forest Meteorology*, **6**, 357–371.

DESJARDINS, R. L., BUCKLEY, D. J., & ST. AMOUR, G. 1984. Eddy flux measurements of CO_2 above corn using a microcomputer system. *Agricultural and Forest Meteorology*, **32**, 257–265.

DOLMAN, A. J., MOORS, E. J., & ELBERS, J. A. 2002. The carbon uptake of a mid latitude pine forest growing on sandy soil. *Agricultural and Forest Meteorology*, **111**(3), 157–170.

DOMEC, J-C., & GARTNER, B. L. 2002. How do water transport and water storage differ in coniferous earlywood and latewood? *Journal of Experimental Botany*, **53**, 2369–2379.

DONGMANN, G., NÜRNBERG, H. W., FÖRSTEL, H., & WAGENER, K. 1974. On the enrichment of $H_2^{18}O$ in the leaves of transpiring plants. *Radiation and Environmental Biophysics*, **11**(1), 41–52.

DONOVAN, L. A., & EHLERINGER, J. R. 1992. Contrasting water-use patterns among size and life-history classes of a semi-arid shrub. *Functional Ecology*, 482–488.

DORMLING, I. 1989. [Role de la photoperiode et de la temperature dans l'induction et la levee de la dormance des plantules de *Pinus sylvestris*L.]. *In: Annales des Sciences Forestieres*.

DOUGLASS, A. E. 1919. *Climatic cycles and tree-growth*. Vol. 1. Carnegie Institution of Washington.

DOWNES, G., BEADLE, C., & WORLEDGE, D. 1999. Daily stem growth patterns in irrigated Eucalyptus globulus and E. nitens in relation to climate. *Trees*, **14**(2), 102–111.

DREW, D. M., & DOWNES, G. M. 2009. The use of precision dendrometers in research on daily stem size and wood property variation: a review. *Dendrochronologia*, **27**(2), 159–172.

DREW, D. M., SCHULZE, E. D., & DOWNES, G. M. 2009. Temporal variation in $\delta^{13}C$, wood density and microfibril angle in variously irrigated *Eucalyptus nitens*. *Functional plant biology*, **36**(1), 1–10.

DUFOUR, B., & MORIN, H. 2007. Focusing modelling on the tracheid development period–an alternative method for treatment of xylogenesis intra-annual data. *Dendrochronologia*, **25**, 125–133.

DUPOUEY, J-L., LEAVITT, S., CHOISNEL, E., & JOURDAIN, S. 1993. Modelling carbon isotope fractionation in tree rings based on effective evapotranspiration and soil water status. *Plant, Cell & Environment*, **16**(8), 939–947.

DUQUESNAY, A., BREDA, N., STIEVENARD, M., & DUPOUEY, J. L. 1998. Changes of tree-ring δ13C and water-use efficiency of beech (*Fagus sylvatica L.*) in north-eastern France during the past century. *Plant, Cell & Environment*, **21**(6), 565–572.

EDWARDS, T. W. D., GRAF, W., TRIMBORN, P., STICHLER, W., LIPP, J., & PAYER, H. D. 2000. $\delta^{13}C$ response surface resolves humidity and temperature signals in trees. *Geochimica et Cosmochimica Acta*, **64**(2), 161–167.

EHLERINGER, J. R., & COOPER, T. A. 1988. Correlations between carbon isotope ratio and microhabitat in desert plants. *Oecologia*, **76**(4), 562–566.

EHLERINGER, J. R., FIELD, C. B., LIN, Z-F., & KUO, C-Y. 1986. Leaf carbon isotope and mineral composition in subtropical plants along an irradiance cline. *Oecologia*, **70**(4), 520–526.

EILMANN, B., BUCHMANN, N., SIEGWOLF, R., SAURER, M., CHERUBINI, P., & RIGLING, A. 2010. Fast response of Scots pine to improved water availability reflected in tree-ring width and $\delta^{13}C$. *Plant, cell & environment*, **33**(8), 1351–1360.

EPSTEIN, S., KRISHNAMURTHY, R. V., OESCHGER, H., EDDY, J. A., & PECKER, J-C. 1990. Environmental information in the isotopic record in trees [and discussion]. *Philosophical Transactions of the Royal Society of London. Series A, Mathematical and Physical Sciences*, **330**(1615), 427–439.

ESPER, J., COOK, E. R., & SCHWEINGRUBER, F. H. 2002. Low-frequency signals in long tree-ring chronologies for reconstructing past temperature variability. *Science*, **295**(5563), 2250–2253.

FAJARDO, A., PIPER, F. I., & HOCH, G. 2013. Similar variation in carbon storage between deciduous and evergreen treeline species across elevational gradients. *Annals of Botany.*

FARQUHAR, G. D., O'LEARY, M. H., & BERRY, J. A. 1982. On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. *Australian Journal of Plant Physiology,* **9**, 121–137.

FARQUHAR, G. D., EHLERINGER, J. R., & HUBICK, K. T. 1989. Carbon isotope discrimination and photosynthesis. *Annual review of plant biology,* **40**(1), 503–537.

FEBRUARY, E. C., & STOCK, W. D. 1999. Declining Trend in the ^{13}C / ^{12}C Ratio of Atmospheric Carbon Dioxide from Tree Rings of South African *Widdringtonia cedarbergensis.* Quaternary Research, **52***(2), 229–236.*

FENG, X. *1998. Long-term c_i/c_a response of trees in western North America to atmospheric CO_2 concentration derived from carbon isotope chronologies.* Oecologia, **117***(1-2), 19–25.*

FENG, X., & EPSTEIN, S. *1995a. Carbon isotopes of trees from arid environments and implications for reconstructing atmospheric CO_2 concentration.* Geochimica et Cosmochimica Acta, **59***(12), 2599–2608.*

FENG, X., & EPSTEIN, S. *1995b. Climatic temperature records in δD data from tree rings.* Geochimica et Cosmochimica Acta, **59***(14), 3029–3037.*

FISCHER, C., & HÖLL, W. *1991. Food reserves of Scots pine (Pinus sylvestris L.). Trees,* **5**(4), 187–195.

FISCHER, C., & HÖLL, W. 1992. Food reserves of scots pine (*Pinus sylvestris* L.). *Trees,* **6**(3), 147–155.

FOKEN, T. 2006. 50 years of the Monin-Obukhov similarity theory. *Boundary-Layer Meteorology,* **119**, 431–447.

FRANCEY, R. J., & FARQUHAR, G. D. 1982. An explanation of $^{13}C/^{12}C$ variations in tree rings. *Nature,* **297**, 28–31.

FRANCEY, R. J., MANNING, M. R., ALLISON, C. E., CORAM, S. A., ETHERIDGE, D. M., LANGENFELDS, R. L., LOWE, D. C., & STEELE, L. P. 1999. A history of delta C-13 in atmospheric CH_4 from the Cape Grim air archive and antarctic firn air. *Journal of geographical research-atmospheres,* **104**(D19), 23631–23643.

FRANK, D., ESPER, J., & COOK, E. R. 2006. On variance adjustments in tree-ring chronology development. *Tree rings in archaeology, climatology and ecology, TRACE*, **4**, 56–66.

FRANKENSTEIN, C., ECKSTEIN, D., & SCHMITT, U. 2005. The onset of cambium activity–a matter of agreement? *Dendrochronologia*, **23**(1), 57–62.

FRASER, P. J. B., FRANCEY, R. J., & PEARMAN, G. I. 1978. Stable carbon isotopes in tree rings as climatic indicators. *DSIR Bull*, **220**, 67–73.

