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Xylem formation in *Fagus sylvatica* during one growing season

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Abstract: The study analyses the activity of cambium and the increment of wood during one growing season of European beech (*Fagus sylvatica* L.) in the central part (region) of the Drahanská vrchovina, Czech Republic. The research plot was situated at an altitude of 630 m a.s.l. The following parameters were studied: the beginning and end of cambial activity, differentiation of wood fibres and vessels and the total increment of wood during the growing season in six trees. Samples were taken during the growing season of 2010 in weekly intervals from the beginning of April to the end of October. The dormant cambium consisted of 5.3 cells on average; their number rose gradually after reactivation. The maximum number of cells (10 to 14, 9.1 on average) in the cambial zone persisted for 8 weeks; in mid-August the cambium ended its division activity, while the differentiation process continued till mid-September. The first fully lignified vessels were formed 5 to 6 weeks after their formation in the cambial zone. Vessels and adjacent wood fibres were the first elements to become fully lignified. The maximum production of cells (wood increment) was recorded from June 11 to June 24. 57% of the total ring width was formed in June. The mean ring width calculated by means of Gompertz function is 1777 μm (ranging from 1226 μm to 2423 μm).

Additional key words: European beech, cambium, wood formation, Gompertz function

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Introduction

European beech (*Fagus sylvatica* L.) is economically the most significant broadleaved species in the Czech Republic; its proportion in current stands is about 7% but in newly reforested and rehabilitated plots have about 21%. The recommended proportion of beech in the stands of the Czech Republic is 18% (Report on the State of Forests and Forestry in the Czech Republic by 2011). Beech covers about 14 million hectares of forests within Europe. Beech stands are valuable both from economic (production of precious wood biomass with good physical and mechanical properties) and ecological points of view (stabilization of ecosystems, stabilization of the water regime of the landscape and regeneration of soils poor in minerals). For these reasons and also with respect to the expected climate change, we need to devote attention to cambial activity and the process of wood formation at cellular level.

While dendroclimatology, which is used to study tree growth and climate, is based on analysis of a completed annual ring width and its relation to climatic factors (e.g. Rybníček et al. 2010), to study how the annual ring is formed need to use a repeated sampling method throughout the growing season

(Wodzicki 1971; Horáček et al. 1999; Deslauriers et al. 2003; Gričar et al. 2006; Rossi et al. 2006b; Gričar 2010; Čufar et al. 2011; Prislan et al. 2011). Most of wood formation studies examined coniferous species (Deslauriers et al. 2003; Gričar et al. 2006; Rossi et al. 2006b; Gryc et al. 2011 and 2012). However, recent studies are also focused to broadleaved species including European beech (*Fagus sylvatica)* (Schmitt et al. 2000; van der Werf et al. 2007; Čufar et al. 2008ab; Prislan et al. 2009, 2011).

Beech is a dicotyledon with diffuse porous wood. With vessels not exceeding 100 μm in diameter can be observed within a tree ring. The wood structure and quality depend on the activity of the cambium and the process of wood formation.Wood formation process is therefore crucial for structure and properties of wood.

There are only few studies (Čufar et al. 2008a, b; Prislan et al. 2011) on description of cambial activity and wood formation processes in European beech (*Fagus sylvatica*) for Central Europe. Considering the necessary transformation of Czech forests – increasing of oaks and beeches in forests (Report on the State of Forests and Forestry in the Czech Republic by 2011), the expected climate change (e.g. Bauer et al. 2010) and the need to understand the relationship between wood structure and its properties, studies of cambium activity and the following process of wood formation in beech (*Fagus sylvatica* L.) are highly significant. The aim of the study is to analyse seasonal dynamics of the cambial activity and the process of wood formation at cellular level in the selected European beech (*Fagus sylvatica* L.) trees at the Rájec-Domanka site in the Czech Republic during the growing season of 2010.

