



Research paper

Comparing the intra-annual wood formation of three European species (*Fagus sylvatica*, *Quercus petraea* and *Pinus sylvestris*) as related to leaf phenology and non-structural carbohydrate dynamics

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Monitoring cambial phenology and intra-annual growth dynamics is a useful approach for characterizing the tree growth response to climate change. However, there have been few reports concerning intra-annual wood formation in lowland temperate forests with high time resolution, especially for the comparison between deciduous and coniferous species. The main objective of this study was to determine how the timing, duration and rate of radial growth change between species as related to leaf phenology and the dynamics of non-structural carbohydrates (NSC) under the same climatic conditions. We studied two deciduous species, *Fagus sylvatica* L. and *Quercus petraea* (Matt.) Liebl., and an evergreen conifer, *Pinus sylvestris* L. During the 2009 growing season, we weekly monitored (i) the stem radial increment using dendrometers, (ii) the xylem growth using microcoring and (iii) the leaf phenology from direct observations of the tree crowns. The NSC content was also measured in the eight last rings of the stem cores in April, June and August 2009. The leaf phenology, NSC storage and intra-annual growth were clearly different between species, highlighting their contrasting carbon allocation. Beech growth began just after budburst, with a maximal growth rate when the leaves were mature and variations in the NSC content were low. Thus, beech radial growth seemed highly dependent on leaf photosynthesis. For oak, earlywood quickly developed before budburst, which probably led to the starch decrease quantified in the stem from April to June. For pine, growth began before the needles unfolding and the lack of NSC decrease during the growing season suggested that the substrates for radial growth were new assimilates of the needles from the previous year. Only for oak, the pattern determined from the intra-annual growth measured using microcoring differed from the pattern determined from dendrometer data. For all species, the ring width was significantly influenced by growth duration and not by growth rate, which differs from previous studies. The observed between-species difference at the intra-annual scale is key information for anticipating suitability of future species in temperate forests.

Keywords: carbohydrates, climate, European beech, intra-annual growth, microcore, Scots pine, sessile oak, tree ring.

Introduction

Global warming and increases in the frequency and severity of extreme droughts, hot extremes and heat waves (Christensen et al. 2007) change plant phenology (reviewed by Cleland et al.

2007) and lead to decreases in forest productivity (Ciais et al. 2005, Loustau et al. 2005, Granier et al. 2007, Reichstein et al. 2007) and tree radial growth (e.g., Orwig and Abrams 1997, Charru et al. 2010, Lebourgeois et al. 2010, Michelot et al. 2012). High-resolution observations of the cambial

phenology and intra-annual growth dynamics are useful approaches for understanding the tree growth response to climate change. New photoassimilates transported in phloem sap are substrates used for radial growth increment. Leaf phenology (i.e., budburst, leaf development and yellowing) could thus influence intra-annual wood formation, underlining the interest in studying these traits in parallel, like in several studies for deciduous species (e.g., Suzuki et al. 1996, Bréda and Granier 1996, Cufar et al. 2008, Sass-Klaassen et al. 2011) and in fewer studies for conifers (see Rossi et al. 2009). The time lags between leaf and growth phenologies change according to species, leading to differences in carbon allocation. In deciduous species, budburst generally occurs following the radial growth for ring-porous species, whereas for diffuse-porous species, radial growth is initiated after budburst (e.g., Suzuki et al. 1996).

Non-structural carbohydrates (NSC) are also considered to be a part of growth substrates. NSC are mainly starch for deciduous species and lipids for coniferous species (see Hoch et al. 2003). The seasonal variations in the lipid pools are low according to the results of Fischer and Höll (1992) and Hoch et al. (2003). NSC are stored in all organs (i.e., leaf, branch, root and stem) at different concentrations (Barbaroux et al. 2003), which could vary during the growing season according to their use or storage (Fischer and Höll 1992, Barbaroux and Bréda 2002, Hoch et al. 2003). The NSC content and intra-annual growth could be linked, as recently demonstrated by Deslauriers et al. (2009) for *Populus*.

During one growing season, the timing, duration and rate of radial growth could differ among species under the same climatic conditions (Rossi et al. 2006b, Rathgeber et al. 2011a). Recent studies showed that the rate of wood growth (Cuny et al. 2012, Rathgeber et al. 2011b) and the timing of growth onset (Lupi et al. 2010) significantly influenced the ring width. Abiotic and biotic factors impacted radial growth increments. With respect to abiotic factors, temperature increases induced cambial reactivation for both deciduous (Begum et al. 2007) and coniferous species (Oribe et al. 2001, Rossi et al. 2007, Deslauriers et al. 2008, Begum et al. 2010). The maximum growth rate of conifers was either synchronized with the warmest temperatures (e.g., Mäkinen et al. 2003) or with the maximum day length (Rossi et al. 2006c). This seasonal growth plasticity was also observed in response to biotic factors, such as competition (Linares et al. 2009), tree size and social status (Rathgeber et al. 2011b) or tree vigour (Gricar et al. 2009). Other factors, such as tree age (reviewed in Ryan et al. 1997) or available water capacity (Lebourgeois et al. 2005, Charru et al. 2010), are known to influence annual radial growth.

Different methodologies were used to assess the intra-annual radial increment with high temporal resolution. Band dendrometers have been used to measure the circumference,

including the wood, phloem and bark increments of trees (e.g., Zweifel and Häsler 2000, Deslauriers et al. 2003b). Repeated stem microcore sampling using specifically designed tools has also been successfully used to determine the intra-annual cambial dynamics (e.g., Forster et al. 2000, Rossi et al. 2006a). In contrast to band dendrometry, microcoring can measure the growth of wood separately from other tissues in one radial direction. Some studies have compared the radial wood increments obtained from dendrometry and microcoring; these studies were focused on coniferous species in boreal zones (Deslauriers et al. 2003b, Mäkinen et al. 2008), Mediterranean ecosystems (Linares et al. 2009, Camarero et al. 2010) or high-altitude sites in the alpine valley (Zweifel et al. 2006, Oberhuber and Gruber 2010 also on one deciduous species). All the studies highlighted similar patterns of intra-annual growth dynamics with occasional time lags in the beginning of growth. Intra-annual studies of wood formation using microcoring are scarce in lowland temperate forests for both deciduous (e.g., Cufar et al. (2008) for beech, Gricar (2010) for oak and van der Werf et al. (2007) for both species) and coniferous species (Wodzicki 1971, Rathgeber et al. 2011a). The comparison of the intra-annual wood formation between deciduous and evergreen species in a lowland temperate forest is lacking.

During the 2009 growing season, we compared the intra-annual wood formation, leaf phenology and NSC dynamics of three major species in Europe (*Fagus sylvatica* L., *Quercus petraea* (Matt.) Liebl. and *Pinus sylvestris* L.). These species have contrasting leaf phenology and wood anatomy. The primary objective of this study was to understand how the timing, duration and rate of radial growth differ among species with respect to leaf phenology and NSC dynamics. The general hypothesis is that the association between intra-annual growth, leaf phenology and NSC dynamics is species specific under the same climatic conditions and reveals a contrasting carbon allocation. To limit the influence of external factors in the species comparison, dominant and mature trees with close stand characteristics were selected. Moreover, we tested the hypothesis that dendrometry and microcoring are two methodologies that measure similar patterns of radial increment with time lags at the beginning of growth. Finally, we examined whether the growth rate was more determinant than growth duration for the total ring width, as recently demonstrated for other climate types.

Materials and methods

Study site and tree sampling

This study was conducted in the Fontainebleau forest, a large managed forested area extending over 17,000 ha in the south-east of Paris (48°25N, 2°40E, 120 m a.s.l.). The attenuated

oceanic temperate climate was homogeneous over the whole forest, with a mean annual temperature of 10.6 °C and mean precipitation of 750 mm, which was well distributed throughout the year. From 1960 to 2009, the mean maximal temperature from April to August (i.e., the growing season) was 21.1 ± 1.1 °C, and the mean sum of precipitation was 307 ± 83 mm. The soil texture was comprised of Stampian sand mixed with loam and clay at different depths.