FREYER, H. D., & BELACY, N. 1983. C-13 C-12 records in northern hemispheric trees during the past 500 years - Anthropogenic impact and climatic superpositions. *journal of geophysical research-oceans and atmospheres*, **88**(NC11), 6844–6852.

FRITTS, H. C. 1976. *Tree rings and climate*. Academic Press, New York.

FUCHIGAMI, L. H., WEISER, C. J., KOBAYASHI, K., TIMMIS, R., & GUSTA, L. V. 1982. A degree growth stage (GS) model and cold acclimation in temperate woody plants. *Plant cold hardiness and freezing stress*, **2**, 93–116.

FUJII, T., SALANG, A. T., & FUJIWARA, T. 1999. Growth periodicity in relation to the xylem development in three Shorea spp.(Dipterocarpaceae) growing in Sarawak. *Tree-ring analysis: biological, methodological and environmental aspects*, 169–183.

GAGEN, M., MCCARROLL, D., & EDOUARD, J-L. 2004. Latewood width, maximum density, and stable carbon isotope ratios of pine as climate indicators in a dry subalpine environment, French Alps. *Arctic, Antarctic, and Alpine Research*, **36**(2), 166–171.

GAGEN, M., MCCARROLL, D., LOADER, N. J., ROBERTSON, I., JALKANEN, R., & ANCHUKAITIS, K. J. 2007. Exorcising thesegment length curse': summer temperature reconstruction since AD 1640 using non-detrended stable carbon isotope ratios from pine trees in northern Finland. *The Holocene*, **17**(4), 435–446.

GAGEN, M., MCCARROLL, D., ROBERTSON, I., LOADER, N. J., & JALKANEN, R. 2008. Do tree ring δ^{13}C series from *Pinus sylvestris* in northern Fennoscandia contain long-term non-climatic trends? *Chemical Geology*, **252**(1), 42–51.

GARNER, W. W., & ALLARD, H. A. 1923. *Further studies in photoperiodism: the response of the plant to relative length of day and night*. US Government Printing Office.

GARRATT, J. R. 1992. *The Atmospheric Boundary Layer.* Cambridge University Press.

GESSLER, A., SCHREMPP, S., MATZARAKIS, A., MAYER, H., RENNENBERG, H., & ADAMS, M. A. 2001. Radiation modifies the effect of water availability on the carbon isotope composition of beech (*Fagus sylvatica*). *New Phytologist,* **150**(3), 653–664.

GESSLER, A., BRANDES, E., BUCHMANN, N., HELLE, G., RENNENBERG, H., & BARNARD, R. L. 2009. Tracing carbon and oxygen isotope signals from newly assimilated sugars in the leaves to the tree-ring archive. *Plant, cell & environment,* **32**(7), 780–795.

GONFIANTINI, R. 1984. *Advisory Group Meeting on Stable Isotope Reference Samples for Geochemical and Hydrological Investigations: IAEA, Vienna, 19-21 September 1983: Report to the Director General.* International Atomic Energy Agency.

GRIČAR, J., ZUPANČIČ, M., ČUFAR, K., & OVEN, P. 2007. Regular cambial activity and xylem and phloem formation in locally heated and cooled stem portions of Norway spruce. *Wood Science and Technology,* **41**(6), 463–475.

GRIFFITHS, H. 1998. Stable isotopes, integration of biological, ecological and geochemical processes (Environmental Plant Biology series). *Bios, Oxford,* pp. 303–321.

HANNINEN, H., & KRAMER, K. 2007. A framework for modelling the annual cycle of trees in boreal and temperate regions. *Silva Fennica,* **41**(1), 167.

HÄNNINEN, H., & TANINO, K. 2011. Tree seasonality in a warming climate. *Trends in plant science,* **16**(8), 412–416.

HARLOW, B. A., MARSHALL, J. D., & ROBINSON, A. P. 2006. A multi-species comparison of delta C-13 from whole wood, extractive-free wood and holocellulose. *Tree physiology,* **26**(6), 767–774.

HEIDE, O. M. 2003. High autumn temperature delays spring bud burst in boreal trees, counterbalancing the effect of climatic warming. *Tree Physiology,* **23**(13), 931–936.

HEIDE, O. M., BUSH, M. G., & EVANS, L. T. 1985. Interaction of photoperiod and gibberellin on growth and photosynthesis of high-latitude *Poa pratensis. Physiologia Plantarum,* **65**(2), 135–145.

HELLE, G., & SCHLESER, G. H. 2004. Beyond CO_2-fixation by Rubisco–an interpretation of $^{13}C/^{12}C$ variations in tree rings from novel intra-seasonal studies on broad-leaf trees. *Plant, Cell & Environment*, **27**(3), 367–380.

HEMMING, D., FRITTS, H. C., LEAVITT, S. W., WRIGHT, W., LONG, A., & SHASHKIN, A. 2001. Modelling tree-ring $\delta 13C$. *Dendrochronologia*, **19**(1), 23–38.

HEMMING, D., YAKIR, D., AMBUS, P., AURELA, M., BESSON, C., BLACK, K., BUCHMANN, N., BURLETT, R., CESCATTI, A., & CLEMENT, R. 2005. Pan-European $\delta^{13}C$ values of air and organic matter from forest ecosystems. *Global Change Biology*, **11**(7), 1065–1093.

HEMMING, D. L., SWITSUR, V. R., WATERHOUSE, J. S., HEATON, T. H. E., & CARTER, A. H. C. 1995. Climate and the stable carbon isotope composition of tree ring cellulose: an intercomparison of three tree species. *Tellus*, **50B**, 25–32.

HEMMING, D. L., SWITSUR, V. R., WATERHOUSE, J. S., HEATON, T. H. E., & CARTER, A. H. C. 1998. Climate variation and the stable carbon isotope composition of tree ring cellulose: an intercomparison of *Quercus robur, Fagus sylvatica*and *Pinus silvestris*. *Tellus B*, **50**(1), 25–33.

HERZOG, K. M., HÄSLER, R., & THUM, R. 1995. Diurnal changes in the radius of a subalpine Norway spruce stem: their relation to the sap flow and their use to estimate transpiration. *Trees*, **10**(2), 94–101.

HESTERBERG, R., & SIEGENTHALER, U. 1991. Production and stable isotope composition of CO_2 in a soil near Bern, Switzerland. *Tellus*, **43**(B), 197–205.

HILL, S. A., WATERHOUSE, J. S., FIELD, E. M., SWITSUR, V. R., & AP REES, T. 1995. Rapid recycling of triose phosphates in oak stem tissue. *Plant, Cell & Environment*, **18**(8), 931–936.

HOCH, G., POPP, M., & KÖRNER, C. 2002. Altitudinal increase of mobile carbon pools in *Pinus cembra*suggests sink limitation of growth at the Swiss treeline. *Oikos*, **98**(3), 361–374.

HÖGBERG, P., JOHNNISSON, C., HÖGBERG, M., HÖGBOM, L., NÄSHOLM, T., & HÄLLGREN, J-E. 1995. Measurements of abundances of ^{15}N and ^{13}C as tools in retrospective studies of N balances and water stress in forests: A discussion of preliminary results. *Plant and Soil*, **168**(1), 125–133.

HUGHES, M. K. 2002. Dendrochronology in climatology - the state of the art. *Dendrochronologia*, **20**, 95–116.

HUGHES, M. K., & FUNKHOUSER, G. 1998. Extremes of moisture availability reconstructed from tree rings for recent millennia in the great Basin of western North America. *Lectures Notes in Earth Sciences*, **74**, 99–107.