Material and methods

Study site

Research was carried out at the permanent field research site Rájec-Němčice of the Department of Forest Ecology, Mendel University in Brno in the central part (region) of the Drahanská vrchovina Upland. The research plot Rájec-Domanka (49°27’49’’N and 16°42’00’’E) is situated in the Mensdorff-Pouilly Forests of Benešov near Boskovice, about 2.5 km north of the permanent field research site. The research plot is situated at an altitude of 630 m a.s.l. The soil type of the area is modal oligotrophic Cambisol with humus form “moder” (Fabiánek et al. 2009). Acid granodiorite of the Brno massif is the parent rock of the area. Research plot ranks among the set of the forest type 5S1 – oligo-mesotrophic silver fir beech forest with *Oxalis acetosella* (Plíva 1987). Mean annual temperature is 6.3°C (station Protivanov, 11 km far from research plot), with the highest monthly mean temperature in July (15.8°C) and the lowest –4.1°C in January. The annual mean of precipitation amounts to 638 mm (Pivec 1992). Climatic diagram (2010) of Rajec-Domanka research plot is presented in Figure 1. For the experiment, six European beech (*Fagus sylvatica* L.) with a stem of 32–41 cm in diameter, 31–37 m in height, and 130 years of age were chosen. The selected trees were of good health and the absence of tension wood was assumed.

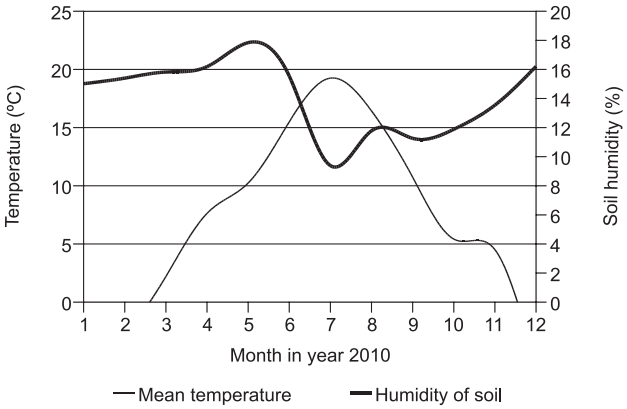

Fig. 1. Climatic diagram of Rajec-Domanka research plot. Monthly mean temperature (°C) and mean soil humidity (%) for year 2010.

Micro-coring and sample preparation

Tissue samples were taken at weekly intervals, from end of March to October 2010. Sampling was carried out by means of the Trephor tool (Rossi et al. 2006a). The microcores (1.8 mm in diameter) were taken at the breast height around the stem perimeter, so that they contained phloem, cambium and xylem of the developing tree ring. The distance between two neighbouring microcores was 2 cm so that the samples did not contain traumatic tissue. Immediately after sampling, the microcores were immersed in FAA (formalin-alcohol-acetic acid) (Gričar 2010), where they were left for a week; afterwards, they were stored in 30% ethanol (Gryc et al. 2011).

Microcores were dehydrated in an alcohol series (70%, 70%, 90%, 95%, 100%, and 100%), then cleaning in xylene followed (Gryc et al. 2011). The actual paraffin infiltration of microcores was carried out in a laboratory drying oven at a temperature of 60°C for 4 hours. Paraffin was poured by means of the Leica EG1120 dispenser and the microcores were put in histological cases to be mounted in the microtome. Then the Leica RM2235 rotation microtome was used to make cross sections 12 μm thin. An adhesive was used for better adhesion of the sections on glass slides. The sections were dried in an oven at a temperature of 60°C for 30 minutes. Further steps were the removal of the paraffin (xylene), dehydration (ethanol) and staining of the sections by safranin and Astra blue. The sections were mounted in Canada balsam.

To monitor and scan the microsections we used the Leica DMLS microscope with the Leica DFC 280 digital camera. The cross sections were used to identify cambial cells and differentiating wood cells. The cells in the cambial zone (CC) were identified based on the thin cell wall and a small radial dimension. In the phase of postcambial growth (PC) the cells still had a thin cell wall, lumina included protoplast and the radial dimensions were at least double in comparison with cambial cells. Application of polarized light enabled us to distinguish cells in the phase of secondary cell wall deposition (SW) from the phase of postcambial growth. During the phase of secondary cell wall deposition cellulose microfibrils are deposited in the cell walls, which causes glistening in the polarized light. The lignification process was detected based on cell wall colour change. Non-lignified cells were dyed blue with astra blue solution, safranin solution dyed the cells red due to the reaction with lignin. Mature wood (MT) had red-stained cell walls and empty lumina without protoplast. To measure wood radial increment we used the ImageJ open source program (Abramoff et al. 2004).