Three pure and mature stands (one per species) were selected with a maximal distance of 9 km (Table 1). These stands were part of a larger dendroecological project (3 stands/species and 15 trees/stand) studying the impact of climatic variations and soil water deficits on tree growth during the period 1960–2007 (Michelot et al. 2012). Stands with a relatively low available water capacity (AWC) were chosen to limit the influence of this factor on growth. The intra-annual growth of beech, oak and pine was monitored weekly using manual band dendrometry and microcore sampling of five dominant trees per species from April to November 2009. The trees were selected according to their wide ring widths and similar inter-annual growth variations from 1960 to 2007. The age of maturity was different among species and it should be considered in the intra-annual growth comparison, as recently underlined by Cuny et al. (2012). Pine has optimal growth at younger ages than the deciduous species and its productivity then rapidly decreases to become the lowest of the three species. Pine is a pioneer species, while oak is an intermediate- and beech is a late-successional species. Thus, for the species comparison, we selected younger pines than deciduous trees and younger beeches than oaks. For each tree, the final earlywood, latewood and total ring widths were measured to the nearest 1/10 mm using a magnifier ($\times 10$, Peak, Japan) on one core (10 mm diameter) sampled in December 2009. As beech is a diffuse-porous species, only the total ring widths were measured for this species. The height and diameter at breast height (DBH) of the 15 sampled trees were measured in March 2009 before installing the dendrometers.

Climatic data and soil water content

The mean, maximal and minimal temperatures and precipitation were recorded daily at the Fontainebleau weather station.

Measurements of the soil water content (SWC) were conducted from 29 April to 16 November 2009 for each stand at intervals of 2 weeks to determine the influence of SWC on intra-annual tree growth. Three soil samples per stand at 40 cm deep were extracted with a soil auger. The augers were situated within a 2-m radius of the stem of three of the five trees studied. The moist soil was weighed and dried after 48 h at 100 °C. The SWC (%) was calculated for each date:

$$\text{SWC} = \frac{W_m - W_d}{W_d} \times 100 \quad (1)$$

where W_m and W_d are the weights of the moist and dry soils (g), respectively.

Leaf phenology monitoring

Budburst observations were monitored from 1 April to 25 May 2009 on all trees sampled at 3–7-day intervals. The evolution of the percentage of leaves (or needles for pine) that had just unfolded in the crown was recorded. For each tree, the budburst date was computed when 50% of the leaves (or needles) had unfolded in the crown. This date could be obtained using a linear interpolation from the percentage evolution for each tree. Similarly, for the deciduous species, the colouring evolution was monitored at weekly intervals from 6 October to 16 November 2009.

Dendrometry and wood formation monitoring

The radial increment was measured using manual band dendrometers (DB20, Jiří Kučera, Brno, Czech Republic), which were installed at breast height on the 15 selected trees in early March 2009. To ensure a smooth contact between the band and trunk, the outer bark was slightly brushed off. The dendrometer readings were conducted weekly prior to microcore sampling. The start of the radial increment was determined as the date when the dendrometer data exceeded the previous value. Wood microcores (2 mm in diameter and 15 mm in length) from the stem were collected to monitor the xylem development from 1 April to 16 November at weekly intervals (i.e., 34 weeks). The microcore samples were collected at breast height using a Trephor® tool (Vitzani, Perarolo

Table 1. Mean stand characteristics: basal area (BA) in 1995, available water capacity (AWC), soil type and C/N of the organic layer (soil horizon A) in 2004 and mean (\pm SD) structural parameters of the sampled trees in 2009: age, diameter at breast height (DBH) and tree height.

Stand	Species	Stand BA (m ² ha ⁻¹)	Stand AWC (mm) ¹	Soil type ¹	Soil C/N ¹	Age (years) ¹	DBH (cm)	Tree height (m)
B12	<i>F. sylvatica</i>	20.1	101	Haplic Albeluvisol	18.7	93 \pm 6	51.8 \pm 2.8	26.6 \pm 1.1
O4	<i>Q. petraea</i>	31.3	115	Haplic Albeluvisol	18.7	152	64.4 \pm 8.3	32.1 \pm 2.9
P3	<i>P. sylvestris</i>	25.9	118	Albic Podzol	20.1	61 \pm 4	41.2 \pm 5.0	22.8 \pm 0.8

¹See the details of data acquisition in Michelot et al. (2012).

di Cadore (BL), Italy), following an ascending spiral pattern with a spacing of 2 cm between each sampling to avoid wound reaction (Deslauriers et al. 2003a, Rossi et al. 2006a). The 510 samples were placed in a water:ethanol solution (1 : 1 v/v) and stored at 4 °C to avoid tissue deterioration of the cambial zone.

Each sample was oriented under a stereomicroscope at a $\times 10$ –20 magnification, and the transverse side was marked with a pencil. The microcores were successively cleaned, dehydrated and submerged in immersion baths containing ethanol, d-limonene and paraffin using an automatic tissue processor (STP121; MM France, Francheville, France), according to Rossi et al. (2006a). The microcores were subsequently embedded in paraffin blocks using an embedding station (EC 350, MM France). The paraffin blocks were thinned with a rotary microtome (HM 355S, MM France) until they reached the microcore plane and immersed in water to facilitate the cutting of microcore sections. Transverse 7- μ m-thick sections were generated, placed on glass slides and dried for at least 1 h at 50 °C. The dried sections were successively immersed in d-limonene, ethanol, cresyl violet

acetate (0.16% in water) and distilled water. The sections were dried and permanently mounted on glass slides using Histolaque LMR® (Paris, France).

The thin sections were observed under an optical microscope (Orthoplan, Leitz, Germany) with visible and polarized light at $\times 125$ –400 magnification to distinguish cells in the cambial zone and to differentiate xylem cells (Figure 1). For each sample, the ring width was measured on three radial files from the first enlarging cell in the xylem (i.e., after the last cambial cell) to the end of the latewood ring of the previous year. The cumulative ring width of each tree was calculated for each date as the mean of the three radial measurements. Cambial cells were characterized by the presence of thin cell walls and small radial diameters.

Cambium phenology

Different phenological phases were determined from observations of the microcores (i.e., the beginning and ending of growth and earlywood–latewood transition for oak and pine). The dates were defined in Julian days as the average of the sampling dates prior to and upon observation of the event. For