INOUE, I. 1958. An aerodynamic measurement of photosynthesis over a paddy field. *Pages 211–214 of: Procedure Seventh Japan National Congress of Applied Mechanics*.

IQBAL, M. 1994. Structural and operational specializations of the vascular cambium of seed plants. *Growth patterns in vascular plants. Dioscorides Press: Oregon*, 211–271.

JÄGGI, M, SAURER, M, FUHRER, J, & SIEGWOLF, R. 2002. The relationship between the stable carbon isotope composition of needle bulk material, starch, and tree rings in Picea abies. *Oecologia*, **131**(3), 325–332.

JAHREN, A. H., & STERNBERG, L. S. L. 2008. Annual patterns within tree rings of the Arctic middle Eocene (ca. 45 Ma): Isotopic signatures of precipitation, relative humidity, and deciduousness. *Geology*, **36**(2), 99–102.

JAMES, J. C., GRACE, J., & HOAD, S. P. 1994. Growth and photosynthesis of *Pinus sylvestris* at its altitudinal limit in Scotland. *Journal of Ecology*, 297–306.

JARVIS, P. G., JAMES, G. B., & LANDSBERG, J. J. 1976. *Coniferous forest. Vegetation and the Atmosphere*. Vol. 2. Academic Press.

JONES, P. D., OSBORN, T. J., & BRIFFA, K. R. 2001. The Evolution of Climate Over the Last Millennium. *Science*, **292**(5517), 662–667.

JORDAN, M. O., & MARIOTTI, A. 1997. Can carbon isotopic discrimination in young peach trees be considered as a tool to understand the seasonal dynamic of the stored carbon? *Pages 327–336 of: IV International Peach Symposium 465*.

KAGAWA, A., NAITO, D., SUGIMOTO, A., & MAXIMOV, T. C. 2003. Effects of spatial and temporal variability in soil moisture on widths and $\delta^{13}C$ values of eastern Siberian tree rings. *Journal of Geophysical Research: Atmospheres (1984–2012)*, **108**(D16).

KAGAWA, A., SUGIMOTO, A., & MAXIMOV, T. C. 2006. 13CO2 pulse-labelling of photoassimilates reveals carbon allocation within and between tree rings. *Plant, Cell & Environment*, **29**(8), 1571–1584.

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KAIMAL, J. C., & FINNIGAN, J. J. 1994. *Atmospheric Boundary Layer Flows.* Oxford University Press.

KALCSITS, L. A., SILIM, S., & TANINO, K. 2009. Warm temperature accelerates short photoperiod-induced growth cessation and dormancy induction in hybrid poplar (Populus× spp.). *Trees,* **23**(5), 971–979.

KAWASE, M., & NITSCH, J. P. 1958. Growth substances and the photoperiodic control of growth in Betula pubescens. *Plant Physiol,* **33**, xix.

KELLY, C. K., & WOODWARD, F. I. 1995. Ecological Correlates of Carbon Isotope Composition of Leaves: A Comparative Analysis Testing for the Effects of Temperature, CO_2 and O_2 Partial Pressures and Taxonomic Relatedness on $\delta^{13}C$. *Journal of Ecology,* 509–515.

KING, G., FONTI, P., NIEVERGELT, D., BÜNTGEN, U., & FRANK, D. 2013. Climatic drivers of hourly to yearly tree radius variations along a 6 C natural warming gradient. *Agricultural and Forest Meteorology,* **168**, 36–46.

KITAGAWA, H., & MATSUMOTO, E. 1995. Climatic implications of δ13C variations in a Japanese cedar (*Cryptomeria japonica*) during the last two millenia. *Geophysical Research Letters,* **22**(16), 2155–2158.

KLEIN, T., HEMMING, D., LIN, T., GRÜNZWEIG, J. M, MASEYK, K., ROTENBERG, E., & YAKIR, D. 2005. Association between tree-ring and needle $\delta^{13}C$ and leaf gas exchange in *Pinus halepensis* under semi-arid conditions. *Oecologia,* **144**(1), 45–54.

KLJUN, N., CALANCA, P., ROTACH, M. W., & SCHMID, H. P. 2004. A Simple Parameterisation for Flux Footprint Predictions. *Boundary-Layer Meteorology,* **112**(3), 503–523.

KÖRNER, C. 2003a. *Alpine plant life: functional plant ecology of high mountain ecosystems; with 47 tables.* Springer.

KÖRNER, C. 2003b. Carbon limitation in trees. *Journal of Ecology,* **91**(1), 4–17.

KÖRNER, C. 2006. Plant CO_2 responses: an issue of definition, time and resource supply. *New phytologist,* **172**(3), 393–411.

KÖRNER, C., & BASLER, D. 2010. Phenology under global warming. *Science,* **327**(5972), 1461–1462.

KÖRNER, C., FARQUHAR, G. D., & WONG, S. C. 1991. Carbon isotope discrimination by plants follows latitudinal and altitudinal trends. *Oecologia*, **88**(1), 30–40.

KORPILAHTI, E. 1988. *Photosynthetic production of Scots pine in the natural environment.* Suomen metsätieteellinen seura.

KOSKI, V., & SIEVANEN, R. 1985. Timing of growth cessation in relation to the variations in the growing season. *Crop physiology of forest trees/compiled and edited by Peter MA Tigerstedt, Pasi Puttonen and Veikko Koski.*

KOSKI, V., & SIEVÄNEN, R. 1982. *Timing of growth cessation in relation to the variations in the growing season.* Crop physiology of forest trees. Helsinki University Press, Helsinki, Finland.

KOZLOWSKI, T. T., & PALLARDY, S. G. 2002. Acclimation and adaptive responses of woody plants to environmental stresses. *The Botanical Review*, **68**(2), 270–334.

KOZLOWSKI, T. T., & WINGET, C. H. 1964. Diurnal and seasonal variation in radii of tree stems. *Ecology*, **45**(1), 149.

KRAMER, P. J. 1936. Effect of variation in length of day on growth and dormancy of trees. *Plant Physiol*, **11**(1), 127–137.

KRAMER, P. J., & KOZLOWSKI, T. T. 1960. *Physiology of Trees.* McGraw-Hill: New York.

KRANABETTER, J. M., SIMARD, S. W., GUY, R. D., & COATES, K. D. 2010. Species patterns in foliar nitrogen concentration, nitrogen content and ^{13}C abundance for understory saplings across light gradients. *Plant and soil*, **327**(1-2), 389–401.

KRESS, A., YOUNG, G. H. F., SAURER, M., LOADER, N. J., SIEGWOLF, R. T. W., & MCCARROLL, D. 2009. Stable isotope coherence in the earlywood and latewood of tree-line conifers. *Chemical Geology*, **268**(1), 52–57.

KRISHNAMURTHY, R. V. 1996. Implications of a 400 year tree ring based $^{13}C/^{12}C$ chronology. *Geophysical Research Letters*, **23**, 371–374.

LAGERGREN, F., LINDROTH, A., DELLWINK, E., IBROM, A., LANKREIJER, H., LAUNIAINEN, S., MOLDER, M., KOLARI, P., PILEGAARD, K., & VESALA, T. 2008. Biophysical controls on CO_2 fluxes of three Northern forests based on long-term eddy covariance data. *Tellus*, **60**, 143–152.

LaMarche Jr., V. C. 1974. Palaeoclimate inferences from long tree-ring records. *Science*, **183**, 1043–1048.