The xylem formation of the tree ring has been analysed with Gompertz function (Rossi et al. 2003, Dufour and Morin 2007) using equation:

$$y = A \cdot e^{-e^{B-k \cdot t}}$$

y – weekly cumulative cells, t – day of year, A – upper asymptote, representing the maximum number of cells, B – place on x axis, estimating the beginning of cambial activity, k – inflection point on the curve.

Results

Cambium

The number and the shape of the cells in cambial zone differ considerably during the growing season (Fig. 2). At the beginning of the growing season (April 8) there were 4 to 6 cells (5.3 on average) in the cambial zone and these were flat in their radial dimensions (see Fig. 3A). The beginning of cambial activity is characterized by an expansion of the radial dimensions of cells in the cambial zone; at the same time their number increases. The number of cells in the cambial zone in our samples increased gradually and the maximum values (7 to 11, 9.1 on average) were achieved at the end of May (May 27); the number of cells in the cambial zone remained constant during June. Starting from the second half of July, the average number of cells in the cambial zone decreased gradually and the division activity ended in mid-August. At the beginning of September (September 2) the average number of cells in the cambial zone (5.3) was the same as at the beginning of the growing season (Fig. 2).

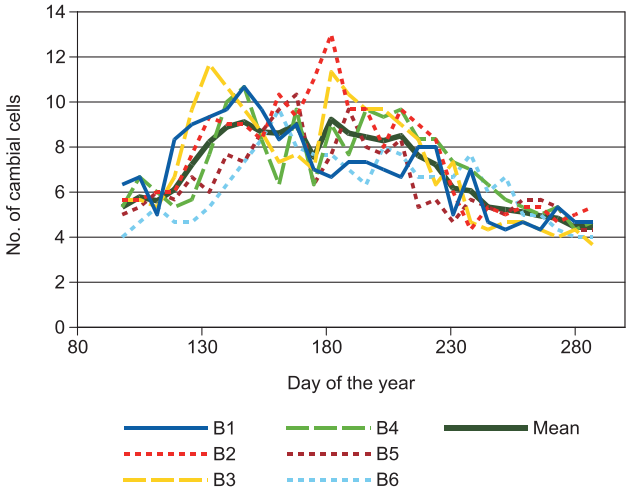

Fig. 2. Number of cambium cells in individual sample trees during growing season 2010 (day 80 = 21 March, 130 = 10 May, 180 = 29 June, 230 = 17 August, 280 = 7 October)

Differentiation of xylem

As soon as wood mother cells, originated by cambium initials or mother cell derivatives, start expanding their dimensions and lose the meristematic character, they cease to be parts of the cambial zone and the process of their differentiation into a specific wood anatomical element starts. In the case of beech wood, these are vessels, fibres, tracheids (fibrous and vascular) and parenchymatic cells (Wagenführ 1996). Our attention mainly focused on the differentiation process of vessels and fibres (without distinguishing between fibres and tracheids).

The first vessels in the phase of postcambial growth were observed between 13 May and 20 May. Two more weeks were needed for the vessels to reach their final dimensions and form secondary cell walls. In the following 1–2 weeks lignification of vessel cell walls started as confirmed by the change of colour of the cell walls from blue (dyed by Astra blue) to red (dyed by safranin) (Fig. 3). The first fully lignified vessels were observed between June 10 and June 24, i.e. 5 or 6 weeks after they were formed in the cambial zone.

All wood cells were formed by the cambium by mid-August (between 12 August and 19 August), while the differentiation process continued in fibres. During the first half of September fibre lignification process finished (between September 2 and September 16).

Figure 4 shows radial increment of wood in the examined sample trees. The decrease in the ring width during the growing season is caused by the sampling around the stem perimeter and unequal wood increment. 70% of the ring width had been formed by mid-July.