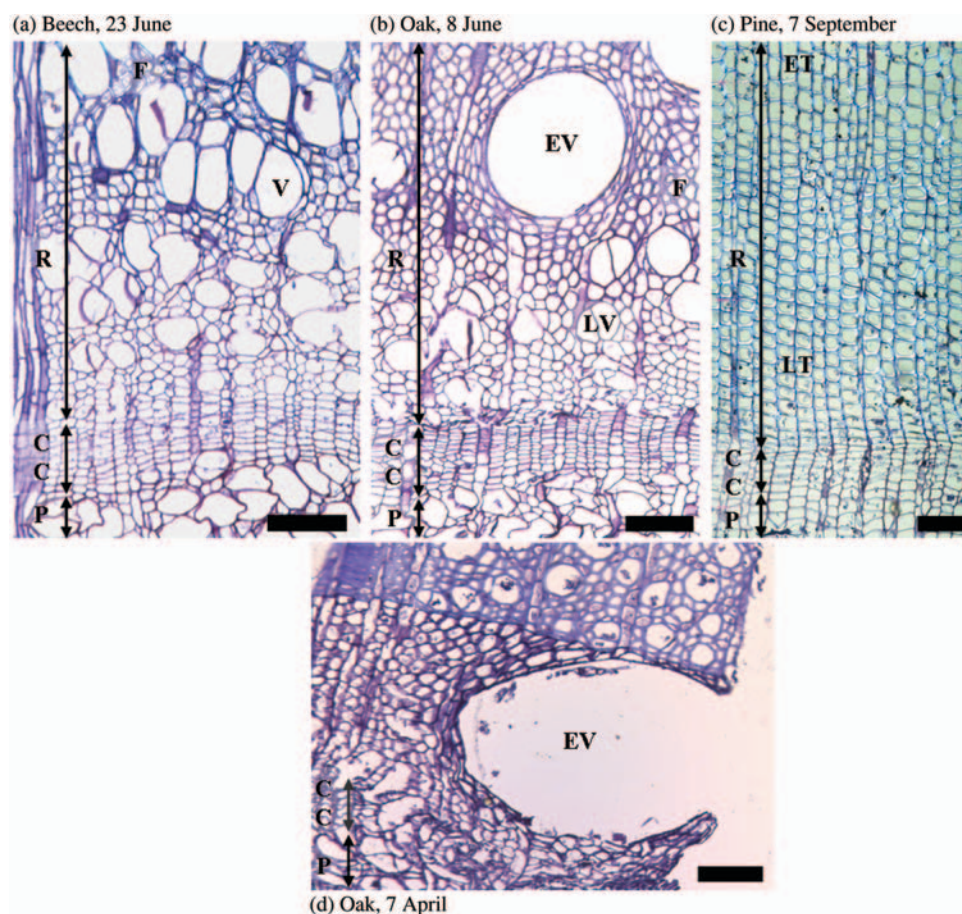


Figure 1. Microcore sections from the three species in 2009 observed at different dates under an optical microscope at $\times 80$. Phloem (P), cambial cells (CC), vessel (V), fibre (F), current ring (R), earlywood vessel (EV), latewood vessel (LV), earlywood tracheids (ET) and latewood tracheids (LT). The scale bars represent 100 μ m.

deciduous species, growth began when the first vessels were formed. For pine, the first enlarging cell indicated the beginning of growth. The cells in radial enlargement were larger than the cambial cells and presented thin pink–violet walls that were not birefringent under polarized light. For pines and three oak trees, growth began prior to the first sampling date (1 April). We therefore extrapolated the initial date of growth using a linear interpolation from the first dataset collected for the cumulative ring width curve.

For the three species, growth was complete when all newly formed cells near the cambial zone began lignification (i.e., no cell is in the enlargement phase). The growth duration was calculated as the difference between the growth end and the growth beginning dates (in Julian days). For oak, the beginning of latewood growth was determined as the date when the first latewood cells were observed. In contrast, for pine the earlywood–latewood transition was difficult to directly observe in the sampled sections. Thus, the final earlywood width and the total number of earlywood cells were determined in two or three sections when the growth was completed (in October–November). From the fitted ring width increment curve (see the next section), we identified the date when the earlywood reached its final width, which corresponded to the date of the earlywood–latewood transition. We counted the cells of the earlywood in the sections (the earlywood cells were more elongated and had thinner cell walls than latewood cells) to determine the date of the earlywood–latewood transition on the optical microscope.

Fitted functions obtained from the microcore measurements

For each tree, the cumulative ring width of the microcore samples was fitted using a non-linear estimation from a statistical software package (Statistica; Statsoft, Tulsa, OK, USA). This method estimates the value of parameters to minimize the sum of squares (SS). For each fit, we determined the asymptotic t -statistic for the parameters, the residual distribution and the resulting R^2 . The Gompertz function was used to fit the cumulative ring width of the beech and pine trees according to the following formula:

$$y = A \exp[-e^{(\beta - \kappa t)}] \quad (2)$$

where y is the weekly cumulative ring width (μm); t is the day of the year (Julian day); A is the upper asymptote (μm), fixed according to the observed final ring; β is the placement parameter, where the lower asymptote starts and κ is the rate of change parameter. For all species, the Gompertz function was also used to fit the mean cumulative radial increment measured using dendrometers.

For oak, we used a double sigmoid function to correctly fit the slow growth observed in May. The first part of the sigmoid function represented the cumulative width of the earlywood, and the second part of the function represented that of the latewood, as indicated in the following formula:

$$y = \frac{u}{1 + \exp^{-K_1(t-M_1)}} + \frac{A-u}{1 + \exp^{-K_2(t-M_2)}} \quad (3)$$

where u is the asymptote of the earlywood formation (μm), fixed at the value of the final earlywood width; κ_1 is the rate of change parameter for the earlywood formation; M_1 is the time of maximum growth of the earlywood; κ_2 is the rate of change parameter for latewood formation and M_2 is the time of maximum growth of the latewood.

The maximal growth rate (r_{max}) was obtained from each fitted curve. The fits were calculated using all the microcore data obtained from the beginning of growth to the identified growth end, except for three outlier points for the tree P6 and one for the tree F12 (see Appendices A and B for fit details).

Carbohydrate analysis

One core (5 mm in diameter and 100 mm in length) was extracted from each tree stem at breast height on 22 April (or 21 April for beech), 1 June and 18 August 2009. The cores were stored in a cooler during sampling and subsequently stored at -80°C until they were freeze-lyophilized. The last eight rings (i.e., 2001–2009) were cut and finely ground in a ball mill (MM200; Retsch, Haan, Germany). The NSC were enzymatically quantified from each wood powder according to Barbaroux and Bréda (2002). Soluble sugars were extracted twice from 10 to 11 mg of powder using 80% ethanol (1 ml) at 80°C for 30 min. The extracts were centrifuged at 12,000 g for 10 min and the supernatants were dried for 2 days at 45°C . The dried extracts were rehydrated in 0.5 ml of 0.02 N NaOH, and the soluble sugar contents (i.e., glucose, fructose and sucrose) were determined colorimetrically at 340 nm (Boehringer 1984). The pellets were dried for 2 h at 45°C . They were rehydrated in 1 ml of 0.02 N NaOH at 90°C for 1 h. The starch was hydrolysed to glucose using α -amylglucosidase (EC 3.2.1.3, Boehringer Mannheim Biochemicals, Mannheim, Germany) in 0.32 M citrate buffer, pH 4.2 at 50°C for 30 min. The glucose content was assessed as described above (Boehringer 1984). The starch was quantified as glucose equivalents.

Statistical analysis

Pearson's correlation coefficients were calculated to quantify the correlations between the variables. An analysis of variance was performed to determine whether the 'species' was a factor that significantly influenced the mean of the phenological variables (i.e., budburst date, date of growth beginning, date

of growth end, growth duration and date of earlywood–latewood transition). The carbohydrate contents were compared between the species and dates using *t*-tests at the 95% confidence level. The homoscedasticity was examined using a Levene test.

Results

Climatic conditions

The climatic conditions from April to August 2009, corresponding to the growing season, were warmer (+1.2 °C) than the regional 1960–2007 mean, while the rainfall was near the average (−18 mm, Figure 2a). The monthly mean temperatures in April and August were +2.4 and +2 °C warmer, respectively, than the averages from 1960 to 2007. August was particularly dry, with a monthly precipitation of 16 mm. For the three stands, the SWC constantly decreased from mid-June to mid-October 2009, except for a slight increase in late July (Figure 2b). The lowest SWC was observed in mid-July for the beech stand and in early October and late August for the oak and pine stands, respectively.

Calendar of leaf phenology and intra-annual growth

The mean budburst date was much earlier for the deciduous species (19 April ± 5 days, mean date ± standard deviation

(SD), for beech and 13 April ± 2 days for oak) compared with the needle unfolding of pine (12 May ± 5 days, analysis of variance (ANOVA), $F = -60.8$, $P < 0.001$, Figure 3). The mean date of leaf yellowing was similar for beech (28 October ± 1 days) and oak (28 October ± 14 days). With respect to the radial increment, the beginning of the oak and pine growths (i.e., the first cell in enlargement phase on microcore sections) occurred 14 and 40 days before budburst, respectively. In contrast, the beech growth began 2 days after budburst. The date of growth beginning was significantly earlier for oak (30 March ± 4 days) and pine (2 April ± 3 days) than for beech (21 April ± 8 days, ANOVA, $F = 24.4$, $P < 0.001$). The first row of earlywood vessels was quickly completed for all oak trees between 14 April and 21 April. The earlywood–latewood transition occurred significantly earlier for oak (16 May ± 6 days) than for pine (4 June ± 11 days, ANOVA, $F = -10.8$, $P < 0.05$). The date of growth end was highly variable between the trees and occurred significantly earlier for oak (24 July ± 8 days) than for beech (12 August ± 14 days) and pine (28 August ± 19 days, ANOVA, $F = -6.9$, $P < 0.01$). The growth duration was clearly longer for pine (148 ± 21 days) compared with that of beech (112 ± 17 days) and oak (116 ± 6 days, ANOVA, $F = 7.7$, $P < 0.01$).