Larson, P. R. 1960. A physiological consideration of the springwood summerwood transition in Red Pine (*Pinus resinosa*). *Forest Science*, **6**, 110–22.

Leavitt, J. 1969. Growth and survival of plants at extremes of temperature–a unified concept. *Page 395 of: Symposia of the Society for Experimental Biology*, vol. 23.

Leavitt, S. W. 1993. Seasonal $^{13}C/^{12}C$ changes in tree rings: species and site coherence, and a possible drought influence. *Canadian Journal of Forest Research*, **23**(2), 210–218.

Leavitt, S. W. 2002. Prospects for reconstruction of seasonal environment from tree-ring δ^{13}C: baseline findings from the Great Lakes area, USA. *Chemical Geology*, **192**(1), 47–58.

Leavitt, S. W. 2007. Regional expression of the 1988 U.S. Midwest drought in seasonal $\delta^{13}C$ of tree rings. *Journal of Geophysical Research: Atmospheres*, **112**(D6), n/a–n/a.

Leavitt, S. W., & Lara, A. 1994. South American tree-rings show declining δ^{13}C trend. *Tellus*, **46(**(2), 152–157.

Leavitt, S. W., & Long, A. 1982. Evidence for $^{13}C/^{12}C$ fractionation between tree leaves and wood. *Nature*.

Leavitt, S. W., & Long, A. 1984. Sampling strategy for stable carbon isotope analysis of tree rings in pine. *Nature*.

Leavitt, S. W., & Long, A. 1986. Stable-carbon isotope variability in tree foliage and wood. *Ecology*, **67**(4), 1002–1010.

Leavitt, S. W., & Long, A. 1991. Seasonal stable-carbon isotope variability in tree rings: possible paleoenvironmental signals. *Chemical Geology: Isotope Geoscience section*, **87**(1), 59–70.

Leavitt, S. W., & Newberry, T. 1992. Systematics of stable-carbon isotopic differences between gymnosperm and angiosperm trees. *Plant Physiol*, **11**, 257–262.

Leavitt, S. W., Idso, S. B., Kimball, B. A., Burns, J. M., Sinha, A., & Stott, L. 2003. The effect of long-term atmospheric CO_2 enrichment on the intrinsic water-use efficiency of sour orange trees. *Chemosphere*, **50**(2), 217–222.

LEINONEN, I., & HANNINEN, H. 2002. Adaptation of the timing of bud burst of Norway spruce to temperate and boreal climates. *Silva Fennica*, **36**(3), 695–701.

LEMON, E. R. 1960. Photosynthesis under field conditions. II. An aerodynamic method for determining the turbulent carbon dioxide exchange between the atmosphere and a corn field. *Agronomy Journal*, **52**, 697–703.

LI, Z.-H., LEAVITT, S. W., MORA, C. I., & LIU, R-M. 2005. Influence of earlywood–latewood size and isotope differences on long-term tree-ring $\delta^{13}C$ trends. *Chemical geology*, **216**(3), 191–201.

LINDROTH, A., GRELLE, A., & MORÉN, A-S. 1998. Long-term measurements of boreal forest carbon balance reveal large temperature sensitivity. *Global Change Biology*, **4**(4), 443–450.

LIPP, J., TRIMBORN, P., FRITZ, P., MOSER, H., BECKER, B., & FRENZEL, B. 1991. Stable isotopes in tree ring cellulose and climatic change. *Tellus B*, **43**(3), 322–330.

LIPP, J., TRIMBORN, P., EDWARDS, T., WAISEL, Y., & YAKIR, D. 1996. Climatic effects on the $\delta^{18}O$ and $\delta^{13}C$ of cellulose in the desert tree *Tamarix jordanis*. Geochimica et Cosmochimica Acta, **60***(17), 3305-3309.*

LIU, Y., WU, Z. D., LEAVITT, S. W., & HUGHES, M.K. *1996. Stable carbon isotope in tree rings from Huangling, China and climatic variation.* Science in China Series D-Earth Sciences, **39***(2), 152-161.*

LIVINGSTON, N. J., & SPITTLEHOUSE, D. L. *1996. Carbon isotope fractionation in tree ring early and late wood in relation to intra-growing season water balance.* Plant, Cell & Environment, **19***(6), 768-774.*

LIVINGSTON, N. J., WHITEHEAD, D., KELLIHER, F. M., WANG, Y-P., GRACE, J. C., WALCROFT, A. S., BYERS, J. N., McSEVENY, T. M., & MILLARD, P. *1998. Nitrogen allocation and carbon isotope fractionation in relation to intercepted radiation and position in a young Pinus radiata D. Don tree.* Plant, Cell & Environment, **21***(8), 795-803.*

LIVINGSTON, N. J., GUY, R. D., SUN, Z. J., & ETHIER, G. J. *1999. The effects of nitrogen stress on the stable carbon isotope composition, productivity and water use efficiency of white spruce (Picea glauca (Moench) Voss) seedlings. Plant, Cell & Environment*, **22**(3), 281–289.

LOADER, N. J. 2013. Loader in Press, 2013. *Loader in Press, 2013.*

LOADER, N. J., & SWITSUR, V. R. 1995. Reconstructing past environmental change using stable isotopes in tree rings. *Botanical Journal of Scotland*, **48**, 65–78.

LOADER, N. J., ROBERTSON, I., BARKER, A. C., SWITSUR, V. R., & WATERHOUSE, J. S. 1997. A modified method for the batch processing of small whole wood samples to α-cellulose. *Chemical Geology*, **136**, 313–317.

LOADER, N. J., ROBERTSON, I., & MCCARROLL, D. 2003. Comparison of stable carbon isotope ratios in the whole wood, cellulose and lignin of oak tree-rings. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **196**(3), 395–407.

LUPI, C., MORIN, H., DESLAURIERS, A., & ROSSI, S. 2010. Xylem phenology and wood production: resolving the chicken-or-egg dilemma. *Plant, cell & environment*, **33**(10), 1721–1730.

LUYSSAERT, S., INGLIMA, I., & M., JUNG. 2009. *Global Forest Ecosystem Structure and Function Data for Carbon Balance Research. Data set. Available on-line [http://daac.ornl.gov/]*. Tech. rept. Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, U.S.A.

MÄKINEN, H., NÖJD, P., & SARANPÄÄ, P. 2003. Seasonal changes in stem radius and production of new tracheids in Norway spruce. *Tree Physiology*, **23**(14), 959–968.

MÄKINEN, H., SEO, J-W., NÖJD, P., SCHMITT, U., & JALKANEN, R. 2008. Seasonal dynamics of wood formation: a comparison between pinning, micro-coring and dendrometer measurements. *European Journal of Forest Research*, **127**(3), 235–245.

MANN, M. E., AMMANN, C. M., BRADLEY, R. S., BRIFFA, K. R., CROWLEY, T.J., HUGHES, M. K., JONES, P. D, OPPEN HEIMER, M., OSBORN, T. J., OVERPECK, J. T., RUTHERFORD, S., TRENBERTH, K. E., & WIGLEY, T. M. L. 2003. On past temperatures and anomalous late-20th-century warmth. *Eos, Transactions American Geophysical Union*, **84**(27), 256–256.

MANTGEM, P. J. VAN, & STEPHENSON, N. L. 2004. Does coring contribute to tree mortality? *Canadian Journal of Forest Research*, **34**(11), 2394–2398.

MARTIN, B., & SUTHERLAND, E. K. 1990. Air pollution in the past recorded in width and stable carbon isotope composition of annual growth rings of Douglas-fir. *Plant, Cell & Environment*, **13**(8), 839–844.