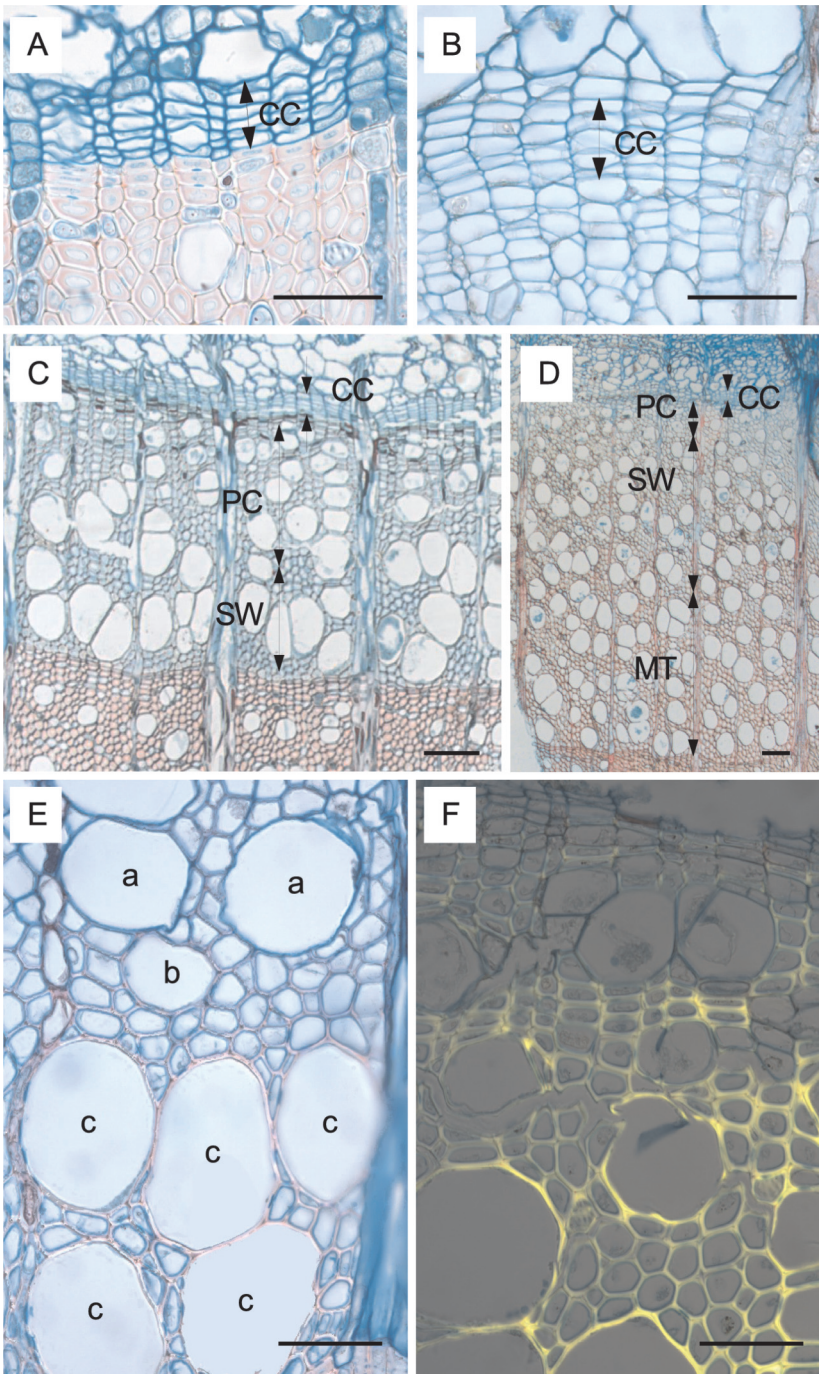

Fig. 3. The cambial zone and the process of ring formation in beech (*Fagus sylvatica* L.) in 2010. A – dormant cambium (CC) on 31 March, B – active cambium (CC) on 10 June; C – the structure of a newly forming ring with the phases of postcambial growth (PC) and secondary cell wall formation (SW) on 17 June; D – the part of the ring with completely mature cells (MT) on 22 July; E – a detail of the vessel lignification process on 10 June, where a – non-lignified vessels, b – vessel lignification beginning, c – lignified vessels, F – detection of lignified cells (yellow) on 10 June using fluorescence microscopy. Scale bars: A, B, E, F = 50 μm, C, D = 100 μm.