Dynamics of intra-annual growth

The maximal cumulative radial growth measured using dendrometers was higher than that fitted from the microcore data for all species (Figure 4a–c). The beginning of the radial increment in three of the five beech trees measured using dendrometers occurred between 1 and 2 weeks earlier than the ring increment measured from the microcores. For oak, the dendrometer data were correctly fitted using the Gompertz function, whereas the microcore measurements were better fitted using a double-sigmoid function because the slow growth in May was only detected using microcoring.

Comparison of microcore fittings showed that the growth slope of oak was highest in April. Consequently, 30% of the total ring width was already developed by the end of April for oak compared with 19 and 1% for pine and beech, respectively. In May, only 13% of the ring width was produced for oak versus 31% for both beech and pine. Among the three species, beech had the steepest slope of ring growth from May to June. The 50% ring development occurred at the same time for the two deciduous species (11 June for beech and 10 June for oak) and at approximately 10 days earlier for pine (31 May). For all species, the maximum ring growth rate occurred earlier than the warmest period, which was in August. The maximum growth rate was not significantly different between the species ($33.0 \pm 6.0 \mu\text{m day}^{-1}$ for beech, $33.4 \pm 14.0 \mu\text{m day}^{-1}$ for oak and $28.7 \pm 8.6 \mu\text{m day}^{-1}$ for pine, mean ± SD, ANOVA, $F = 0.33$, $P = 0.72$).

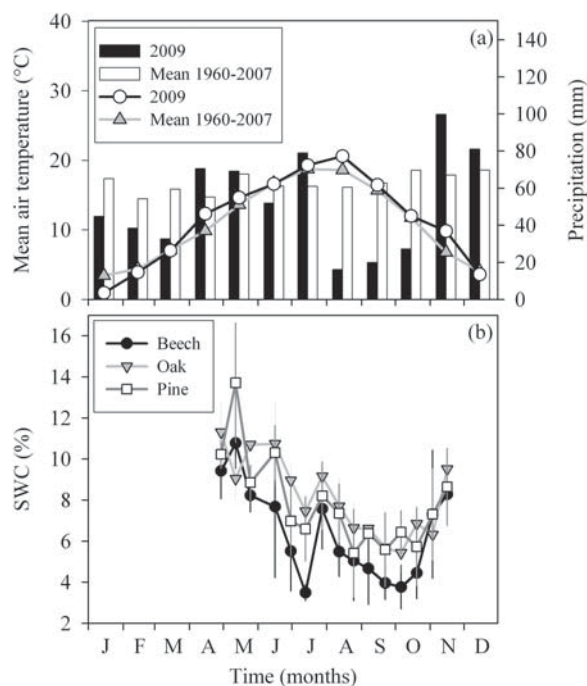


Figure 2. Comparison between mean climatic conditions from 1960 to 2007 and during 2009 (monthly mean air temperature: lines and monthly sums of precipitation: bars, (a)). The mean soil water content at 40 cm depth for each stand in 2009 (b). The error bars represent ± SD.

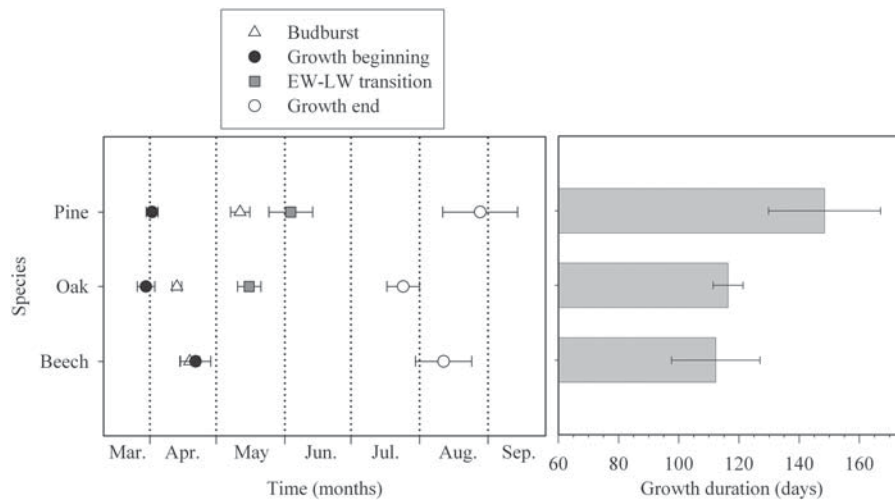


Figure 3. Dates of budburst, growth beginning, earlywood–latewood (EW–LW) transition and growth end (left), as well as growth duration (right) for beech, oak and pine in 2009. The horizontal bars correspond to the 95% confidence limits of the mean ($N = 5$ trees per species).

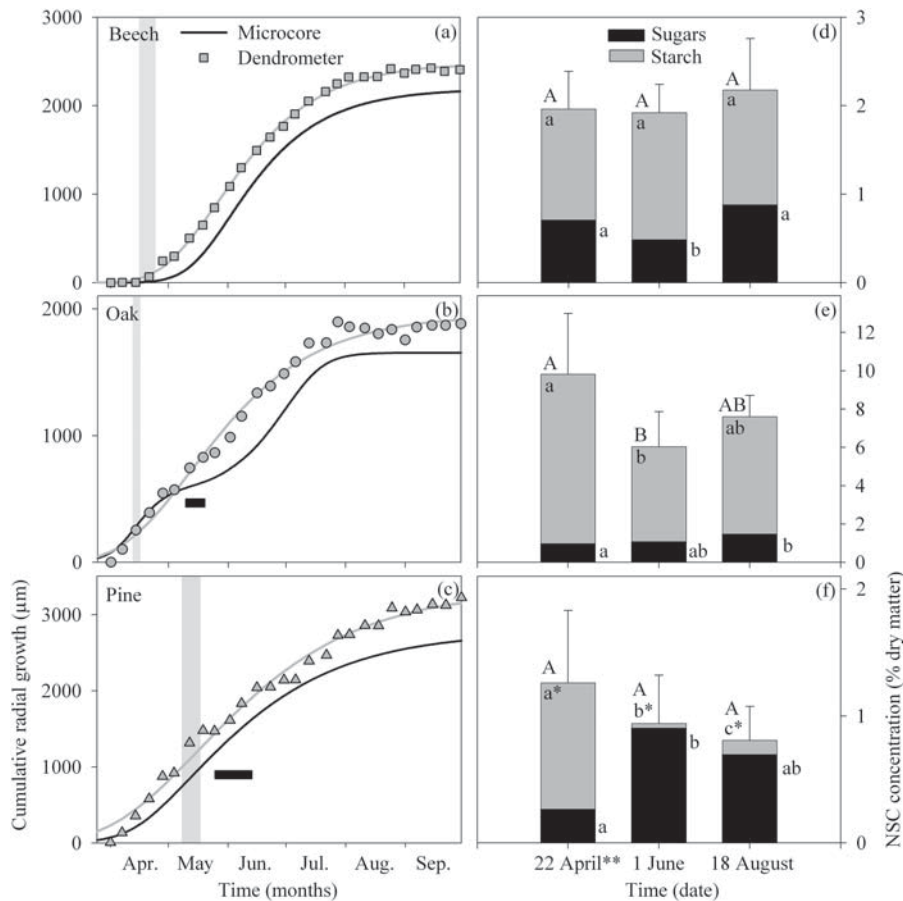


Figure 4. Cumulative radial growth fitted from the microcore measurements and obtained by dendrometer readings (a–c) and non-structural carbohydrate concentrations in the rings from 2001 to 2009 (d–f) for beech, oak and pine. The grey lines represent the Gompertz functions fitted from the dendrometer data. The grey and black bands correspond to the 95% confidence limits of the mean budburst date and the mean earlywood–latewood transition date, respectively. The errors bars represent \pm SD and the capital letters indicate significant differences in NSC content among the sampling dates for each species (t -test, $P < 0.05$). The lower-case letters on the left indicate starch and the lower-case letters on the right indicate sugars. *A logarithmic transformation was conducted to determine homoscedasticity. **This sampling was conducted on 21 April for beech.