MATTHEWS, D. E., & HAYES, J. M. 1978. Isotope-ratio-monitoring gas chromatography-mass spectrometry. *Analytical Chemistry*, **50**(11), 1465–1473.

MATZNER, S. L., RICE, K. J., & RICHARDS, J. H. 2001. Factors affecting the relationship between carbon isotope discrimination and transpiration efficiency in blue oak (*Quercus douglasii*). *Functional Plant Biology*, **28**(1), 49–56.

MAUSETH, J. D. 2003. *Botany: An Introduction to Plant Biology 3rd Edition*. Jones and Barlett: Boston.

MAZANY, T., LERMAN, J. C., & LONG, A. 1980. Carbon-13 in tree-ring cellulose as an indicator of past climates. *Nature*.

MCCARROLL, D., & LOADER, N. J. 2004. Stable isotopes in tree rings. *Quaternary Science Reviews*, **23**(7), 771–801.

MCCARROLL, D., & PAWELLEK, F. 1998. Stable carbon isotope ratios of latewood cellulose in *Pinus sylvestris* from northern Finland: variability and signal-strength. *Holocene*, **8**(6), 675–684.

MCCARROLL, D., & PAWELLEK, F. 2001. Stable carbon isotope ratios of *Pinus sylvestris* from northern Finland and the potential for extracting a climate signal from long Fennoscandian chronologies. *The Holocene*, **11**(5), 517–526.

MCCARROLL, D., JALKANEN, R., HICKS, S., TUOVINEN, M., PAWELLEK, F., GAGEN, M., ECKSTEIN, D., SCHIMTT, U., AUTIO, J., & HEIKKINEN, O. 2003. Multiproxy dendroclimatology: a pilot study in northern Finland. *The Holocene*, **13**, 829–838.

MCDOWELL, N. G., PHILLIPS, N., LUNCH, C., BOND, B. J., & RYAN, M. G. 2002. An investigation of hydraulic limitation and compensation in large, old Douglas-fir trees. *Tree Physiology*, **22**(11), 763–774.

MENZEL, A., SPARKS, T. H., ESTRELLA, N., KOCH, E., AASA, A., AHAS, R., ALM-KÜBLER, K., BISSOLLI, P., BRASLAVSKÁ, O., & BRIEDE, A. 2006. European phenological response to climate change matches the warming pattern. *Global Change Biology*, **12**(10), 1969–1976.

MONTEITH, J. L., & SZEICZ, G. 1960. The CO_2 flux over a field of sugar beets. *Quarterly Journal of the Royal Meteorological Society*, **86**, 205Â–214.

MOSER, L., FONTI, P., BÜNTGEN, U., ESPER, J., LUTERBACHER, J., FRANZEN, J., & FRANK, D. 2010. Timing and duration of European larch growing season along altitudinal gradients in the Swiss Alps. *Tree physiology*, **30**(2), 225–233.

NAKATSUKA, T., OHNISHI, K., HARA, T., SUMIDA, A., MITSUISHI, D., KU-RITA, N., & UEMURA, S. 2004. Oxygen and carbon isotopic ratios of tree-ring cellulose in a conifer-hardwood mixed forest in northern Japan. *GEOCHEMI-CAL JOURNAL-JAPAN-*, **38**(1), 77–88.

NITSCH, J. P., & NITSCH, C. 1957. Auxin-dependent growth of excised Helianthus tuberosus tissues. II. Organic nitrogenous compounds. *American Journal of Botany*, 555–564.

NOCTOR, G., & FOYER, C. H. 1998. A re-evaluation of the ATP: NADPH budget during C3 photosynthesis: a contribution from nitrate assimilation and its associated respiratory activity? *Journal of Experimental Botany*, **49**(329), 1895–1908.

OFFERMANN, C., FERRIO, J. P., HOLST, J., GROTE, R., SIEGWOLF, R., KAYLER, Z., & GESSLER, A. 2011. The long way down—are carbon and oxygen isotope signals in the tree ring uncoupled from canopy physiological processes? *Tree physiology*, **31**(10), 1088–1102.

OGLE, N., & MCCORMAC, F. G. 1994. High-resolution $\delta^{13}C$ measurements of oak show a previously unobserved spring depletion. *Geophysical Research Letters*, **21**(22), 2373–2375.

OHTAKI, E. 1984. Application of an infrared carbon dioxide and humidity instrument to studies of turbulent transport. *Boundary-Layer Meteorology*, **29**, 85–107.

OLDFIELD, F., & ALVERSON, K. 2003. *The societal relevance of paleoenvironmental research.* Springer, berlin.

O'LEARY, M. H. 1981. Carbon Isotope fractionations in plants. *Phytochemistry*, **20**, 553–567.

PACHAURI, R. K., & REISINGER, A. 2007. *Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.*

PANEK, J. A., & GOLDSTEIN, A. H. 2001. Response of stomatal conductance to drought in *ponderosa pine*: implications for carbon and ozone uptake. *Tree physiology*, **21**(5), 337–344.

PANEK, J. A., & WARING, RICHARD H. 1995. Carbon isotope variation in Douglas-fir foliage: improving the δ13C–climate relationship. *Tree Physiology*, **15**(10), 657–663.

PANEK, J. A., & WARING, RICHARD H. 1997. Stable carbon isotopes as indicators of limitations to forest growth imposed by climate stress. *Ecological Applications*, **7**(3), 854–863.

PANOFSKY, H. A., & DUTTON, J. A. 1984. *Atmospheric turbulence: Models and methods for engineering applications.* Wiley (New York).

PATE, J., & ARTHUR, D. 1998. δ^{13}C analysis of phloem sap carbon: novel means of evaluating seasonal water stress and interpreting carbon isotope signatures of foliage and trunk wood of Eucalyptus globulus. *Oecologia*, **117**(3), 301–311.

PENG, T-H., BROECKER, W. S., FREYER, H. D., & TRUMBORE, S. 1983. A deconvolution of the tree ring based δ^{13}C record. *Journal of Geophysical Research: Oceans (1978-2012)*, **88**(C6), 3609–3620.

PERRY, T. O. 1971. Dormancy of trees in winter. *Science*, **171**(3966), 29–36.

PESONEN, E., MIELIKÄINEN, K., & MÄKINEN, H. 2004. A new girth band for measuring stem diameter changes. *Forestry*, **77**(5), 431–439.

PHILLIPS, I. D. J., & WAREING, P. F. 1958. Studies in dormancy of sycamore I. Seasonal changes in the growth-substance content of the shoot. *Journal of Experimental Botany*, **9**(3), 350–364.

POMEROY, M. K., SIMINOVITCH, D., & WIGHTMAN, F. 1970. Seasonal biochemical changes in the living bark and needles of red pine (*Pinus resinosa*) in relation to adaptation to freezing. *Canadian Journal of Botany*, **48**(5), 953–967.

PONS, T. L., & HELLE, G. 2011. Identification of anatomically non-distinct annual rings in tropical trees using stable isotopes. *Trees*, **25**(1), 83–93.

PONTON, S., DUPOUEY, J-L., BRÉDA, N., FEUILLAT, F., BODENES, C., & DREYER, E. 2001. Carbon isotope discrimination and wood anatomy variations in mixed stands of *Quercus robur* and *Quercus petraea*. *Plant, Cell & Environment*, **24**(8), 861–868.

PORTÉ, A., & LOUSTAU, D. 2001. Seasonal and interannual variations in carbon isotope discrimination in a maritime pine (*Pinus pinaster*) stand assessed from the isotopic composition of cellulose in annual rings. *Tree Physiology*, **21**(12-13), 861–868.