Xylem tree ring

The wood increments measured in the sample trees were fitted with the Gompertz function. The following parameters were analysed for each sample tree: the final ring width, the daily rate of wood formation, the maximum daily rate of wood formation, the date of maximum daily rate and the duration of wood formation (Table 1). The calculated model ring width was 1.77 mm and ranged between 1.22 mm and 2.42 mm in the sample trees. The average value of daily increment within all sample trees was 30 μm, ranging from 16 to 40 μm. The maximum daily incre-

Table 1. Parameters of Gompertz function for 2010 xylem ring formation in European beech in Rajec-Domanka, Czech Republic

Tree	B1	B2	B3	B4	B5	B6	Mean
Final ring width (μm)	1226	2015	2423	1441	1912	1644	1777
Daily rate of wood formation (μm)	16	44	40	18	33	28	30
Maximum daily rate of wood formation (μm)	24	62	58	27	48	40	43
Date of maximum daily rate	11 Jun	22 Jun	17 Jun	25 Jun	26 Jun	14 Jun	19 Jun
Duration of wood formation (day)	75	46	61	78	58	59	63

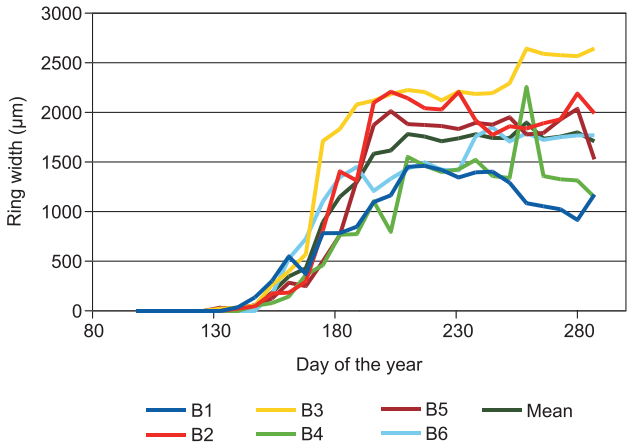

Fig. 4. Dynamics of xylem formation during the growing season of 2010 in individual trees (day 80 = 21 March, 130 = 10 May, 180 = 29 June, 230 = 17 August, 280 = 7 October)

ment calculated by the Gompertz function was found between June 11 and June 26 and its value was 24 to 62 μm (Fig. 5). The trees at the Rájec-Domanka site needed 63 days on average to form a xylem tree ring, with the value ranging between 46 and 75 days.

The time needed for formation of most of the xylem as calculated by the Gompertz function is different from observations by light microscope. Observations performed using permanent microscopic slides show that the cambium ended its division activity 4 weeks later. The difference is caused by the fact that the cambium was less active in the second half of the growing season and formed only a few cells during several weeks.

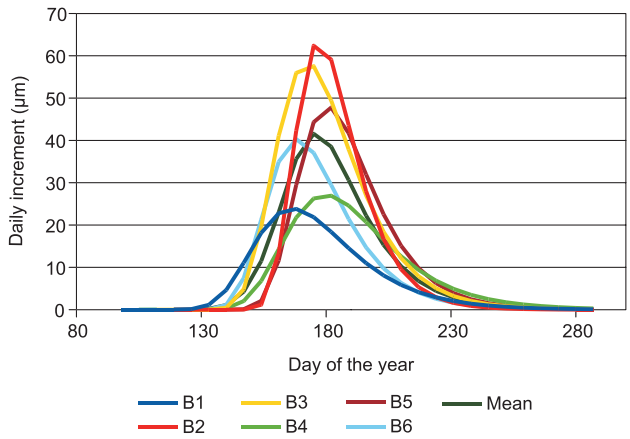

Fig. 5. Daily increment of xylem formation derived from the Gompertz function in the growing season of 2010 (day 80 = 21 March, 130 = 10 May, 180 = 29 June, 230 = 17 August, 280 = 7 October)

Discussion

The results on cambial activity and wood increments in European beech (*Fagus sylvatica* L.) from the research site Rájec-Domanka can be compared with studies on beech carried out by Čufar et al. (2008a, b) and Prislan et al. (2011) during 2006 and 2008 growing season, respectively. Their site in Slovenia (Panška reka) was at similar altitude (400 m a.s.l.) to ours (650 m a.s.l.).