Changes in carbohydrates content during the growing season

The mean NSC content in the rings from 2001 to 2009 (i.e., mean of five trees over three dates) was significantly higher for oak ($7.8 \pm 1.6\%$ DM) compared with beech ($2.0 \pm 0.4\%$ DM, t -test, $t = 7.9$, $P < 0.001$) and pine ($1.0 \pm 0.4\%$ DM, $t = 9.5$, $P < 0.001$). The starch content in the oak rings was 5 and 16 times higher than that of the beech and pine, respectively. For beech, the changes in NSC content during the growing season were not significant at the 95% confidence level, but the sugar content was significantly reduced between April and June ($t = -2.4$, $P < 0.05$) and increased between June and August ($t = 2.6$, $P < 0.05$, Figure 4d). On the contrary, oak showed significant differences in NSC content among the three dates, with a significant decrease in starch content between April and June ($t = -2.4$, $P < 0.05$) and a significant increase of sugar content between April and August ($t = 3.7$, $P < 0.01$, Figure 4e). For pine, no significant difference in the NSC content was observed among the three dates. However, between April and June, the starch content was significantly decreased ($t = -3.8$, $P < 0.01$), whereas the sugar content was increased ($t = 3.6$, $P < 0.01$). Moreover, the starch content significantly increased between June and August ($t = 3.1$, $P < 0.05$).

Duration versus growth rate

The linear relationship between the date of growth end and ring width was positive and highly significant ($r = 0.924$, $P < 0.001$, Figure 5a), whereas the date of growth beginning was not significantly correlated with the ring width ($r = 0.195$, $P > 0.10$). The growth duration was a better indicator of ring width ($r = 0.933$, $P < 0.001$, data not shown) than r_{\max} ($r = 0.076$, $P > 0.10$, Figure 5b). The linear relationship between r_{\max} and the date of growth end was not significant ($r = 0.072$, $P > 0.10$, Figure 5c).

Discussion

Leaf phenology, carbohydrates and intra-annual growth

Despite similar climatic variations and close edaphic conditions, the leaf phenology, carbohydrate storage and intra-annual growth were different among the three species, which highlighted their contrasting carbon allocation. Our results indicated that the beech radial growth was mainly dependent on leaf photosynthesis. The radial growth of beech, a diffuse-porous species, began just after budburst, which is consistent with many studies showing beech cambial reactivation at 0–10 days after budburst (e.g., Lachaud and Bonnemain 1981, Suzuki et al. 1996, Barbaroux and Bréda 2002, Cufar

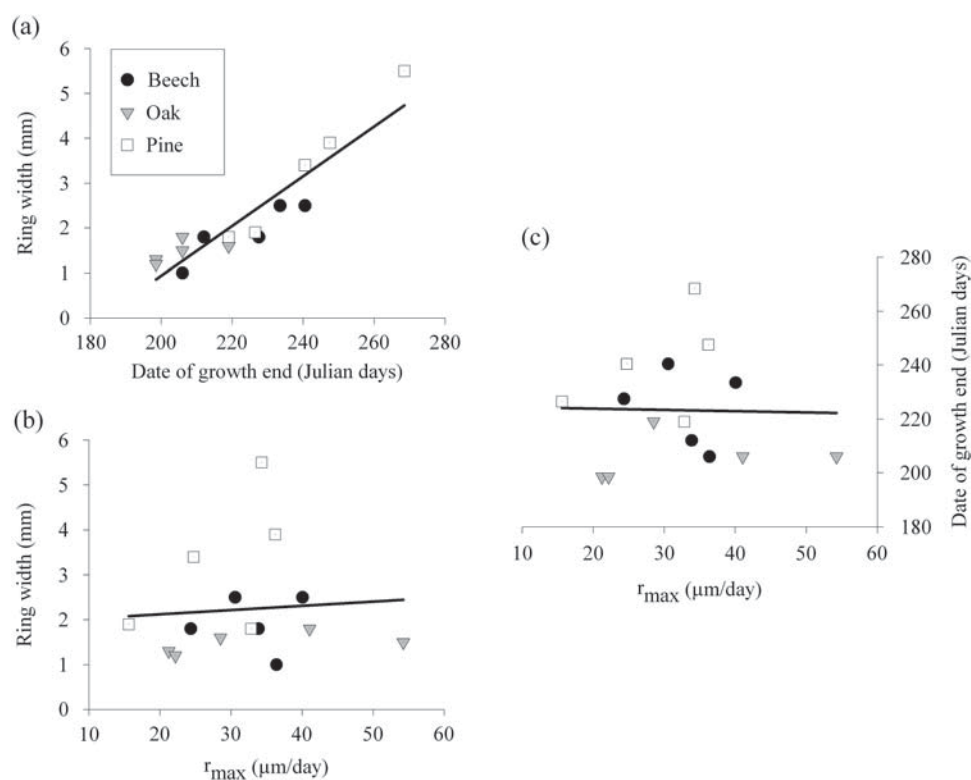


Figure 5. Relationships among the ring width, date of growth end and maximal growth rate (r_{\max}). The black lines represent linear regressions: (a) $y = 0.055x - 10.119$, $r = 0.924$, $P < 0.001$; (b) $y = 0.009x + 1.933$, $r = 0.076$, $P > 0.10$; (c) $y = -0.048x + 224.810$, $r = 0.072$, $P > 0.10$.

et al. 2008). When the leaves were not developed in April, beech showed the slowest growth rate compared with the other species. The NSC content did not decrease between the budburst and maximal growth rate of the beech, although the sugar content was slightly decreased, consistent with Barbaroux and Bréda (2002) and Hoch et al. (2003). This result could suggest that the stem NSC are not used for the radial growth of beech, provided no NSC was stored in the stems during this period. The beech growth rate was considerably increased in May and June, exceeding that of the other species. In contrast to the results of Deslauriers et al. (2009) for *Populus*, a diffuse-porous species, the maximal values for the sugar content were not synchronized with the maximum growth rate of beech. The fast maturation of beech leaves from May (i.e., in 10 days for leaf area and 2–3 weeks for leaf mass area, see Eglin et al. 2009) likely promotes fast ring formation. Our finding that the beech maximum growth rate occurred in June, which is the month when the leaves reach their maximum leaf mass area and photosynthetic rate (see Eglin et al. 2009), supported the assumption that beech growth is highly dependent on leaf phenology.

For oak, a ring porous species, growth began 2 weeks before budburst, which is consistent with results of Bréda and Granier (1996), Zweifel et al. (2006) and Sass-Klaassen et al. (2011). The early growth prior to leaf budburst is associated with the winter embolism of large xylem vessels, which requires that the restoration of the water flow pathway occurs each spring before the onset of transpiration (Essiamah and Eschrich 1986). Moreover, we found that the first row of oak earlywood vessels was constructed rapidly in approximately 2–3 weeks. The observed rapid enlargement of oak earlywood might occur through the division of undifferentiated vessel elements formed at the end of the previous vegetation period that overwintered in the cambium (Zasada and Zahner 1969, Frankenstein et al. 2005, Fonti et al. 2007). The beginning of the radial increment prior to photoassimilate synthesis and the high growth rate during earlywood formation could explain the high starch decrease between April and June. This carbon pool was stored during the previous years and was probably used for the earlywood growth of oak. This reserve use for oak growth could also explain the seasonal pattern of intra-ring carbon isotopic composition during earlywood formation (Helle and Schleser 2004, Eglin et al. 2010, Michelot et al. 2011).