PRESTON, T., & OWENS, N. J. P. 1983. Interfacing an automatic elemental analyser with an isotope ratio mass sepectrometer: the potential for fully automated total nitrogen and nitrogen-15 analysis. *Analyst*, **108**(1289), 971–977.

PRESTON, T., & OWENS, N. J. P. 1985. Preliminary ^{13}C measurements using a gas chromatograph interfaced to an isotope ratio mass spectrometer. *Biological Mass Spectrometry*, **12**(9), 510–513.

RAFFALLI-DELERCE, G., MASSON-DELMOTTE, V., DUPOUEY, J. L., STIEVE-NARD, M., BREDA, N., & MOISSELIN, J. M. 2004. Reconstruction of summer droughts using tree-ring cellulose isotopes: A calibration study with living oaks from Brittany (western France). *Tellus B*, **56**(2), 160–174.

RAMESH, R., BHATTACHARYA, S. K., & GOPALAN, K. 1986. Climatic correlations in the stable isotope records of silver fir (*Abies pindrow*) tree from Kashmir, India. *Earth and Planetary Science Letters*, **79**, 66–74.

REBETEZ, M., SAURER, M., & CHERUBINI, P. 2003. To What Extent Can Oxygen Isotopes in Tree Rings and Precipitation Be Used to Reconstruct Past Atmospheric Temperature? A Case Study. *Climatic Change*, **61**(1-2), 237–248.

REYNOLDS, A. 1895. On the dynamical theory of incompressible viscous fluids and the determinatino of the criterion. *Philosophical Transactions of the Royal Society of London*, **186**, 123–164.

RICE, D. L., & TENORE, K. R. 1981. Dynamics of carbon and nitrogen during the decomposition of detritus derived from esturine macrophytes. *Esturine, Coastal and Shelf Sciences*, **13**, 681–690.

RICHARDSON, S. D., & DINWOODIE, J. M. 1960. Studies on the physiology of xylem development. *Journal of the Institute of Wood Science*, **12**.

RIGLING, A., BRÄKER, O., SCHNEITER, G., & SCHWEINGRUBER, F. 2002. Intra-annual tree-ring parameters indicating differences in drought stress of *Pinus sylvestris*forests within the Erico-Pinion in the Valais (Switzerland). *Plant Ecology*, **163**(1), 105–121.

ROBERTSON, I., SWITSUR, V. R., CARTER, A. H. C., BARKER, A. C., WATERHOUSE, J. S., BRIFFA, K. R., & JONES, P. D. 1997a. Signal strength and climate relationships in 13C/12C ratios of tree ring cellulose from oak in east England. *Journal of Geophysical Research: Atmospheres (1984–2012)*, **102**(D16), 19507–19516.

ROBERTSON, I., ROLFE, J., SWITSUR, V. R., CARTER, A. H. C., HALL, M. A., BARKER, A. C., & WATERHOUSE, J. S. 1997b. Signal strength and climate relationships in $^{13}C/^{12}C$ ratios of tree ring cellulose from oak in southwest Finland. *Geophysical Research Letters*, **24**(12), 1487–1490.

ROBERTSON, I., LOADER, N. J., MCCARROLL, D., CARTER, A. H. C., CHENG, L., & LEAVITT, S. W. 2004. δ13C of tree-ring lignin as an indirect measure of climate change. *Pages 531–544 of: Biogeochemical Investigations of Terrestrial, Freshwater, and Wetland Ecosystems across the Globe.* Springer.

RODEN, J. S., JOHNSTONE, J. A., & DAWSON, T. E. 2009. Intra-annual variation in the stable oxygen and carbon isotope ratios of cellulose in tree rings of coast redwood (*Sequoia sempervirens*). *The Holocene*, **19**(2), 189–197.

ROESKE, C. A., & O'LEARY, M. H. 1984. Carbon isotope effects on the enzyme-catalyzed carboxylation of Ribulose Bisphosphate. *Biochemistry*, **23**, 6275–6284.

ROSENBERG, N. J., BLAD, B. L., & VERMA, S. B. 1983. *Microclimate. The biological environment.* A Wiley-interscience publication.

ROSSI, S., & DESLAURIERS, A. 2007. Intra-annual time scales in tree rings. *Dendrochronologia*, **25**(2), 75–77.

ROSSI, S., DESLAURIERS, A., & MORIN, H. 2003. Application of the Gompertz equation for the study of xylem cell development. *Dendrochronologia*, **21**(1), 33–39.

ROSSI, S., DESLAURIERS, A., & ANFODILLO, T. 2006a. Assessment of cambial activity and xylogenesis by microsampling tree species: an example at the Alpine timberline. *Iawa Journal*, **27**, 383.

ROSSI, S., DESLAURIERS, A., ANFODILLO, T., MORIN, H., SARACINO, A., MOTTA, R., & BORGHETTI, M. 2006b. Conifers in cold environments synchronize maximum growth rate of tree-ring formation with day length. *New Phytologist*, **170**(2), 301–310.

ROSSI, S., DESLAURIERS, A., ANFODILLO, T., & CARRARO, V. 2007. Evidence of threshold temperatures for xylogenesis in conifers at high altitudes. *Oecologia*, **152**(1), 1–12.

ROSSI, S., MORIN, H., & DESLAURIERS, A. 2012. Causes and correlations in cambium phenology: towards an integrated framework of xylogenesis. *Journal of Experimental Botany*, **63**(5), 2117–2126.

RYAN, M. G., & YODER, B. J. 1997. Hydraulic limits to tree height and tree growth. *Bioscience.*

SAN JOSE, J., RUBEN, M., & NIKONOVA, N. 2007. Seasonal patterns of carbon dioxide, water vapour and energy fluxes in pineapple. *Agricultural and Forest Meteorology*, **147**(1-2), 16–34.

SARVAS, R. 1972. Investigations on the annual cycle of development of forest trees. Active period. *Metsantutkimuslaitoksen Julkaisuja*, **76**(3).

SAURER, M., & SIEGENTHALER, U. 1989. $^{13}C/^{12}C$ isotope ratios in trees are sensitive to relative humidity. *Dendrochronologia*, **7**, 9–13.

SAURER, M., SIEGENTHALER, U., & SCHWEINGRUBER, F. 1995. The climate-carbon isotope relationship in tree-rings and the significance of site conditions. *Tellus, Serie B*, **47**(3), 320–330.

SAURER, M., AELLEN, K. A. S. R., & SIEGWOLF, R. 1997. Correlating δ^{13}C and δ^{18}O in cellulose of trees. *Plant, Cell & Environment*, **20**(12), 1543–1550.

SAURER, M., CHERUBINI, P., & SIEGWOLF, R. 2000. Oxygen isotopes in tree rings of Abies alba: The climatic significance of interdecadal variations. *Journal of Geophysical Research: Atmospheres*, **105**(D10), 12461–12470.

SCHEIDEGGER, Y., SAURER, M., BAHN, M., & SIEGWOLF, R. 2000. Linking stable oxygen and carbon isotopes with stomatal conductance and photosynthetic capacity: a conceptual model. *Oecologia*, **125**, 350–357.

SCHELHAAS, M. J., NABUURS, G. J., JANS, W., MOORS, E., SABAT, S., & DAAMEN, W. P. 2004. Closing the carbon budget of a Scots pine forest in the Netherlands. *Climatic Change*, **67**(2-3), 309–328.