The cells in the dormant cambium at the Rájec-Domanka site had the same shape and distribution as presented by Čufar et al. (2008a) and Prislan et al. (2011) for *Fagus sylvatica* in Slovenia. Also the average number of cells in dormant cambium was similar. The beginning of the cambial division activity at Rájec-Domanka site was observed in the second half of April. It was a similar time to beech in Slovenia (Prislan et al. 2011). Similarly to Slovenia, the number of cells in the cambial zone increased gradually and reached maximum values at the end of May. The maximum number of cells in the cambial zone was observed for the time of 8 weeks; in Slovenia it was only 6 weeks (Prislan et al. 2011). The differences are not significant and they correspond to the variability caused by differing site and climatic conditions on each site in particular years. The maximum number of cells in the cambial zone of our sample trees was observed until mid-July, thus later than in Slovenia (Prislan et al. 2011).

The duration of cambium activity depends on soil conditions and the climate of the growing season and the social position of the tree in the stand (Larson 1994). Temperature (fall of average daily temperatures below 8°C) seems to be the determining factor in the ending of cambium activity, in critical situations it is also the decrease in soil moisture (the decrease in water storage to the limit or below the limit of reduced availability), or a combination of both (Matovič 1985). It is probable that ending of the cambium activity at the Rájec-Domanka site in 2010 was caused by lack of water in the soil (see Fig. 1) and a

decrease in photoperiod. The ending of cambial division activity has been observed in our trees in mid August similarly as in Slovenia (Prislan et al. 2011). On the contrary study in the Netherlands in *Fagus sylvatica* showed that cambial activity ended at the end of October (van der Werf et al. 2007). Also studies in other species show later cessation of cambial activity, e.g. in *Acer platanoides* in mid-September (Marion et al. 2007), for *Quercus robur* at the turn of October (Horáček et al. 2003).

During the xylem cell differentiation we followed two phases: (1) postcambial growth, and (2) secondary cell wall formation and lignification that is finished by programmed cell death. The first formed vessels at Rájec-Domanka site started to lignify within 2 weeks after their formation by the cambial zone and they were fully lignified two weeks later (June 24). As also other studies dealing with the differentiation process of cells confirm, the first vessels or fibres in contact with the conductive system are fully lignified earlier than libriform fibres and tracheids (Prislan et al. 2009 and 2011; Oladi et al. 2011; Romagnoli et al. 2011).

The growth of tree ring in our trees followed an S-shaped curve of growth, which agrees with van der Werf et al. (2007), Čufar et al. (2008a and 2011) and Oladi et al. (2011). At least 65 % of the entire tree-ring width on average was formed from the beginning of the growing season to the end of June. The same result was found by Bouriaud et al. (2004) whose studied *Fagus sylvatica* in France (55 year old, 300 m a.s.l.). In contrary, Čufar et al. (2008b) presented that approximately 76% of tree ring was formed until the end of June. Previous studies on beech already pointed out the influence of June as the most important month for wood formation (Bouriaud et al. 2004; van der Werf et al. 2007; Čufar et al. 2008b).

The maximum daily rate of wood formation calculated by the Gompertz function occurs between June 11 and June 26, which is before (for three sample trees) and after (for the other three sample trees) the summer solstice (21 June), when the photoperiod is the longest. By contrast, Čufar et al. (2008a) found the maximum weekly production of wood for *Fagus sylvatica* was more than 2 weeks before the summer solstice. The calculated daily rate of wood formation 30 μm at Rájec-Domanka site is very similar to the value found in Slovenia – 26 μm. The final tree ring at the Rájec-Domanka site (1.77 mm) is lower than total increment in Slovenia (2.55 mm) (Čufar et al. 2008a).

Several studies showed that the dynamics of wood formation varies from year to year (e.g. Rossi et al. 2008; Romagnoli et al. 2011), therefore we will need to analyse longer time series to create specific models describing the relation of the climate and the particular phases of a forming ring.

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