For pine, the growth beginning occurred largely before the needles unfolding. These results indicated that cambial reactivation occurred before the current needle elongation, as observed by Rossi et al. (2009) for three coniferous species in the eastern Italian Alps. From April to June, starch was probably hydrolysed in the sugars because the starch content decreased, but the sugar content increased in parallel. Thus, the NSC content did not significantly decrease during this season,

suggesting that old carbon reserves were not mobilized for radial increment. Our findings supported the recent conclusions of Eilmann et al. (2010), which suggested that an immediate and direct transfer of newly synthesized assimilates is required for pine radial growth in the Alpine valley. The photosynthetic capacity of the needles in previous years, even in the winter (Guehl 1985), could promote the beginning of radial growth in early spring. The decrease in pine growth rate early in the growing season could result from an adaptation to complete cell wall formation and lignification before winter, as shown by Rossi et al. (2006c), or from a high below-ground demand for carbohydrates to ensure resource acquisition during the decrease of SWC in the summer (Oberhuber and Gruber 2010). For pine, the growth duration was longer than for the deciduous species, but the growth rate was low during the last month of the growing season. The scarce studies on the Scots pine growing under temperate climatic conditions in lowland forests showed similar growth durations. Wodzicki (1971) found that pine growth lasted from mid-April to mid-September in Poland, and Rathgeber et al. (2011a) showed a mean pine growth duration of 162 days in the forests of Northeast France, a result similar to those obtained in our study (148 days). This growth duration lasted until late August only for the pine, which could explain our recent observations of influences of late summer climatic conditions on inter-annual growth from 1960 to 2007 (Michelot 2011, Michelot et al. 2012). For the studied species, an additional study of trees growing on the same stand would be necessary to ensure that no external factors influenced the between-species differences in intra-annual growth.

In addition to contrasting carbon allocations, other biotic factors could result in growth differences between the stands, such as slight differences in stand basal area, tree DBH, edaphic conditions and tree age. Concerning tree age, Rossi et al. (2008) showed that growth duration was shortened by 2–3 weeks, and the wood production was lower for the old coniferous trees (200–300 years) compared with the young coniferous trees (50–80 years old) of the same species. In our study, the maximal growth rate of pine could thus be lower if pines had the same age as the deciduous species. This change will be in agreement with the idea that early-successional species present a lower rate of production than late-successional species because they are less efficient at converting environmental resources into growth (see Cuny et al. 2012). However, in our study, the age effect was lower than that in the study of Rossi et al. (2008) because our tree selection considered the age maturity differences among species and the maximal age difference between stands was <100 years.

Dendrometry and microcoring methodologies

Although dendrometers recorded the growth of all tissues (bark, phloem and xylem), we hypothesized that the patterns

of intra-annual growth were similar between dendrometry and microcoring, which is consistent with previous studies comparing dendrometry and microcoring methodologies (Deslauriers et al. 2003b, Zweifel et al. 2006, Makinen et al. 2008, Linares et al. 2009, Camarero et al. 2010). However, our results for oak highlighted different patterns between the two methodologies. The radial increment derived from the dendrometers was fitted using the Gompertz function, whereas the growth measured from microcoring was predicted using a double-sigmoid function. Thus, the bimodal wood growth, corresponding to the earlywood and latewood increment phases, was not observable from the dendrometer data. According to the results of Gricar (2010) in a temperate forest, the annual phloem increment of oak is not negligible and could represent ~20% of the xylem increment. Moreover, the dendrometers on some beech trees recorded stem expansion 1–2 weeks earlier than those obtained from the microcore data. This difference could be due to stem rehydration in the early spring, which could mislead the interpretation of the beginning of radial growth using only dendrometer readings (see Deslauriers et al. 2003b). In contrast to Makinen et al. (2008), this time lag in the data obtained from the dendrometer and microcore measurements was not observed in pine, as indicated in the studies of Oberhuber and Gruber (2010) and Zweifel et al. (2006) conducted in the Alpine valley.

Influence of growth duration on ring width

For all species, the date of growth end highly influenced the total ring width of each tree in contrast to the growth beginning or growth rate. We did not expect this result according to the recent studies. In the boreal forest, Lupi et al. (2010) observed a significant influence of the date of xylogenesis beginning on the total number of cells in the total ring (which is strongly correlated with the total ring width) for *Picea mariana* from 2006 to 2009. For several coniferous species in a mild continental temperate climate, Rathgeber et al. (2011b) and Cuny et al. (2012) showed that 75% of the tree-ring width variability was attributable to the rate of cell production and that only 25% was attributable to its duration. In our oceanic-attenuated climate, we assume that summer SWC causes the variability in the growth ending and total ring width among different tree species. The trees most sensitive to summer SWC could have the earliest growth ending. This hypothesis could be reinforced by the recent results of Eilmann et al. (2011), who showed that the non-irrigated Scots pine had a noticeably shorter period of wood formation and a significantly lower increment compared with irrigated trees. The tree growth observed in our study could be particularly sensitive to SWC variations because of the low stand AWC, which strongly modulates ring characteristics and climate–growth relationships, as demonstrated by

Lebourgeois et al. (2005) on French beech plots. The measurement and comparison of tree water status could help in confirming this hypothesis.

Conclusions

Timing, duration and rate of radial growth were contrasted between different tree species, and the associations with leaf phenology and NSC highlighted differences in carbon allocation. We concluded that the beech radial growth was highly dependent on leaf photosynthesis because of their growth beginning after budburst, maximal growth rate when the leaves became mature and low change of NSC content during the growing season. For oak, we noted that the high starch decrease in the stem from April to June was probably due to a strong carbon demand for a quick constitution of earlywood in addition to growth beginning before budburst. For pine, the cambial reactivation began largely before the needles unfolding, and no decrease in NSC content was observed during the growing season. These results suggest that the needles from the previous year directly provided substrates for current radial growth. In contrast to previous studies of coniferous species, microcoring recorded different patterns of intra-annual growth for oak than dendrometry, with two phases corresponding to earlywood and latewood growth. Finally, the ring width was largely influenced by growth duration, particularly by the growth end date, which contrasts with the results observed under other climate types. It is necessary to validate the observed inter-species differences over several years to anticipate species growth in response to future climate change.

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Conflict of interest

None declared.