SCHLESER, G. H. 1990. Investigations of the δ13C Pattern in Leaves of Fagus sylvatica L. *Journal of experimental botany*, **41**(5), 565–572.

SCHLESER, G. H. 1995. Parameters determining carbon isotope ratios in plants. *Paläoklimaforschung*, **15**, 71–96.

SCHLESER, G. H., HELLE, G., LÜCKE, A., & VOS, H. 1999. Isotope signals as climate proxies: the role of transfer functions in the study of terrestrial archives. *Quaternary Science Reviews*, **18**(7), 927–943.

SCHLESER, G.H., & JAYASEKERA, R. 1985. $\delta^{13}C$C-variations of leaves in forests as an indication of reassimilated CO2 from the soil. *Oecologia*, **65**(4), 536–542.

SCHOLLAEN, K., HEINRICH, I., & HELLE, G. 2014. UV-laser-based microscopic dissection of tree rings–a novel sampling tool for δ13C and δ18O studies. *New Phytologist*, **201**(3), 1045–1055.

SCHUBERT, B. A., & JAHREN, A. H. 2011. Quantifying seasonal precipitation using high-resolution carbon isotope analyses in evergreen wood. *Geochimica et Cosmochimica Acta*, **75**(22), 7291–7303.

SCHULZE, B., WIRTH, C., LINKE, P., BRAND, W. A., KUHLMANN, I., HORNA, V., & SCHULZE, E-D. 2004. Laser ablation-combustion-GC-IRMS: a new method for online analysis of intra-annual variation of $\delta^{13}C$ in tree rings. *Tree Physiology*, **24**(11), 1193–1201.

SCHWEINGRUBER, F. H. 1996. *Tree rings and Environment: Dendroecology*. Paul Haupt, Berne.

SELLERS, P. J., MINTZ, Y. C. S. Y., SUD, Y. C. E AL, & DALCHER, A. 1986. A simple biosphere model (SiB) for use within general circulation models. *Journal of the Atmospheric Sciences*, **43**(6), 505–531.

SEO, J.-W., ECKSTEIN, D., JALKANEN, R., RICKEBUSCH, S., & SCHMITT, U. 2008. Estimating the onset of cambial activity in Scots pine in northern Finland by means of the heat-sum approach. *Tree Physiology*, **28**(1), 105–112.

SHEU, D. D., KOU, P., CHIU, C. H., & CHEN, M-J. 1996. Variability of tree-ring $\delta^{13}C$ in Taiwan fir: Growth effect and response to May–October temperatures. *Geochimica et Cosmochimica Acta*, **60**(1), 171–177.

SIMARD, S., GIOVANNELLI, A., TREYDTE, K., TRAVERSI, M. L., KING, G. M., FRANK, D., & FONTI, P. 2013. Intra-annual dynamics of non-structural carbohydrates in the cambium of mature conifer trees reflects radial growth demands. *Tree physiology*, **33**(9), 913–923.

SKOMARKOVA, M. V., VAGANOV, E. A., MUND, M., KNOHL, A., LINKE, P., BOERNER, A., & SCHULZE, E-D. 2006. Inter-annual and seasonal variability of radial growth, wood density and carbon isotope ratios in tree rings of beech (*Fagus sylvatica*) growing in Germany and Italy. *Trees*, **20**(5), 571–586.

SMITH, B. N., OLIVER, J., & MCMILLAN, C. 1976. Influence of carbon source, oxygen concentration, light intensity and temperature on $^{13}C/^{12}C$ ratios in plant tissues. *Botanical Gazette*, **137**(2), 99–104.

SOLFJELD, I., & JOHNSEN, O. 2006. The influence of root-zone temperature on growth of *Betula pendula* Roth. *Trees*, **20**(3), 320–328.

STUDHALTER, R. A., GLOCK, W. S., & AGERTER, S. R. 1963. Tree growth. *The Botanical Review*, **29**(3), 245–365.

STUIVER, M., & BRAZIUNAS, T. F. 1987. Tree cellulose $^{13}C/^{12}C$ isotope ratios and climatic change. *Nature*, **328**(6125), 58–60.

STULL, R. B. 1988. *An Introduction to Boundary Layer Meteorology.* Kluwer Academic Publishers.

SWITSUR, V. R., WATERHOUSE, J. S., FIELD, E. M., CARTER, A. H. C., & LOADER, N. J. 1995. Stable isotope studies in tree rings from oak: techniques and some preliminary results. *Paläoklimaforschung*, **15**, 129–140.

SWITSUR, V. R., WATERHOUSE, J. S., FIELD, E. M., & CARTER, A. H. C. 1996. Climatic signals from stable isotopes in oak tree rings from East Anglia, Great Britain. *Tree Rings, Environment and Humanity Radiocarbon*, 637–645.

TANG, K., FENG, X., & FUNKHOUSER, G. 1999. The $\delta^{13}C$ of tree rings in full-bark and strip-bark bristlecone pine trees in the White Mountains of California. *Global Change Biology*, **5**(1), 33–40.

TANINO, K. K., KALCSITS, L., SILIM, S., KENDALL, E., & GRAY, G. R. 2010. Temperature-driven plasticity in growth cessation and dormancy development in deciduous woody plants: a working hypothesis suggesting how molecular and cellular function is affected by temperature during dormancy induction. *Plant molecular biology*, **73**(1-2), 49–65.

TANJA, S., BERNINGER, F., VESALA, T., MARKKANEN, T., HARI, P., MÄKELÄ, A., ILVESNIEMI, H., HÄNNINEN, H., NIKINMAA, E., & HUTTULA, T. 2003. Air temperature triggers the recovery of evergreen boreal forest photosynthesis in spring. *Global Change Biology*, **9**(10), 1410–1426.

TARDIF, J., FLANNIGAN, M., & BERGERON, Y. 2001. An analysis of the daily radial activity of 7 boreal tree species, northwestern Quebec. *Environmental Monitoring and Assessment*, **67**(1-2), 141–160.

TENG, Y., TANABE, K., TAMURA, F., & ITAI, A. 1999. Translocation of ^{13}C-assimilates in the spring following fall assimilation of $^{13}CO_2$ by 'Nijisseiki' pear (*Pyrus pyrifolia* Nakai). *Japanese Society for Horticultural Science*, **68**, 248–255.

TOFT, N. L., ANDERSON, J. E., & NOWAK, R. S. 1989. Water use efficiency and carbon isotope composition of plants in a cold desert environment. *Oecologia*, **80**(1), 11–18.

TREHARNE, K. J., & COOPER, J. P. 1969. Effect of temperature on the activity of carboxylases in tropical and temperature gramineae. *Journal of Experimental Botany*, **20**, 170–175.

TREYDTE, K., SCHLESER, G. H., SCHWEINGRUBER, F. H., & WINIGER, M. 2001. The climatic significance of $\delta^{13}C$ in subalpine spruces (Lötschental, Swiss Alps). *Tellus B*, **53**(5), 593–611.

TREYDTE, K. S., FRANK, D. C., SAURER, M., HELLE, G., SCHLESER, G. H., & ESPER, J. 2009. Impact of climate and CO_2 on a millennium-long tree-ring carbon isotope record. *Geochimica et Cosmochimica Acta*, **73**(16), 4635–4647.

TROUGHTON, J. H., & CARD, K. A. 1975. Temperature effects on the carbon-isotope ratio of C_3, C_4 and crassulacean-acid-metabolism (CAM) plants. *Planta*, **123**, 185–190.