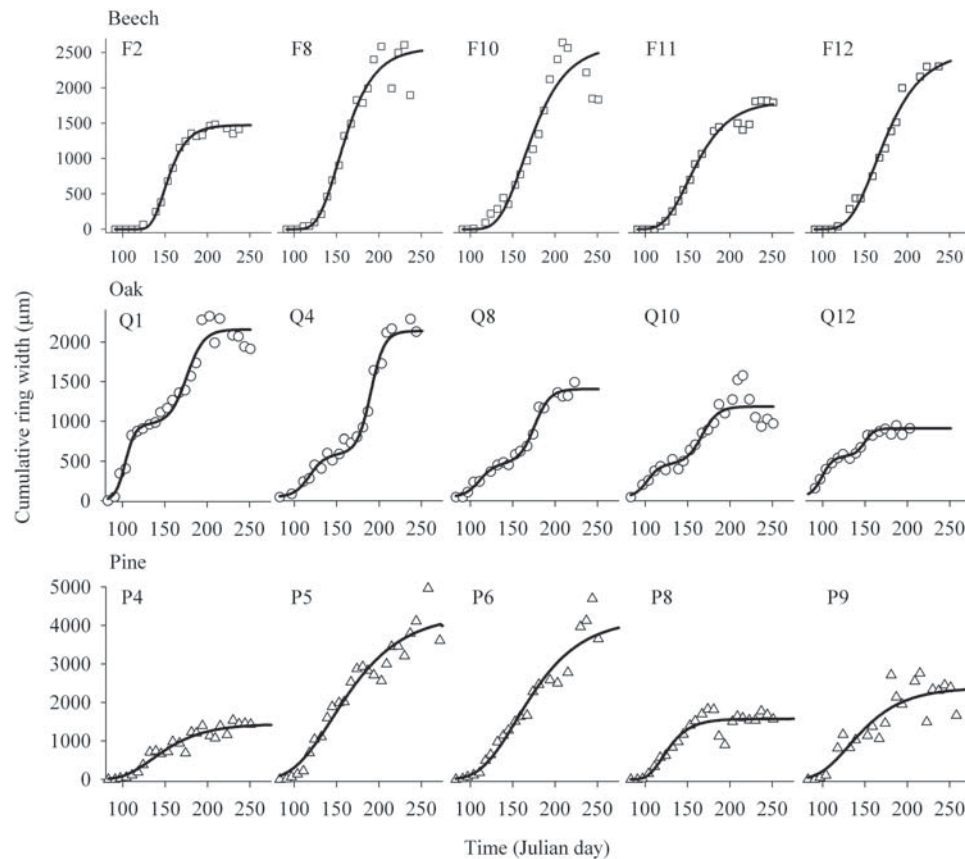
References

- Barbaroux, C. and N. Bréda. 2002. Contrasting distribution and seasonal dynamics of carbohydrate reserves in stem wood of adult ring-porous sessile oak and diffuse-porous beech trees. *Tree Physiol.* 22:1201–1210.
- Barbaroux, C., N. Bréda and E. Dufrêne. 2003. Distribution of above-ground and below-ground carbohydrate reserves in adult trees of two contrasting broad-leaved species (*Quercus petraea* and *Fagus sylvatica*). *New Phytol.* 157:605–615.
- Begum, S., S. Nakaba, Y. Oribe, T. Kubo and R. Funada. 2007. Induction of cambial reactivation by localized heating in a deciduous hardwood hybrid poplar (*Populus sieboldii* × *P. grandidentata*). *Ann. Bot.* 100:439–447.
- Begum, S., S. Nakaba, Y. Oribe, T. Kubo and R. Funada. 2010. Cambial sensitivity to rising temperatures by natural condition and artificial heating from late winter to early spring in the evergreen conifer *Cryptomeria japonica*. *Trees Struct. Funct.* 24:43–52.
- Boehringer, S.A. 1984. Methods of enzymatic food analysis using single reagents. *Boehringer Mannheim GmbH, Mannheim, Germany*, 79 p.
- Bréda, N. and A. Granier. 1996. Intra- and interannual variations of transpiration, leaf area index and radial growth of a sessile oak stand (*Quercus petraea*). *Ann. For. Sci.* 53:521–536.
- Camarero, J.J., J.M. Olano and A. Parras. 2010. Plastic bimodal xylogenesis in conifers from continental Mediterranean climates. *New Phytol.* 185:471–480.
- Charru, M., I. Seynave, F. Morneau and J.D. Bontemps. 2010. Recent changes in forest productivity: an analysis of national forest inventory data for common beech (*Fagus sylvatica* L.) in north-eastern France. *For. Ecol. Manag.* 260:864–874.
- Christensen, J.H., B. Hewitson, A. Busuioc, et al. Whetton. 2007. Regional climate projections. In *Climate Change 2007: The Physical Science Basis*. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Eds. S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller. Cambridge University Press, Cambridge, UK, pp 849–940.
- Ciais, P., M. Reichstein, N. Viovy, et al. 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature* 437:529–533.
- Cleland, E.E., I. Chuine, A. Menzel, H.A. Mooney and M.D. Schwartz. 2007. Shifting plant phenology in response to global change. *Trends Ecol. Evol.* 22:357–365.
- Cufar, K., P. Prislan and J. Gricar. 2008. Cambial activity and wood formation in beech (*Fagus sylvatica*) during the 2006 growth season. *Wood Res.* 53:1–12.
- Cuny, H., C.B.K. Rathgeber, F. Lebourgeois, M. Fortin and M. Fournier. 2012. Life strategies in intra-annual dynamics of wood formation: example of three conifer species in a temperate forest in northeast France. *Tree Physiol.* 32:612–625.
- Deslauriers, A., H. Morin and Y. Begin. 2003a. Cellular phenology of annual ring formation of *Abies balsamea* in the Quebec boreal forest (Canada). *Can. J. For. Res.* 33:190–200.
- Deslauriers, A., H. Morin, C. Urbinati and M. Carrer. 2003b. Daily weather response of balsam fir (*Abies balsamea* (L.) Mill.) stem radius increment from dendrometer analysis in the boreal forests of Quebec (Canada). *Trees Struct. Funct.* 17:477–484.
- Deslauriers, A., S. Rossi, T. Anfodillo and A. Saracino. 2008. Cambial phenology, wood formation and temperature thresholds in two contrasting years at high altitude in southern Italy. *Tree Physiol.* 28:863–871.
- Deslauriers, A., A. Giovannelli, S. Rossi, G. Castro, G. Fragnelli and L. Traversi. 2009. Intra-annual cambial activity and carbon availability in stem of poplar. *Tree Physiol.* 29:1223–1235.
- Eglin, T., C. Fresneau, C. Lelarge-Trouverie, C. Francois and C. Damesin. 2009. Leaf and twig $\delta^{13}\text{C}$ during growth in relation to biochemical composition and respired CO_2 . *Tree Physiol.* 29:777–788.
- Eglin, T., C. Francois, A. Michelot, N. Delpierre and C. Damesin. 2010. Linking intra-seasonal variations in climate and tree-ring $\delta^{13}\text{C}$: a functional modelling approach. *Ecol. Model.* 221:1779–1797.
- Eilmann, B., N. Buchmann, R. Siegwolf, M. Saurer, P. Cherubini and A. Rigling. 2010. Fast response of Scots pine to improved water availability reflected in tree-ring width and $\delta^{13}\text{C}$. *Plant Cell Environ.* 33:1351–1360.
- Eilmann, B., R. Zweifel, N. Buchmann, E.G. Pannatier and A. Rigling. 2011. Drought alters timing, quantity, and quality of wood formation in Scots pine. *J. Exp. Bot.* 62:2763–2771.
- Essiamah, S. and W. Eschrich. 1986. Water uptake in deciduous trees during winter and the role of conducting tissue in spring reactivation. *IAWA Bull.* 7:31–38.
- Fischer, C. and W. Höll. 1992. Food reserves of scots pine (*Pinus sylvestris* L.) II. Seasonal changes and radial distribution of carbohydrate and fat reserves in pine wood. *Trees Struct. Funct.* 6:147–155.
- Fonti, P., N. Solomonoff and I. Garcia-Gonzalez. 2007. Earlywood vessels of *Castanea sativa* record temperature before their formation. *New Phytol.* 173:562–570.
- Forster, T., F.H. Schweingruber and B. Denneler. 2000. Increment puncher—a tool for extracting small cores of wood and bark from living trees. *IAWA J.* 21:169–180.
- Frankenstein, C., D. Eckstein and U. Schmitt. 2005. The onset of cambium activity—a matter of agreement? *Dendrochronologia* 23:57–62.
- Granier, A., M. Reichstein, N. Bréda, et al. 2007. Evidence for soil water control on carbon and water dynamics in European forests during the extremely dry year: 2003. *Agric. For. Meteorol.* 143:123–145.
- Gricar, J. 2010. Xylem and phloem formation in sessile oak from Slovenia in 2007. *Wood Res.* 55:15–22.
- Gricar, J., L. Krze and K. Cufar. 2009. Number of cells in xylem, phloem and dormant cambium in silver fir (*Abies alba*), in trees of different vitality. *IAWA J.* 30:121–133.
- Guehl, J.-M. 1985. Etude comparée des potentialités hivernales d'assimilation carbonée de trois conifères de la zone tempérée (*Pseudotsuga menziesii* Mirb, *Abies alba* Mill et *Picea excelsa* Link). *Ann. For. Sci.* 42:23–38.
- Helle, G. and G.H. Schleser. 2004. Beyond CO_2 -fixation by Rubisco—an interpretation of $^{13}\text{C}/^{12}\text{C}$ variations in tree rings from novel intra-seasonal studies on broad-leaf trees. *Plant Cell Environ.* 27:367–380.
- Hoch, G., A. Richter and C. Körner. 2003. Non-structural carbon compounds in temperate forest trees. *Plant Cell Environ.* 26:1067–1081.
- Lachaud, S. and J.L. Bonnemain. 1981. Xylogénèse chez les Dicotylédones arborescentes. I. Modalités de la remise en activité du cambium et de la xylogénèse chez les hêtres et les chênes âgés. *Can. J. Bot.* 59:1222–1230.
- Lebourgeois, F., N. Bréda, E. Ulrich and A. Granier. 2005. Climate-tree-growth relationships of European beech (*Fagus sylvatica* L.) in the French Permanent Plot Network (RENECOFOR). *Trees Struct. Funct.* 19:385–401.
- Lebourgeois, F., C.B.K. Rathgeber and E. Ulrich. 2010. Sensitivity of French temperate coniferous forests to climate variability and extreme events (*Abies alba*, *Picea abies* and *Pinus sylvestris*). *J. Veg. Sci.* 21:364–376.
- Linares, J.C., J.J. Camarero and J.A. Carreira. 2009. Plastic responses of *Abies pinsapo* xylogenesis to drought and competition. *Tree Physiol.* 29:1525–1536.