TURCOTTE, A., MORIN, H., KRAUSE, C., DESLAURIERS, A., & THIBEAULT-MARTEL, M. 2009. The timing of spring rehydration and its relation with the onset of wood formation in black spruce. *Agricultural and Forest Meteorology*, **149**(9), 1403–1409.

UGGLA, C., MAGEL, E., MORITZ, T., & SUNDBERG, B. 2001. Function and dynamics of auxin and carbohydrates during earlywood/latewood transition in Scots pine. *Plant Physiology*, **125**(4), 2029–2039.

UREY, H. 1947. The thermodynamic properties of isotopic subtances. *Journal of the Chemical Society*, **1**, 562–581.

VAGANOV, E. A., HUGHES, M. K., & SHASHKIN, A. V. 2006. *Introduction and Factors Influencing the Seasonal Growth of Trees*. Springer.

VAGANOV, E.A., SCHULZE, E-D., SKOMARKOVA, M.-V., KNOHL, A., BRAND, W. A., & ROSCHER, C. 2009. Intra-annual variability of anatomical structure and $\delta^{13}C$ values within tree rings of spruce and pine in alpine, temperate and boreal Europe. *Oecologia*, **161**(4), 729–745.

VAN DE WATER, P. K., LEAVITT, S. W., & BETANCOURT, J. L. 2002. Leaf $\delta^{13}C$ variability with elevation, slope aspect, and precipitation in the southwest United States. *Oecologia*, **132**(3), 332–343.

VAN DER MERWE, N. J., & MEDINA, E. 1991. The canopy effect, carbon isotope ratios and foodwebs in Amazonia. *Journal of Archaeological Science*, **18**(3), 249–259.

VERHEYDEN, A., ROGGEMAN, M., BOUILLON, S., ELSKENS, M., BEECKMAN, H., & KOEDAM, N. 2005. Comparison between $\delta^{13}C$ of α-cellulose and bulk wood in the mangrove tree *Rhizophora mucronata* : Implications for dendro-chemistry. *Chemical Geology*, **219**(1), 275–282.

VERMA, S. B., BALDOCCHI, D. D., ANDERSON, D. E., MATT, D. R., & CLEMENT, R. E. 1986. Eddy fluxes of CO_2 water vapor, and sensible heat over a deciduous forest. *Boundary-Layer Meteorology*, **36**, 71–91.

VERMA, S. B., KIM, J., & CLEMENT, R. J. 1989. Carbon dioxide, water vapor and sensible heat fluxes over a tall grass prairie. *Boundary-Layer Meteorology*, **46**, 53–67.

VESALA, T. 1998. On the concept of leaf boundary layer resistance for forced convection. *Journal of theoretical biology*, **194**(1), 91–100.

VIHERÄ-AARNIO, A., HÄKKINEN, R., PARTANEN, J., LUOMAJOKI, A., & KOSKI, V. 2005. Effects of seed origin and sowing time on timing of height growth cessation of *Betula pendula* seedlings. *Tree physiology*, **25**(1), 101–108.

VOGEL, J. C. 1980. *Fractionation of the carbon isotopes during photosynthesis.* Springer.

WALCROFT, A. S., SILVESTER, W. B., WHITEHEAD, D., & KELLIHER, F. M. 1997. Seasonal changes in stable carbon isotope ratios within annual rings of *Pinus radiata* reflect environmental regulation of growth processes. *Functional Plant Biology*, **24**(1), 57–68.

WARREN, C. R., MCGRATH, J. F., & ADAMS, M. A. 2001. Water availability and carbon isotope discrimination in conifers. *Oecologia*, **127**(4), 476–486.

WEISER, C. J. 1970. Cold Resistance and Injury in Woody Plants Knowledge of hardy plant adaptations to freezing stress may help us to reduce winter damage. *Science*, **169**(3952), 1269–1278.

WIGLEY, T. M. L., BRIFFA, K. R., & JONES, P. D. 1984. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *Journal of Climate and Applied Meteorology*, **23**(2), 201–213.

WILLIAMS, L. D., & WIGLEY, T. M. L. 1983. A comparison of evidence for late Holocene summer temperature variations in the Northern Hemisphere. *Quaternary Research*, **20**(3), 286–307.

WILSON, A. T., & GRINSTED, M. J. 1975. Palaeotemperatures from tree rings and the D/H ratio of cellulose as a biochemical thermometer. *Nature*.

WILSON, A. T., & GRINSTED, M. J. 1977. $^{12}C/^{13}C$ in cellulose and lignin as palaeothermometers. *Nature*, **265**(5590), 133–135.

WILSON, A. T., & GRINSTED, M. J. 1978. The possibilities of deriving past climate information from stable isotope studies on tree rings. *Stable Isotopes in the Earth Sciences, Department of Scientific and Industrial Research Bulletin, Science Information Division*, 61–66.

WIMMER, R. 2002. Wood anatomical features in tree-rings as indicators of environmental change. *Dendrochronologia*, **20**, 21–36.

WIMMER, R., DOWNES, G. M., & EVANS, R. 2002. Temporal variation of microfibril angle in *Eucalyptus nitens* grown in different irrigation regimes. *Tree physiology*, **22**(7), 449–457.

WODZICKI, T. 1964. Photoperiodic control of natural growth substances and wood formation in larch (*Larix decidua* DC). *Journal of experimental botany*, **15**(3), 584–599.

WOLTER, K. E. 1968. A new method for marking xylem growth. *For Sci*, **14**, 102–104.

YAKIR, D., ISSAR, A., GAT, J., ADAR, E., TRIMBORN, P., & LIPP, J. 1994. ^{13}C and ^{18}O of wood from the Roman siege rampart in Masada, Israel (Ad 70–73): Evidence for a less arid climate for the region. *Geochimica et Cosmochimica Acta*, **58**(16), 3535–3539.

YIN, C., WANG, X., DUAN, B., LUO, J., & LI, C. 2005. Early growth, dry matter allocation and water use efficiency of two sympatric *Populus* species as affected by water stress. *Environmental and experimental botany*, **53**(3), 315–322.

YIN, C., PANG, X., & CHEN, K. 2009. The effects of water, nutrient availability and their interaction on the growth, morphology and physiology of two poplar species. *Environmental and experimental botany*, **67**(1), 196–203.

YODA, K., SUZUKI, M., & SUZUKI, H. 2000. Development and evaluation of a new type of opto-electronic dendrometer. *IAWA JOURNAL*, **21**(4), 425–434.

YOUNG, G. H. F., MCCARROLL, D., LOADER, N. J., & KIRCHHEFER, A. J. 2010. A 500-year record of summer near-ground solar radiation from tree-ring stable carbon isotopes. *The Holocene*, **20**(3), 315–324.

ZAHNER, R., LOTAN, J. E., & BAUGHMAN, W. D. 1964. Earlywood-latewood features of red pine grown under simulated drought and irrigation. *Forest Science*, **10**, 361–370.

ZIMMERMAN, J. K., & EHLERINGER, J. R. 1990. Carbon isotope ratios are correlated with irradiance levels in the Panamanian orchid *Catasetum viridiflavum*. *Oecologia*, **83**(2), 247–249.

ZIMMERMANN, B., SCHLESER, G. H., & BRAUNING, A. 1997. Preliminary results of a Tibetan stable C-isotope chronology dating from 1200 to 1994. *Isotopes in Environmental and Health Studies*, **33**(1), 157–166.

ZWEIFEL, R., ITEM, H., & HÄSLER, R. 2001. Link between diurnal stem radius changes and tree water relations. *Tree Physiology*, **21**(12-13), 869–877.