- Loustau, D., A. Bosc, A. Colin, et al. 2005. Modeling climate change effects on the potential production of French plains forests at the sub-regional level. *Tree Physiol.* 25:813–823.
- Lupi, C., H. Morin, A. Deslauriers and S. Rossi. 2010. Xylem phenology and wood production: resolving the chicken-or-egg dilemma. *Plant Cell Environ.* 33:1721–1730.
- Makinen, H., P. Nojd and P. Saranpaa. 2003. Seasonal changes in stem radius and production of new tracheids in Norway spruce. *Tree Physiol.* 23:959–968.
- Makinen, H., J.W. Seo, P. Nojd, U. Schmitt and R. Jalkanen. 2008. Seasonal dynamics of wood formation: a comparison between pinning, microcoring and dendrometer measurements. *Eur. J. For. Res.* 127:235–245.
- Michelot, A. 2011. Croissance et $\delta^{13}\text{C}$ des cernes de trois essences forestières tempérées (*Fagus sylvatica*, *Quercus petraea* et *Pinus sylvestris*) face aux variations climatiques à l'échelle interannuelle et saisonnière. Université Paris-Sud 11, Orsay, 196 p. + annexes.
- Michelot, A., T. Eglin, E. Dufrêne, C. Lelarge-Trouverie and C. Damesin. 2011. Comparison of seasonal variations in water-use efficiency calculated from the carbon isotope composition of tree rings and flux data in a temperate forest. *Plant Cell Environ.* 34:230–244.
- Michelot, A., N. Bréda, C. Damesin and E. Dufrêne. 2012. Differing growth responses to climatic variations and soil water deficits of *Fagus sylvatica*, *Quercus petraea* and *Pinus sylvestris* in a temperate forest. *For. Ecol. Manag.* 265:161–171.
- Oberhuber, W. and A. Gruber. 2010. Climatic influences on intra-annual stem radial increment of *Pinus sylvestris* (L.) exposed to drought. *Trees Struct. Funct.* 24:887–898.
- Oribe, Y., R. Funada, M. Shibagaki and T. Kubo. 2001. Cambial reactivation in locally heated stems of the evergreen conifer *Abies sachalinensis* (Schmidt) masters. *Planta* 212:684–691.
- Orwig, D.A. and M.D. Abrams. 1997. Variation in radial growth responses to drought among species, site, and canopy strata. *Trees Struct. Funct.* 11:474–484.
- Rathgeber, C.B.K., F. Longuetaud, F. Mothe, H. Cuny and G. Le Moguédec. 2011a. Phenology of wood formation: data processing, analysis and visualisation using R (package CAVIAR). *Dendrochronologia* 29:139–149.
- Rathgeber, C.B.K., S. Rossi and J.-D. Bontemps. 2011b. Cambial activity related to tree size in a mature silver-fir plantation. *Ann. Bot.* 108:429–438.
- Reichstein, M., P. Ciais, D. Papale, et al. 2007. Reduction of ecosystem productivity and respiration during the European summer 2003 climate anomaly: a joint flux tower, remote sensing and modelling analysis. *Glob. Change Biol.* 13:634–651.
- Rossi, S., T. Anfodillo and R. Menardi. 2006a. Trephor: a new tool for sampling microcores from tree stems. *IAWA J.* 27:89–97.
- Rossi, S., A. Deslauriers and T. Anfodillo. 2006b. Assessment of cambial activity and xylogenesis by microsampling tree species: an example at the alpine timberline. *IAWA J.* 27:383–394.
- Rossi, S., A. Deslauriers, T. Anfodillo, H. Morin, A. Saracino, R. Motta and M. Borghetti. 2006c. Conifers in cold environments synchronize maximum growth rate of tree-ring formation with day length. *New Phytol.* 170:301–310.
- Rossi, S., A. Deslauriers, T. Anfodillo and V. Carraro. 2007. Evidence of threshold temperatures for xylogenesis in conifers at high altitudes. *Oecologia* 152:1–12.
- Rossi, S., A. Deslauriers, T. Anfodillo and M. Carrer. 2008. Age-dependent xylogenesis in timberline conifers. *New Phytol.* 177:199–208.
- Rossi, S., C.B.K. Rathgeber and A. Deslauriers. 2009. Comparing needle and shoot phenology with xylem development on three conifer species in Italy. *Ann. For. Sci.* 66:1–8.
- Ryan, M.G., D. Binkley and J.H. Fownes. 1997. Age-related decline in forest productivity: pattern and process. *Adv. Ecol. Res.* 27: 213–262.
- Sass-Klaassen, U., C.R. Sabajo and J. den Ouden. 2011. Vessel formation in relation to leaf phenology in pedunculate oak and European ash. *Dendrochronologia* 29:171–175.
- Suzuki, M., K. Yoda and H. Suzuki. 1996. Phenological comparison of the onset of vessel formation between ring-porous and diffuse-porous deciduous trees in a Japanese temperate forest. *IAWA J.* 17:431–444.
- van der Werf, G.W., U.G.W. Sass-Klaassen and G.M.J. Mohren. 2007. The impact of the 2003 summer drought on the intra-annual growth pattern of beech (*Fagus sylvatica* L.) and oak (*Quercus robur* L.) on a dry site in the Netherlands. *Dendrochronologia* 25:103–112.
- Wodzicki, T.J. 1971. Mechanism of xylem differentiation in *Pinus sylvestris* L. *J. Exp. Bot.* 22:670–687.
- Zasada, J.C. and R. Zahner. 1969. Vessel element development in earlywood of red oak (*Quercus rubra*). *Can. J. Bot.* 47:1965–1971.
- Zweifel, R. and R. Häsler. 2000. Frost-induced reversible shrinkage of bark of mature subalpine conifers. *Agric. For. Meteorol.* 102:213–222.
- Zweifel, R., L. Zimmermann, F. Zeugin and D.M. Newbery. 2006. Intra-annual radial growth and water relations of trees: implications towards a growth mechanism. *J. Exp. Bot.* 57:1445–1459.

Appendices

Appendix A. Cumulative ring width fitted from microcore measurements for beech, oak and pine trees in 2009.



Appendix B. Parameters and goodness of fit (R^2) of the fitted function used for each studied tree.

Trees	F2	F8	F10	F11	F12
Function used	Gompertz	Gompertz	Gompertz	Gompertz	Gompertz
R^2	99.7	96.3	90.8	98.6	97.1
A	1473.3	2563.2	2602.5	1811.3	2509.8
B	10.0	6.4	5.7	5.5	5.4
K	0.067	0.042	0.035	0.037	0.033
r_{\max} ($\mu\text{m}/\text{day}$)	36.4	40.1	33.9	24.3	30.5
Trees	Q1	Q4	Q8	Q10	Q12
Function used	Double sigmoid	Double sigmoid	Double sigmoid	Double sigmoid	Double sigmoid
R^2	97.5	98.7	99.0	98.0	98.8
A	2155.5	2346.1	1526.1	1278.7	968.2
U	958.6	611.5	474.4	466.3	584.5
K_1	0.171	0.109	0.113	0.134	0.152
K_2	0.098	0.125	0.108	0.105	0.180
M_1	103.5	118.2	110.9	102.5	99.3
M_2	175.8	190.3	175.6	166.9	149.4
r_{\max} ($\mu\text{m}/\text{day}$)	41.0	54.3	28.5	21.2	22.1
Trees	P4	P5	P6	P8	P9
Function used	Gompertz	Gompertz	Gompertz	Gompertz	Gompertz
R^2	94.5	95.2	95.4	90.9	87.2
A	1440.2	4286.3	4173.2	1569.5	2379.7
B	4.0	3.1	3.6	6.9	3.7
K	0.029	0.022	0.024	0.057	0.028
r_{\max} ($\mu\text{m}/\text{day}$)	15.6	34.3	36.2	32.8	24.7